

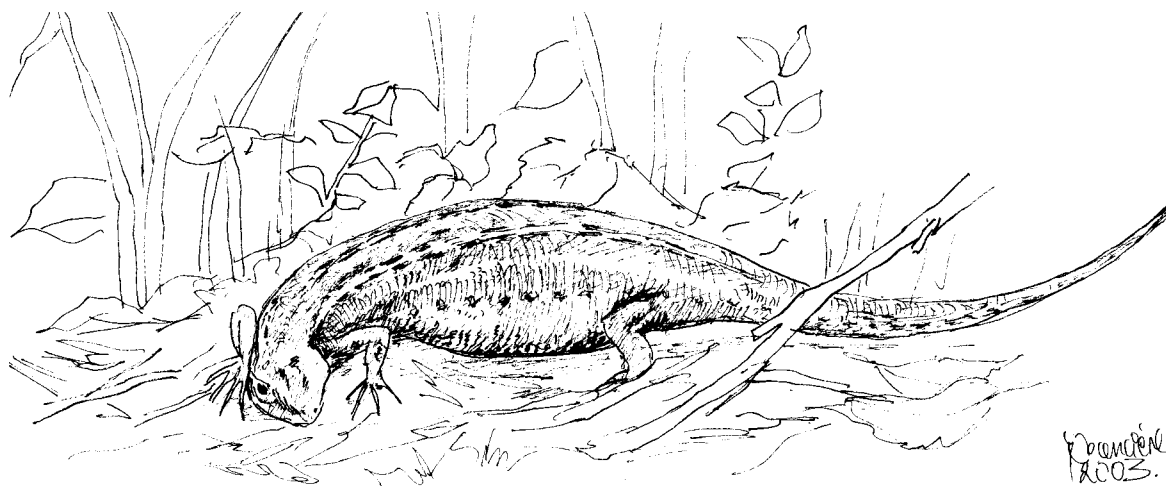
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**INTERACTIONS SOCIALES ET DISPERSION DANS DES POPULATIONS
STRUCTUREES DANS L'ESPACE**



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RÉSUMÉ

L'hétérogénéité spatiale d'une population est engendrée à courte échelle par la portée limitée des interactions sociales et de la mobilité, à laquelle se superpose à plus longue échelle la fragmentation de l'habitat. Des facteurs intrinsèques (stochasticité démographique) et extrinsèques (fluctuations environnementales) génèrent alors de la variabilité spatio-temporelle à ces deux échelles. Cette thèse illustre certaines conséquences proximales et ultimes de cette hétérogénéité sur la dispersion et les interactions sociales.

A l'échelle du voisinage social, la stochasticité démographique permet d'ouvrir l'espace nécessaire à l'expansion d'une population altruiste favorisée par la sélection de parentèle. La variation génétique et démographique qui en résulte rend aussi possible l'évolution de certaines stratégies de dispersion : évitement des interactions avec la mère, de la consanguinité, ou de la compétition pour les ressources, et préférence pour les habitats denses. Elle accroît la valeur sélective de la dispersion par la colonisation de nouveaux habitats. Interactions sociales et dispersion se retrouvent alors associées dans un processus éco-évolutif qui résume les tensions entre coopération et compétition locale.

Mots-clés : dispersion, compétition, coopération, dynamiques adaptatives, hétérogénéité spatiale, valeur sélective.

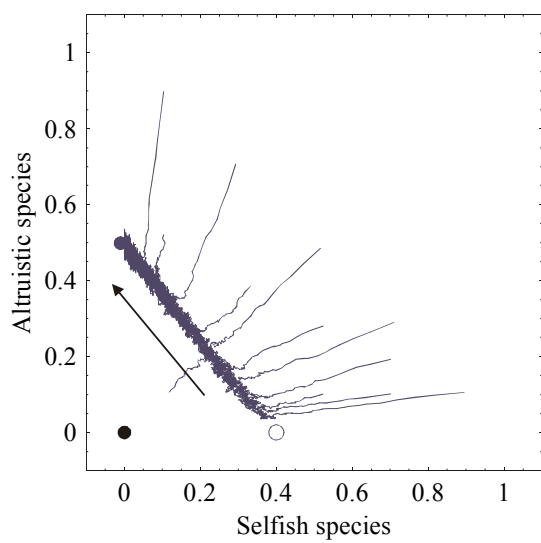
SUMMARY

Population spatial heterogeneity arises at small scales from limited interaction and dispersal ranges and additionally at larger scales from habitat fragmentation. Intrinsic (demographic stochasticity) and extrinsic (environmental fluctuations) factors then combine to generate spatio-temporal variability at these two scales. In this thesis, I illustrate some proximal and ultimate consequences of this heterogeneity on dispersal and social interactions.

At the scale of a social neighbourhood, demographic stochasticity is sufficient to provide the empty space necessary for the spread of an altruistic population favoured by kin selection. Stochasticity also gives rise to a genetical and demographic variation which allows the evolution of some dispersal strategies: avoiding competitive interactions with the mother, inbreeding, or resource competition, and cueing on population density. Fluctuations increase the fitness of dispersal through the colonization of new habitats. Social interactions and dispersal are then entangled in an eco-evolutionary process which summarises the tensions between cooperation and competition.

Keywords : dispersal, competition, cooperation, adaptive dynamics, spatial heterogeneity, fitness.

INTRODUCTION GENERALE



INTERACTIONS

INTERACTIONS SOCIALES

La vie, c'est l'interaction

Un jeune oisillon piaille comme un fou à l'arrivée de son parent et s'accapare toute la nourriture. Une mangouste suricate allaite les petits de sa sœur, puis surveille l'entrée du terrier communal. Elle a faim et attend avec impatience un relais qui tarde tant à venir. Suite à un conflit entre la vieille lionne et l'une de ses filles, la jeune fille doit quitter la troupe de sa mère pour fonder son propre groupe. Dans une prairie d'apparence si paisible, des plantes se combattent en utilisant à foison des armes chimiques libérées par leurs racines et en étouffant leurs voisines de leur ombrage ramifié. Pour le biologiste de l'évolution André Adoutte, la vie pouvait se résumer à trois concepts fondamentaux : un concept d'unité, le support génétique de l'information ; un concept de diversité, la capacité de réplication du support génétique ; et un concept de fonctionnalité, le métabolisme cellulaire. Mais que seraient l'oisillon, la mangouste, la lionne ou cette plante sans toutes ces capacités d'interactions sociales ? Pas grand chose à vrai dire. La vie, c'est donc aussi l'interaction sociale.

Interactions sociales, démographie et évolution

Les interactions sociales siègent au cœur du fonctionnement de toute population et de l'évolution adaptative de tout système biologique. La dynamique de la population est le résultat de l'intégration des effets des interactions sociales individuelles entre congénères et entre espèces sur les paramètres démographiques fondamentaux que sont la mortalité, la natalité et la migration (Caswell, 2001). L'évolution résulte de l'impact de ces paramètres démographiques sur le succès d'une nouveauté génétique, mesurée par sa capacité à envahir la population de son ancêtre (Fisher, 1930; Frank, 1998; Metz et al., 1992; Michod, 1999).

Pour Darwin, la démographie et l'évolution sont modelées par la *compétition* (une interaction sociale négative d'un individu focal envers ses congénères) : compétition entre membres des deux sexes pour la survie, la *sélection naturelle* (Darwin, 1859), ou compétition entre membres du même sexe pour l'accès au partenaire ou l'attraction du partenaire, la *sélection sexuelle* (Darwin, 1871). L'importance de la compétition continue de fasciner les écologistes qui construisent des pans entiers de théories et d'expériences autour de ce concept, depuis l'effet de la compétition sur la dynamique de la population jusqu'au rôle de la compétition dans la diversification des espèces (e.g., Bjørnstad et Grenfell, 2001 ; Dieckmann et Doebeli, 1999).

A l'inverse, pour les écologistes Clements (1916) ou Allee (1949), populations et écosystèmes fonctionnent comme une unité mutualiste, les espèces et les individus étant assimilés à des organes qui

se développent, coopèrent et meurent. Plus récemment, l'intérêt porté au rôle de la *coopération* (une interaction sociale positive d'un individu envers ses congénères) a été stimulé par l'étude de *l'altruisme social* (un comportement de coopération impliquant un coût d'investissement pour l'individu) de certains insectes, vertébrés et micro-organismes (voir Annexe 1), ainsi que par l'étude de « grandes transitions majeures » impliquant la coopération entre des entités indépendantes au sein du génome, de la cellule, de l'individu ou de la colonie sociale (Maynard Smith et Szathmary, 1995).

La séparation entre compétition et coopération n'est cependant pas si claire. D'une part, de nombreuses interactions sociales impliquent à la fois des éléments de coopération, par exemple pour la production de descendants, et de compétition, par exemple entre les jeunes produits de manière coopérative (West et al., 2002). D'autre part, certains contextes sociaux impliquent à la fois une tentation à la compétition et une tentation à la coopération. En effet, l'intérêt privé de l'individu coïncide rarement avec l'intérêt commun des partenaires impliqués dans une interaction sociale (van Baalen et Jansen, 2001). Par exemple, l'intérêt d'un poussin quémandant la becquée auprès de ses parents est d'obtenir une quantité de ressources maximale au détriment de ses frères et sœurs, alors que l'intérêt de ses parents est d'assurer un nourrissage homogène de la descendance.

Voisinage social

Toutes ces interactions sociales ont lieu dans un espace limité autour de chaque individu, que j'appelle le *voisinage social* de l'individu. Par exemple, chez les végétaux terrestres, la sphère racinaire détermine les limites d'interaction dans le sol entre plantes voisines, alors que la surface foliaire et la structure aérienne déterminent les limites d'interaction au-dessus du sol entre plantes voisines (Begon et al., 1996). Chez les animaux, les interactions vont aussi être limitées à un voisinage social qui dépend des capacités de mobilité et de perception des congénères (Wilson, 1975). **De fait, toute population possède un degré plus ou moins prononcé de structuration sociale, qui se reflète dans la distribution des voisinages sociaux autour de chaque individu au sein de la population.**

Prenons l'exemple du modèle biologique de cette thèse, le lézard vivipare *Lacerta vivipara* (voir Annexe 2). A la sortie de l'œuf, le jeune est autonome. Il va explorer et trouver ses ressources dans son habitat de naissance. Pour cet animal, le voisinage social va se construire en fonction (i) des décisions d'interactions sociales prises au cours de sa vie par l'individu ; (ii) des décisions d'interactions sociales prises au cours de leurs vies par ses proches voisins, comme ses frères et sœurs ; ainsi que (iii) d'inévitables variations démographiques, provoquées par la mort de proches congénères ou l'arrivée d'individus non familiaux. Le voisinage social est ainsi caractérisé par une *variabilité temporelle*.

L'environnement social du jeune lézard n'est pas comme tout les autres. D'une part, il coïncide avec le milieu de vie de sa mère et le site de ponte qu'elle a choisie. Ce site contient sûrement quelques éléments particuliers du paysage, car la variabilité spatiale des propriétés physiques et

démographiques de l'habitat est détectable à une échelle de deux ou trois domaines vitaux de distance (Massot com. pers.). D'autre part, ce site est celui de la famille du jeune lézard, en particulier de ses jeunes frères et sœurs, de sa mère et peut-être aussi de son père biologique. Un site sur lequel pourrait déjà résider une lignée familiale impliquant d'autres proches généalogiques (voir O'Connor et Shine, 2003). Le voisinage social de notre jeune lézard focal est donc caractérisé par des *éléments de ressemblance* qui le distinguent d'un voisinage aléatoirement choisi dans la population : il implique à la fois des proches généalogiques et le milieu de vie de ses proches généalogiques.

Tout voisinage social possède ainsi trois propriétés fondamentales : ses **propriétés généalogiques** (par exemple, le degré moyen d'apparentement entre individus : Frank, 1998) ; ses **propriétés écologiques**, comme la structure d'âge chez Ronce et al. (2000) ou la qualité de l'habitat chez McPeck et Holt (1992) ; et ses **propriétés ontogéniques**, c'est-à-dire sa dépendance à l'histoire de l'individu et de ses congénères.

LA DISPERSION

Bouger

Le jeune lézard a pris sa décision quelques jours après sa naissance. Vraiment, cet habitat ne lui convient pas, trop humide à son goût et vraiment surpeuplé. En plus, ses frères et sœurs lui marchent sur les pattes en permanence, et sa mère est omniprésente. Le goût de l'indépendance a pris le dessus, et notre jeune lézard se lance dans une longue marche de plusieurs dizaines de mètres. Quand il a enfin quitté le territoire maternel, il pose ses pattes à l'ombre d'une callune. Il ne lui restera plus que de vagues souvenirs du petit coin de la tourbière où sa mère a mis bas. Contrairement à tous ses frères et sœurs, il a préféré changer d'espace.

Processus

La dispersion est le comportement de mouvement d'un individu de son site de résidence vers un autre site d'établissement. Ce mouvement est caractérisé par trois étapes principales sur lesquelles vont opérer des mécanismes proximaux et ultimes différents : la décision de départ (ou *émigration*), la phase de *transfert* ou d'exploration, et la décision de fixation (ou *immigration*) dans un site d'arrivée (Ims et Yoccoz, 1997). La dispersion est aussi un trait de l'histoire de vie de l'individu, c'est-à-dire une décision fondamentale impliquant des allocations d'énergie et pouvant influencer le succès reproducteur de l'individu, au même titre que l'âge à la première reproduction ou la vitesse de croissance (Stearns, 1992).

La dispersion affecte la répartition spatiale des individus, et influence donc la structure généalogique, les propriétés écologiques et l'histoire du voisinage social d'un individu dispersant

et de ses proches congénères. La dispersion est ainsi une composante fondamentale de la structuration sociale de la population. **En retour, les règles et les pressions de sélection qui régissent les décisions de dispersion vont dépendre de la structure du voisinage social de départ, de transfert et d'arrivée de l'individu.** Dispersion et interactions sociales sont donc impliquées dans une boucle de rétroaction éco-évolutive dont l'élément de contrôle fondamental se situe dans la structure sociale et spatiale de la population (chapitre 1). Il devient donc naturel de considérer conjointement les interactions sociales et la dispersion. La dispersion et les interactions sociales vont affecter mutuellement la dynamique de la population (voir chapitres 1-3, et chapitre 5). L'évolution adaptative de la dispersion va dépendre de l'évolution adaptative des interactions sociales, justifiant une approche conjointe des deux problèmes (voir chapitres 2 et 3).

Capacités locomotrices et phase de transfert

La phase de transfert de la dispersion nécessite des capacités d'exploration et d'interaction relativement élevées. **Les capacités locomotrices apparaissent dans ce contexte comme de bons candidats pour mesurer la compétence d'un individu à explorer son voisinage social car elles traduisent des différences physiologiques et morphologiques se reflétant dans des activités quotidiennes** (voir Annexes 4 et 5). Les capacités de locomotion fournissent une mesure totale de la compétence d'un organisme à se déplacer lors de tâches écologiquement pertinentes (Bennett et Huey, 1990). Par exemple, le régime d'endurance maximale en laboratoire, une mesure de la capacité d'un animal à résister à un effort prolongé, est corrélé à l'activité comportementale *in situ* chez les lézards (Clobert et al., 2000; Garland, 1999).

HETEROGENEITE SPATIALE

Hétérogénéité spatiale à l'échelle de l'habitat et de l'individu

Les paysages écologiques sont structurés à de multiples niveaux, et ceci de manière extrinsèque au fonctionnement démographique de la population. En particulier, il existe dans le paysage des éléments favorables à l'espèce, les *fragments* de la population, et des éléments externes à ces fragments, la *matrice* de la population constituée de corridors ou d'habitats défavorables utilisés lors des mouvements entre fragments (Wiens et al., 1993). Cette structure spatiale peut prendre diverses formes selon les espèces (Hanski, 1998; Harrison et Taylor, 1997), ce qui se reflète dans la diversité des approches théoriques de la structure spatiale en écologie (Kareiva et Wennergren, 1995). Certaines populations fonctionnent comme une collection indépendante de petits fragments isolés par la distance, susceptibles de s'éteindre du fait de leur petite taille, et connectés par des flux d'individus. On parle alors d'une *métapopulation*, et un tel système peut être maintenu dans un équilibre d'extinction et de colonisation (Hanski, 1999; Levins, 1969). Certaines populations fonctionnent au

contraire sous la forme de sites stables, produisant de grandes quantités d'individus (les sources), et de sites instables, qui perdent une grande quantité d'individus (les puits ; Pulliam, 1988). A plus large échelle, on peut aussi considérer que la population est constituée de fragments de tailles très dissemblables, une formulation traduite par la notion de systèmes *continents-îles* (Harrison et al., 1988 ; MacArthur et Wilson, 1967). Globalement, la différenciation entre ces structures spatiales dépend de l'espèce considérée, de la structure de son environnement et de l'échelle spatiale, mais aussi des exigences de précision de l'étude. Il n'existe donc pas une « bonne » approche de la structure spatiale : tout au plus l'approche la plus informative dans le contexte de l'espèce et de l'étude. Par exemple, peu d'espèces de petits mammifères semblent se conformer à un système de métapopulation *sensu stricto* (Harrison et Taylor, 1997; Lambin et al., 2003). Par contre, la théorie des métapopulations fournit des concepts utiles à la description et à la compréhension de ces populations, même si ce n'est qu'en première approximation.

Indépendamment de l'habitat, la distribution des individus au sein des fragments d'habitat est hétérogène si les capacités d'interactions sociales et de dispersion sont limitées par rapport à la taille des fragments. Par exemple, la distribution des plantes adultes dans un habitat homogène dépend de processus internes à la population, en particulier du voisinage de compétition et du voisinage de dispersion. La structure spatiale qui se développe dans une population régulée par des processus compétitifs est définie par la taille des voisinages de compétition et de dispersion (Dieckmann et Law, 2000; Law et Dieckmann, 2000).

Quand la taille des voisinages sociaux est très large, la distribution des individus au sein des fragments converge vers un *champ moyen*. Si les individus perçoivent leur environnement dans les limites de la taille des fragments de la population, alors les processus démographiques individuels dépendront directement de la moyenne globale de la composition démographique de la population (van Baalen, 2000). Cette approximation est vraisemblablement vérifiée dans les systèmes très fragmentés où la taille des fragments correspond à quelques territoires, comme ceux du pika américain (*Ochotona princeps*) à Bodie en Californie (Smith, 1980). Par contre, chez le papillon modèle de la théorie des métapopulations, le fritillaire de Glanville *Melitea cinxia*, les œufs de différentes femelles sont pondus sur une même plante hôte qui constitue ainsi une unité spatiale fondamentale pour les interactions entre frères et sœurs, et pour la compétition entre familles (Hanski, 1999). Cette unité spatiale a une taille bien inférieure à celle des plus petits fragments du réseau d'habitat de l'espèce, ce qui pose la question de la pertinence d'une approche reposant exclusivement sur l'étude et la comparaison de fragments d'habitat. Cette thèse illustrera un contexte dans lequel s'écarter de l'hypothèse en champ moyen apporte une solution à un problème d'évolution des interactions sociales (voir chapitres 1-3).

On conçoit donc que **toute population possède un degré d'hétérogénéité spatiale, qui se reflète dans la distribution des habitats de l'espèce et dans la distribution des individus au sein**

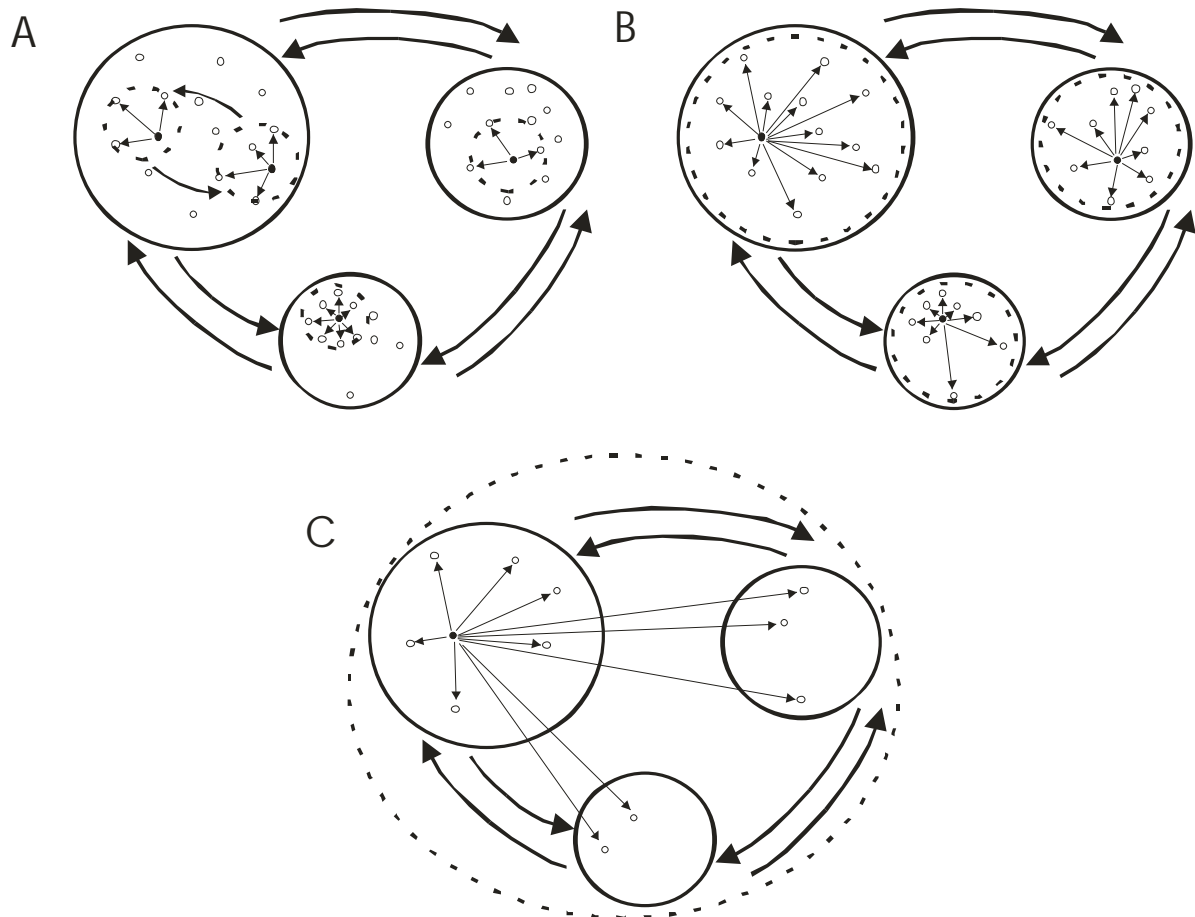
de ces habitats (Fig. 1). On parlera de *populations fragmentées* pour désigner une population structurée en fragments (chapitres 1, 4-6) et de *populations hétérogènes dans l'espace* pour désigner une population à distribution individuelle hétérogène au sein d'un espace continu (chapitres 1-3). Le terme *métapopulation* sera réservé pour désigner des populations fragmentées instables et typiquement asynchrones, tel que Levins (1969) l'a originellement conçu. Ces désignations ne présument pas de l'échelle spatiale de la fragmentation et de l'hétérogénéité ou de l'intensité de la variabilité spatiale.

Cependant, l'organisation réelle de toute population peut être organisée le long d'un continuum : depuis des systèmes très stables (e.g., les populations naturelles du lézard vivipare, Clobert et al., 1994) jusqu'à des systèmes très dynamiques (e.g., le fritillaire de Glanville, Hanski, 1998), depuis des systèmes synchrones vers des systèmes asynchrones (Bjørnstad et al., 1999), ou bien encore depuis des systèmes très structurés à des éléments continus du paysage (Wiens et al., 1993). Dès lors toute classification devient artificielle, et reflète avant tout le pragmatisme de l'approche et la sensibilité du problème au degré de structuration spatiale. Dans le cadre d'une étude de l'écologie et de l'évolution des interactions sociales et de la dispersion, la structuration de la population en voisinages sociaux peut difficilement être ignorée, ainsi que les travaux présentés dans cette thèse le démontrent. On peut alors considérer que la fragmentation de l'habitat vient se superposer à cette structuration sociale pour en affecter la dépendance à la démographie et à la génétique de la population (voir sections suivantes). Par contre, il me semble que la structuration du paysage n'est pas nécessaire à la description des phénomènes envisagés dans cette thèse, d'autant plus qu'elle nécessite de prendre en compte des éléments spécifiques à l'organisation spatiale d'une espèce (Wiens, 1989).

Structuration socio-spatiale

L'interaction entre la structuration sociale et spatiale génère trois organisations socio-spatiales fondamentales de la population (voir la Figure 1). Dans le premier cas, la taille du voisinage social est inférieure à la taille des fragments (Fig. 1A). Les fragments sont alors constitués d'unités sociales au sein desquelles sont déterminés les taux de mortalité et de natalité. La population est une collection de fragments qui échangent des individus. Cette double structuration permet la séparation de deux types d'évènements de dispersion : la *dispersion sociale*, qui a lieu entre les voisinages d'interaction, et la *dispersion d'habitat*, qui a lieu entre les fragments de la population. Dans le troisième cas, la taille du voisinage social est supérieure à la taille des fragments : le voisinage social implique alors des individus appartenant à plusieurs fragments et la dispersion d'habitat a lieu au sein du même voisinage social (Fig. 1C). Dans le cas intermédiaire, on retrouve l'organisation classique de la population fragmentée : la population est composée d'unités sociales correspondant aux fragments (Fig. 1B). Les interactions ont lieu de façon homogène entre tous les individus du même fragment, et les fragments échangent des individus par la dispersion.

Figure 1. Trois types de structuration socio-spatiale. Les individus sont formalisés par des petits ronds, les individus focaux étant indiqués en noir. Le voisinage social d'un individu focal est indiqué par un cercle pointillé. Les flèches droites connectent les congénères qui interagissent socialement avec l'individu focal. Les fragments d'habitat sont indiqués par des cercles pleins. Les flèches incurvées indiquent les mouvements individuels. A. Le voisinage social est structuré à une échelle inférieure à la taille du fragment : la population possède deux niveaux d'organisation. B. Le voisinage social coïncide avec la taille des fragments : la population possède un seul niveau d'organisation. C. Le voisinage social inclut tous les fragments de la population.



Considérons le cas de la Figure 1A que l'on pourrait appeler une *population fragmentée et structurée socialement*. Tout d'abord, natalité et mortalité ne dépendent pas ici directement de la structure démographique du fragment, mais de la structure des voisinages sociaux et de la répartition spatiale des individus au sein de ces voisinages (voir aussi chapitre 1). **Cette dépendance des événements individuels à la structure du voisinage génère une variabilité spatiale, qui vient se superposer à la variabilité existant entre les fragments d'habitat.** Premièrement, la structure sociale impose des variations liées à la *fluctuation* aléatoire entre voisinages, même si les individus sont répartis de façon homogène dans l'espace (Durrett et Levin, 1994). En effet, on peut considérer chaque voisinage comme un échantillon aléatoire d'un nombre fini d'individus de la population

(Dieckmann et Law, 2000). Deuxièmement, si les individus sont répartis de façon hétérogène, la structure spatiale locale impose des variations liées aux *corrélations spatiales*. Le voisinage moyen autour d'un individu est en effet différent de l'environnement moyen en présence de corrélations spatiales. Ces fluctuations aléatoires et ces corrélations spatiales peuvent profondément affecter la démographie de la population (e.g., Harada et Iwasa, 1994; Law et Dieckmann, 2000; Morris, 1997; Rand, 1998; van Baalen, 2000). Par exemple, certaines stratégies démographiques utilisées par des plantes, comme l'exploitation, la colonisation, ou la tolérance, peuvent coexister parce qu'elles exploitent l'espace différemment dans une population hétérogène, mais pas dans un habitat strictement homogène. Une stratégie de colonisation utilise l'agrégation des autres stratégies pour exploiter les sites vides à l'aide d'une dispersion globale. Une stratégie d'exploitation utilise sa dispersion réduite et son avantage de croissance pour exploiter des sites occupés avant d'être remplacée. Une stratégie de tolérance utilise son agrégation et sa résistance à la compétition intraspécifique pour exploiter les sites occupés et les rendre imperméables aux autres stratégies (Bolker et Pacala, 1999).

De plus, la structure en voisinages sociaux engendre une redistribution de la variabilité généalogique, qui dépend du nombre de groupes sociaux impliqués, du mode de dispersion ou du régime de reproduction (e.g., Sugg et al., 1996). Prenons l'exemple de la musaraigne *Crocidura russula*, un mammifère insectivore à reproduction socialement monogame et à dispersion femelle (Favre et al., 1997). Cette espèce territoriale forme différents groupes de reproduction (en général, un jardin) au sein d'un même fragment d'habitat (en général, un village). La variabilité génétique d'une population suisse autour de Lausanne a été échantillonnée à ces deux échelles (Balloux et al., 1998). Les données génétiques mettent en évidence une structuration entre les villages, au sein des villages entre jardins pour les mâles et au sein d'un individu dans un jardin pour les mâles. Donc, la structuration génétique est présente à l'échelle du paysage et de la structure sociale au sein du paysage. La structure sociale produit un apparentement significatif entre voisins au sein d'un même fragment d'habitat pour le sexe philopatride, et s'accompagne d'une consanguinité significative. Enfin, la taille efficace de la population (taille correspondant à une population idéale qui perdrait la variabilité génétique au même taux que la population d'étude) vaut environ 680 individus pour 140 reproducteurs, ce qui témoigne du rôle de la structuration sociale dans le maintien de la variabilité génétique.

Finalement, les voisinages sociaux sont une source de pressions de sélection qui peuvent conduire à l'évolution adaptative de combinaisons innovantes de traits d'histoire de vie, par exemple en favorisant l'émergence de comportements coopératifs familiaux (Emlen, 1997). Les conséquences évolutives des voisinages sociaux sont liées tant à leurs *propriétés écologiques* (chapitre 1), comme la variabilité spatiale, qu'à leurs *propriétés génétiques*, notamment la préservation d'unités d'individus apparentés (van Baalen et Rand (1998), chapitre 2).

POINTS DE VUE DE LA THESE

Ma thèse n'a pas l'ambition de répondre de manière générale aux problèmes posés par l'étude des interactions sociales et de la dispersion dans les populations structurées dans l'espace, de présenter un cadre théorique unifié des structures sociales et spatiales, ou d'en proposer une investigation approfondie et complète dans le cadre du modèle biologique d'étude. Au cours de ce travail, j'ai plutôt développé quatre points de vues complémentaires afin de décrire les effets de l'hétérogénéité et de la variabilité spatiale sur les interactions sociales et la dispersion. Les parties suivantes font une brève présentation des questions abordées dans cette thèse. Ces questions seront traitées en détail dans les chapitres 1 à 6 qui forment le corps du travail de la thèse. Des travaux complémentaires et des éléments de synthèse sont rassemblés dans les Annexes 1 à 5.

Hétérogénéité locale

J'envisage dans cette partie l'évolution de l'altruisme et de la dispersion dans une population hétérogène où les interactions sociales et la dispersion sont limitées aux territoires voisins. Je modélise une structure spatiale hébergeant des individus d'un organisme haploïde caractérisé par un phénotype d'altruisme et de mobilité. Je considère que les valeurs de ces phénotypes sont déterminés génétiquement et peuvent varier par mutation. Je décris le processus de sélection et le résultat de la dynamique adaptative de l'évolution conjointe de ces deux traits.

Les objectifs de la modélisation sont justifiés dans le chapitre 1 et dans l'introduction des chapitres 2 et 3. Le cadre théorique est fixé dans le chapitre 1, ainsi que dans les annexes des chapitres 2 et 3. Un point de vue général et un état des connaissances sur les comportements altruistes est donné dans l'Annexe 1. Il fournit le pesant biologique au déroulement du modèle théorique, et le place dans la perspective plus générale de l'étude de la coopération. Seuls les principes généraux du modèle et de sa construction sont présentés dans les paragraphes qui suivent.

La plupart des modèles d'évolution de l'altruisme et de la dispersion font deux hypothèses majeures : la structuration spatiale est envisagée globalement, c'est-à-dire que le paysage est composé de nombreux fragments connectés à longue distance par la dispersion (voir Fig. 1B), et la composition démographique des fragments d'habitats est donnée une fois pour toutes. Nous modéliserons au contraire une population structurée à une échelle locale et une démographie explicite, rendant compte du tirage aléatoire des événements individuels de naissance, de mort et de mouvement. Par ailleurs, les problèmes de l'évolution de l'altruisme et de la dispersion partagent de nombreux points communs (chapitres 1, 3 et Annexe 1), mais sont classiquement étudiés séparément. Au contraire, nous envisagerons ici l'évolution conjointe de la dispersion et de la coopération. De plus, il est d'usage commun de considérer seulement deux stratégies d'interaction altruiste, comme Coopération et

Egoïste dans la théorie des jeux (Axelrod et Hamilton, 1981). Cette dichotomie recoupe mal la variabilité interindividuelle et interspécifique des comportements de coopération (voir Annexe 1). Au contraire, notre modèle suppose que l'altruisme peut se mesurer à l'échelle individuelle par l'investissement réalisé dans les interactions altruistes, et envisage de décrire les déterminants de la variation adaptative de cet investissement. Finalement, on tiendra compte de la diversité des coûts de la coopération (Heinsohn et Legge, 1999) en modélisant un coût accélérant (plus on investit dans l'altruisme, plus il sera coûteux d'investir plus), un coût linéaire (le coût d'un investissement supplémentaire est constant), et un coût décélérant (plus on investit dans l'altruisme, moins il sera coûteux d'investir plus).

En reprenant les prédictions verbales de Hamilton (1964) et les résultats théoriques de van Baalen et Rand (1998), on prédit une évolution continue de l'altruisme dans la population par un processus de mutation et de sélection de parentèle impliquant l'apparentement entre l'individu et ses proches voisins (Frank, 1998). Dans la mesure où le niveau adaptatif d'altruisme atteint dans la population dépend (i) d'interactions entre les bénéfices indirects de la coopération entre apparentés, les coûts indirects de la compétition entre apparentés et les coûts physiologiques directs de l'altruisme (West et al., 2002), et (ii) de l'effet rétroactif du niveau d'investissement dans l'altruisme sur ces pressions de sélection (Metz et al., 1996), on va s'attacher à décrire formellement ces processus. Cependant, on peut prédire qu'une mobilité réduite renforce l'apparentement, donc favorise probablement l'émergence de phénotypes plus altruistes (Hamilton, 1964). Par ailleurs, on va rechercher des processus permettant de franchir la barrière initiale d'invasion de l'altruisme liée à la disproportion des coûts physiologiques dans la situation où les coûts de l'altruisme décélèrent. Dans un deuxième temps, on va étudier les pressions de sélection contribuant à l'évolution de la mobilité individuelle dans ce type de population, et l'impact de l'évolution de la mobilité sur la persistance évolutive des interactions altruistes.

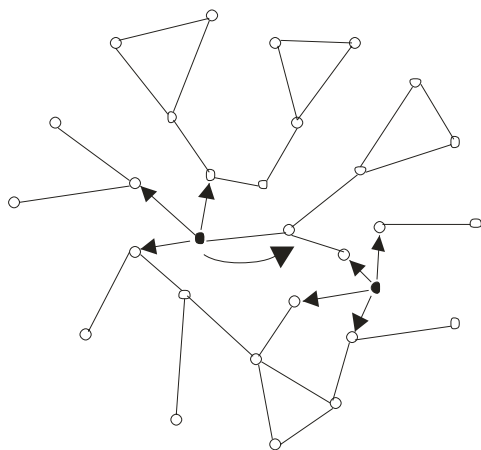


Figure 2. Structuration socio-spatiale du réseau envisagé dans le modèle théorique de la thèse (voir chapitres 1-3). Les liens entre sites voisins sont figurés par les traits fins et les sites par les ronds vides. Autour d'un individu focal (cercle plein), les interactions sociales (flèches droites) et la dispersion (flèche incurvée) sont limitées aux sites voisins.

Plus précisément, on envisage une structuration sociale qui prend la forme d'un voisinage de sites individuels connectés formant une structure globale en *réseau* (Matsuda et al. (1992), Fig. 2). Les interactions sociales et la dispersion ont lieu strictement entre sites voisins. Les liens de voisinage sont tirés aléatoirement entre les sites ou selon des règles qui dépendent de la proximité géographique (voir chapitres 1 et 2). Dans tous les cas, on supposera que le nombre de voisins est fixé *a priori*, dans la mesure où nos résultats ne sont pas fortement sensibles à cette hypothèse (Morris, 1997). On peut considérer ce réseau comme une métapopulation de sites discrets individuels, donc une structure spatiale où les interactions sociales et la dispersion sont limitées par la distance (comparer la Figure 2 à la Figure 1C). On peut aussi considérer ce réseau comme le résultat d'une hétérogénéité interne à un fragment d'habitat, donc une structure purement sociale (comparer la Figure 2 à la Figure 1A).

Par ailleurs, on suppose que l'état du réseau dépend des événements démographiques qui ont lieu dans la population. Les sites sont vidés par la mortalité individuelle qui est supposée constante. Les sites sont remplis par la natalité et la mobilité individuelle à partir des sites voisins. La natalité comprend une part constante et une part influencée par *l'investissement dans l'altruisme* des voisins, qui augmente la natalité de ses voisins de manière additive et linéaire. La natalité résultant de ces deux parts est réduite par la *compétition locale* proportionnellement à la fréquence des sites occupés dans le voisinage. La *mobilité* entre sites voisins est constante, et est aussi réduite par la *compétition locale* proportionnellement à la fréquence des sites occupés dans le voisinage. L'investissement dans l'altruisme et la mobilité sont des traits coûteux, et leurs coûts augmentent en rapport à la valeur de ces deux traits. On envisage des coûts linéaires pour la mobilité, et j'envisage des coûts linéaires, décélérant et accélérant pour l'altruisme. Ces deux coûts affectent la natalité de l'individu.

L'analyse du modèle utilise une description écologique de la population, basée sur une méthode prenant en compte une correction des corrélations spatiales jusqu'au niveau des paires de sites (chapitre 1). La dynamique des sites et des paires de site étant explicitée, on utilise le formalisme des dynamiques adaptatives pour décrire l'évolution adaptative de l'investissement altruiste (chapitres 2 et 3) et de la dispersion (chapitre 3). Une mesure approximative de la valeur sélective d'invasion est dérivée et interprétée à la lumière des pressions de sélection affectant les deux traits. L'analyse complète de l'influence des paramètres du modèle sur cette dynamique adaptative est conduite numériquement. Elle est complétée par une simulation du processus individu centré et par une analyse de l'effet de mutations à effets importants.

Densité et structure généalogique du voisinage social

On étudie ici l'effet de la structure généalogique et de la densité du voisinage de naissance d'un jeune lézard sur son comportement de dispersion natale et son histoire de vie. On manipule la présence de la mère dans l'environnement de naissance du jeune pour tester l'effet des interactions entre la mère et ses enfants sur la dispersion natale du jeune. On manipule le nombre d'individus, toutes classes d'âge et de sexe confondues, pour mettre en évidence un effet de la densité en

congénères sur la dispersion natale du jeune. On croise ces deux manipulations pour tester si l'interaction mère à enfant a un effet sur la dispersion du jeune indépendamment ou non de la densité du voisinage. Les principes et résultats de l'expérience sont présentés dans le chapitre 4, et dans l'Annexe 3. Certains éléments propres à la compétition entre proches génétiques sont aussi discutés dans l'Annexe 1. Les caractéristiques du modèle d'étude sont rassemblées dans l'Annexe 2. Les objectifs de l'expérience et les données récoltées sont présentés dans les paragraphes qui suivent.

Après la naissance, la décision de dispersion du jeune lézard vivipare est rapide dans les populations naturelles (voir l'Annexe 2 pour la biologie de l'espèce). Certains résultats nous invitent à penser que cette décision dépend en partie d'une interaction entre la mère et ses enfants par des mécanismes agissant avant la naissance (de Fraipont et al., 2000; Massot et Clobert, 1995, 1998; Meylan et al., 2002; Sorci et al., 1994) ou après la naissance (Léna et al., 1998; Léna et de Fraipont, 1998). D'une part, certaines caractéristiques maternelles, comme l'âge de la mère ou la condition maternelle, affectent la dispersion natale. Les jeunes provenant de mères sénescences ou en mauvaise condition ont tendance à disperser moins fréquemment (Meylan et al., 2002; Ronce et al., 1998). D'autre part, des manipulations simulant une mauvaise gestation maternelle, comme un faible nourrissage (Massot et Clobert, 1995, 2000), une application hormonale de corticostérone (de Fraipont et al., 2000), ou un parasitisme externe (Sorci et al., 1994) peuvent stimuler la philopatrie des jeunes. Enfin, les jeunes sont capables de discriminer leur mère biologique des autres femelles adultes et utilisent cette information pour choisir leur habitat (Léna et al., 2000; Léna et de Fraipont, 1998). Les réponses comportementales observées dépendent du sexe des jeunes, la réponse étant en général plus prononcée pour les jeunes femelles (Ronce et al., 1998; Sorci et al., 1994); de l'année, la relation pouvant s'inverser d'une année à l'autre (Massot et Clobert, 2000); et des caractéristiques maternelles (Meylan et al., 2002). Ces effets traduisent la dépendance au contexte des effets maternels et l'ambiguïté des messages véhiculés par ces effets : une bonne condition maternelle indique à la fois un risque élevé d'interactions futures entre la mère et ses enfants, mais aussi un bon environnement de naissance (Ims et Hjermmann, 2001). Cependant, les manipulations pré-natales peuvent être confondues par les effets organisationnels de l'environnement maternel sur le développement du jeune et par des contraintes développementales (Dufty et al., 2002). Dans ce contexte, il nous est apparu utile de manipuler directement la présence de la mère afin de contraster des contextes sociaux sans possibilités d'interactions mère à enfants et des contextes sociaux où ces interactions sont possibles. On peut prédire l'effet de cette manipulation sur la dispersion natale en utilisant différentes explications, sous l'hypothèse que la mère n'est pas affectée par l'expérience :

- si la dispersion natale résulte uniquement d'un évitement de la compétition entre la mère et les enfants (Ronce et al., 1998), alors on devrait observer une augmentation de la dispersion natale en présence de la mère ;

- si la dispersion natale résulte uniquement d'un évitement de la consanguinité entre la mère et les enfants (Motro, 1991), alors on devrait observer une augmentation de la dispersion natale des fils en présence de leur mère, la dispersion des filles n'étant pas affectée ;
- si la dispersion natale résulte uniquement d'une facilitation entre la mère et ses enfants (Lambin et al., 2001), alors on devrait observer une diminution de la dispersion natale en présence de leur mère.

La dispersion natale dépend aussi de la présence d'individus non apparentés (ou plutôt, lointainement apparentés) dans le voisinage de l'individu. En particulier, le nombre de voisins traduit chez cette espèce le risque d'une compétition forte pour les ressources et l'espace (Massot et al., 1992). La dispersion devrait donc être augmentée à forte densité du fait des interactions compétitives entre congénères (Metz et Gyllenberg, 2001; Travis et al., 1999). Pour cette raison, on a manipulé conjointement la densité du voisinage social de l'individu en créant deux niveaux de densité, en dessous et au-dessus de la capacité de charge supposée du dispositif expérimental.

L'effet de la présence de la mère sur la dispersion des jeunes pourrait être dilué par des relations avec des individus non apparentés si un mélange entre les territoires familiaux voisins a lieu, si la dispersion adulte rend peu probable la présence d'un parent sur le lieu de naissance du jeune, ou si de nombreux individus partagent le même domaine vital. Chez notre espèce, les domaines vitaux individuels se chevauchent et les variations locales de la densité sont suffisantes pour permettre à la dispersion d'évoluer pour des causes indépendantes des interactions sociales avec la mère. De fait, on a croisé la manipulation de densité du voisinage avec la manipulation de la présence de la mère. On prédit une réponse plus forte à la présence de la mère pour un faible nombre d'individus dans le voisinage social.

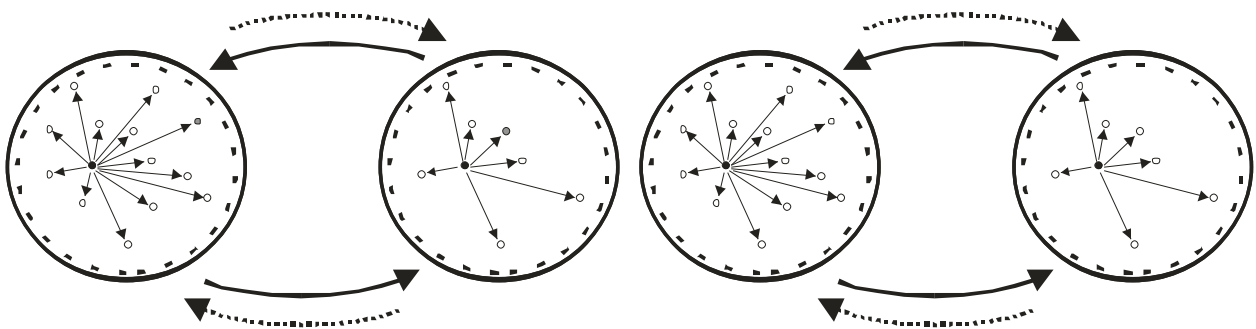


Figure 3. Structuration socio-spatiale de la première expérience de la thèse (voir chapitre 4 et Annexe 3). Autour d'un individu focal (rond noir), les interactions sociales (flèches droites) ont lieu au sein du fragment. La dispersion (flèche incurvée) est limitée à un fragment voisin (flèches pleines : mouvements aller, flèches hachurées : mouvements retour). On manipule la densité du voisinage au sein de la même population, et la présence de la mère (rond gris) dans le voisinage du jeune entre populations.

On réalise cette expérience à l'échelle d'un dispositif expérimental faisant coïncider le voisinage social et la structure spatiale de la population (Fig. 3). Chaque population est composée de deux fragments d'habitat fermés et connectés à l'autre fragment par des corridors. On met en rapport un fragment d'habitat à faible densité et un fragment d'habitat à haute densité au début de l'été 1999. Deux types de populations fragmentées sont établis : dans la moitié des systèmes, les jeunes sont lâchés en présence de la mère, alors que les jeunes sont lâchés en présence d'une femelle adulte non apparentée dans l'autre moitié du système. On laisse le système fonctionner de manière autonome jusqu'à l'été 2001. Chaque année, on identifie les individus dispersant d'un fragment d'habitat à l'autre, on capture à plusieurs reprises (printemps, été, automne) les individus résidant dans les fragments, et on garde les femelles gestantes au laboratoire en juin-juillet. Ce suivi permet d'étudier l'effet des traitements expérimentaux sur le comportement de dispersion, les histoires de vie individuelles (croissance, survie et reproduction), et la démographie de la population. L'analyse des données a été conduite entièrement pour le comportement de dispersion de toutes les classes d'âge (chapitre 4 et son appendice). L'analyse des caractéristiques de l'histoire de vie et de la démographie étant en cours de synthèse, elle sera présentée sous la forme de résultats bruts (Annexe 3).

Variabilité entre fragments d'habitats : occupation du fragment

On analyse ici l'effet de la structure d'occupation des fragments d'habitat sur le comportement d'immigration et l'histoire de vie d'un lézard dispersant. Je manipule la présence des congénères toutes classes d'âge et de sexe dans le fragment d'arrivée d'un dispersant afin de tester l'effet des interactions avec des résidents sur le comportement d'immigration d'un lézard et le succès de l'immigration. Les résultats de l'expérimentation sont présentés dans le chapitre 9.

Après la dispersion, tout individu doit s'établir dans un territoire et faire un choix d'habitat (Danchin et al., 2001). Le succès de l'individu au cours de sa vie va dépendre de ce choix si l'habitat choisi coïncide avec celui occupé en tant qu'adulte. En effet, le succès reproducteur individuel est une fonction de la qualité intrinsèque de l'habitat et des caractéristiques des congénères. Comment l'individu doit-il choisir son milieu de vie ? Quelles sont les conséquences de ce choix sur le succès reproducteur de l'individu au cours de sa vie ?

Une théorie traditionnelle du choix de l'habitat a été formulée par Fretwell et Lucas (1970), et est appelée distribution libre et idéale (Fretwell, 1972). Dans cette théorie, on suppose qu'il existe des habitats stables de qualités différentes, que le succès reproducteur individuel dans un habitat est influencé négativement par les congénères, que les individus ont une connaissance complète de leur environnement et que le choix d'un habitat s'effectue sans aucun coût. La théorie de la distribution libre et idéale prédit une répartition individuelle à l'équilibre évolutif proportionnelle aux différences intrinsèques de qualité de l'habitat (Fretwell, 1972).

On peut cependant supposer que des interactions sociales peuvent aussi avoir des effets positifs sur la démographie, notamment à faible densité (effets de Allee et interactions coopératives, Courchamp et al., 1999). De plus, on sait que de nombreux organismes ont une capacité limitée à accéder à l'information et procèdent par un processus d'échantillonnage pendant la prospection (Stamps, 2001). Dans le cas d'un effet de Allee, on prédit l'évolution d'une stratégie de choix de l'habitat basée sur la présence de congénères. A faible densité, les interactions positives génèrent une attraction envers les congénères, et le contraire est observé à forte densité (Greene et Stamps, 2001). Une telle attraction envers les congénères a été démontrée chez de nombreuses espèces à reproduction coloniale, mais aussi chez quelques espèces territoriales (Stamps, 2001). Par ailleurs, on doit s'attendre à voir évoluer des mécanismes de choix de l'habitat qui conduisent à une réduction des coûts de la prospection et à une augmentation de la qualité de l'information récoltée. Les coûts de prospection sont liés à l'échantillonnage, à des compensations avec d'autres activités et à la compétition entre prospecteurs. La qualité de l'information dépend de sa relation avec le succès reproducteur de l'individu et de sa prédictibilité, liée à l'autocorrélation temporelle de l'environnement (Doligez et al., 2003). Trois mécanismes de sélection de l'habitat ont donc été proposés : l'estimation directe d'un paramètre environnemental, l'attraction pour les congénères (attraction sociale), et l'utilisation du succès reproducteur des congénères (information publique, (Danchin et al., 2001)).

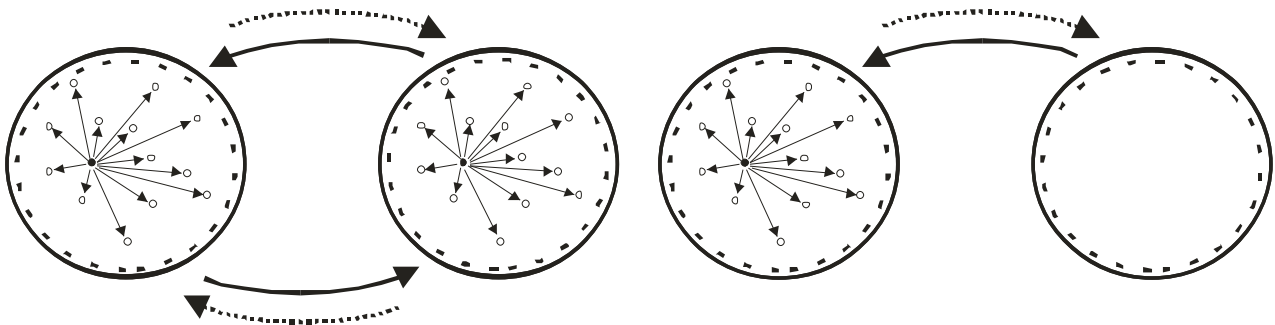


Figure 4. Structuration socio-spatiale de la deuxième expérience de la thèse (voir chapitre 5). Autour d'un individu focal, les interactions sociales ont lieu au sein du fragment. La dispersion est limitée à un fragment voisin. On manipule la présence de congénères au sein du fragment d'arrivée du lézard (gauche : les deux fragments sont occupés, mimant un contexte d'augmentation ; droite : un fragment est vide, mimant un contexte de colonisation depuis une source vers un habitat vide).

Si plusieurs études récentes chez les oiseaux suggèrent qu'un dispersant peut utiliser l'information dérivée du succès reproducteur de ses congénères pour choisir son milieu de vie (Boulinier et al., 2002; Danchin et Wagner, 1997; Doligez et al., 1999, 2002; Frederiksen et Bregnballe, 2001), relativement peu de travaux ont testé l'effet de la présence de congénères sur

l'immigration à l'échelle d'une population et en comparant des individus dispersant (chez les invertébrés marins, voir par exemple Meadows et Campbell (1972) ; pour des expériences en milieu ouvert comparant la fixation d'oiseaux dans le cadre de programmes de réintroduction, voir par exemple Reed et Dobson, 1993). On a donc comparé le comportement d'établissement de lézards dispersant dans des unités expérimentales occupées par des congénères, à une densité proche de l'équilibre démographique du système, et dans des unités expérimentales initialement vides. On s'attendait à une préférence pour les sites vides si cet habitat était associé à un risque plus faible de compétition, surtout pour les individus jeunes. On s'attendait à une préférence pour les sites occupés si cet habitat était associé à un risque plus faible de coûts à l'établissement et la recherche du partenaire sexuel, surtout pour les individus âgés. On a donc aussi mesuré le succès démographique des immigrants dans des habitats occupés ou initialement vides.

On a réalisé cette expérience à l'aide du même dispositif que l'expérience précédente (Fig. 3). Au début de l'été 2001, on a mis en rapport deux fragments d'habitat occupés dans des unités dites d'augmentation, et un fragment d'habitat occupé à un fragment d'habitat vide dans les unités dites de colonisation. Le terme d'augmentation est utilisé en référence à son utilisation en biologie de la conservation et des métapopulations où il fait référence au rôle renforçant de l'immigration sur l'effectif des populations. Trois types de fragments sont donc établis : des fragments « augmentés » connectés deux à deux, des fragments « sources » connectés à un habitat vide, et des fragments initialement vides connectés à des fragments sources. On a laissé le système fonctionner de manière autonome jusqu'à l'été 2002. Un suivi a permis d'étudier l'effet des traitements expérimentaux sur le comportement de dispersion, les histoires de vie individuelles (croissance, survie et reproduction), et la démographie de la population. L'analyse des caractéristiques de l'histoire de vie, de la démographie et de la dispersion est résumée dans le chapitre 5.

Variabilité entre fragments d'habitats : structure de sexe

On envisage maintenant l'effet de la sexe ratio du fragment d'habitat sur le comportement de dispersion, l'histoire de vie et le mode d'appariement d'un lézard. On manipule la structure de sexe de la population adulte, afin de tester l'effet des interactions entre mâles ou femelles et un individu sur (i) son comportement de dispersion, (ii) son histoire de vie, et (iii) la dynamique des appariements. Certains résultats préliminaires sont présentés dans le chapitre 6. L'Annexe 2 donne les éléments fondamentaux de la biologie de la reproduction de notre espèce d'étude.

La dispersion est susceptible de dépendre d'interactions locales impliquant la structure généalogique du voisinage de l'individu (Le Galliard et al., 2003), mais aussi de la structure démographique du voisinage de départ et d'arrivée, comme la densité en congénères (voir par exemple Ozaki (1995) et Crespi et Taylor, 1990). Dans la dernière situation, on a supposé que les interactions étaient symétriques entre individus, en considérant la densité totale du voisinage toutes classes d'âge

et de sexe confondues comme un bon indice du niveau de compétition. On peut cependant penser que la densité dépendance ne se résume pas à un paramètre aussi simple. Pour un vertébré, une stratification de la population s'opère par l'âge et le sexe : l'âge détermine entre autres le rang social de l'individu, les individus adultes étant en général dominants sur les individus jeunes ; et le sexe détermine les paramètres écologiques critiques du succès reproducteur, en dépendance du régime d'appariement. Chez les espèces à reproduction polygyne, les mâles et les femelles ont des stratégies démographiques différentes. Les mâles investissent peu dans les soins parentaux et la reproduction, hormis via la *compétition pour l'accès au partenaire*. Les femelles investissent beaucoup dans la production des jeunes et les soins parentaux (d'autant plus que la fécondation est interne et la reproduction vivipare), et sont en *compétition pour les ressources* (Andersson, 1994; Greenwood, 1980). De fait, les mâles sont plus sensibles que les femelles à des paramètres de la population reflétant la compétition locale pour le partenaire, alors que les femelles sont plus sensibles que les mâles à des paramètres de la population reflétant la compétition locale pour les ressources (e.g., Post et al., 1999). Ces différences entre mâles et femelles dans le régime de compétition ont été utilisées pour prédire une dispersion mâle biaisée chez les espèces polygynes (essentiellement des mammifères, voir Dobson, 1982; Perrin et Goudet, 2001; Perrin et Mazalov, 2000).

Les populations du lézard vivipare n'échappent pas à cette structuration par l'âge et par le sexe. Le régime de reproduction de l'espèce est polygynandrique, avec une variance du succès reproducteur plus forte chez les mâles que chez les femelles (Laloi et al. soumis). D'un point de vue comportemental, les mâles adultes sont dominants sur les femelles adultes, et les adultes sont dominants sur les sub-adultes et les juvéniles (Lecomte, 1993; Lecomte et al., 1994). Les données démographiques suggèrent aussi que les mâles adultes sont en compétition pour les femelles adultes (Massot, 1992; Massot et al., 1992; Pilorge, 1987; Pilorge et al., 1987). Par ailleurs, la dispersion natale est faiblement biaisée en faveur des mâles, et la dispersion de reproduction est plus fortement biaisée en faveur des mâles (Clobert et al., 1994; Massot, 1992), suggérant une asymétrie compétitive entre mâles et femelles dans la population (Perrin et Goudet, 2001). On a donc tenté de tester l'hypothèse selon laquelle la dispersion dépendrait du risque de compétition locale pour les ressources et pour les partenaires en manipulant la sexe ratio adulte de la population :

- si la dispersion de reproduction des femelles résulte d'un évitement de la compétition pour les ressources, on prédit une augmentation de la dispersion des femelles quand la sexe ratio de la population est biaisée en faveur des femelles (resp. mâles). Cette dispersion devrait être synchronisée sur la période estivale pendant laquelle les individus restaurent les réserves dépensées lors de la reproduction, surtout pour les femelles.

- si la dispersion de reproduction des mâles résulte d'un évitement de la compétition pour l'accès au partenaire, on prédit une augmentation de la dispersion des mâles quand la sexe ratio de la population est biaisée en faveur des mâles (resp. femelles). Cette dispersion devrait être synchronisée sur la période printanière pendant laquelle les appariements ont lieu.

Au début de l'été 2002, nous avons établi deux types de fragments d'habitat : la moitié des populations est constituée d'une sexe ratio adulte biaisée en faveur des mâles, et l'autre moitié d'une sexe ratio adulte biaisée en faveur des femelles (Fig. 5). La densité en adultes de la population est maintenue constante, et la structure de la population immature et juvénile est semblable entre les fragments. Nous avons laissé le système fonctionner de manière autonome jusqu'à l'été 2003. Nous avons identifié les individus dispersant d'un fragment d'habitat à l'autre, capturé à plusieurs reprises les individus résidant dans les fragments (été, automne, fin du printemps) et ramené les femelles gestantes au laboratoire à la fin de l'expérience. Contrairement aux expériences précédentes, on ne connecte pas les fragments deux à deux : la dispersion a lieu entre tous les fragments du même traitement. On simule ainsi une dispersion dans un paysage linéaire dont la sexe ratio adulte est déséquilibrée. Nous avons aussi établi la carte allélique des individus introduits et des juvéniles issus de la première génération de cette expérience sur plusieurs loci microsatellites (Boudjemadi et al., 1999). Une analyse préliminaire des comportements de dispersion est résumée dans le chapitre 6. En effet, l'expérience ayant débuté dans la dernière année de la thèse, elle est toujours en cours au moment de l'écriture de ce document.

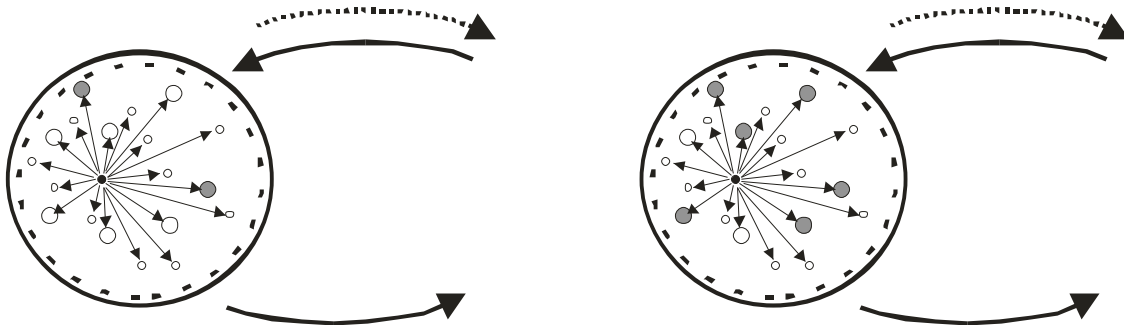


Figure 5. Structuration socio-spatiale de la troisième expérience de la thèse (voir chapitre 6). Autour d'un individu focal, les interactions sociales ont lieu au sein du fragment. La dispersion est limitée à plusieurs fragments du même traitement. On manipule la sexe ratio des congénères adultes (ronds de grande taille, rond gris : femelle, rond vide : mâle) au sein du fragment de vie du lézard (gauche : la sexe ratio est biaisée en faveur des mâles ; droite : la sexe ratio est biaisée symétriquement en faveur des femelles). La structure de la population immature et juvénile (petits cercles) n'est pas perturbée.

Capacités locomotrices

Dans cette dernière partie, on envisage certaines propriétés des capacités locomotrices, une mesure intégrative de la compétence physiologique et morphologique d'un individu à explorer son voisinage social. On a étudié ces variations dans deux contextes particuliers :

- l'effet de l'investissement dans la reproduction des femelles sur les performances locomotrices (Annexe 4) ;

- la relation entre la capacité locomotrice d'un jeune et sa survie pendant la première année de sa vie (Annexe 5).

On a utilisé une démarche corrélative pour répondre à ces questions. Cette démarche consiste à mesurer les performances locomotrices individuelles pour les mettre en relation avec des covariables individuelles. Cette approche est justifiée par le fait qu'il était difficile de manipuler directement les capacités locomotrices des lézards, en tout cas dans le cadre de ces travaux préliminaires (mais voir Miles et al. (2000) pour une étude expérimentale).

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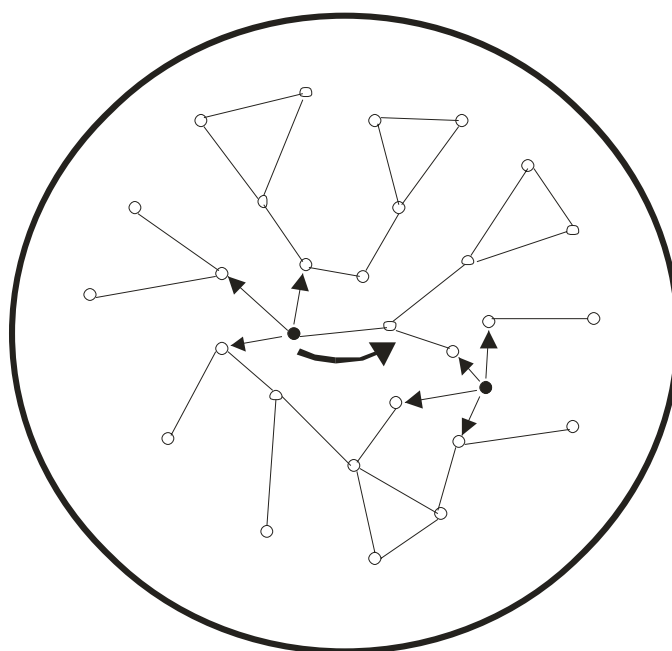
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CHAPITRE 1 – DYNAMIQUES ADAPTATIVES SPATIALISEES



« Explicit spatial models are instructive for they show that fitness (as measured by the likelihood of invasion) depends not on individual property alone but also upon aspects of the spatial environment » R. E. Michod dans *Darwinian dynamics. Evolutionary transitions in fitness and individuality*. 1999. p. 73.

Attention : les appels de chapitre dans cette partie font référence aux chapitres de l'ouvrage dans lequel cette partie a été publiée, pas aux chapitres de la thèse !

VALEUR SELECTIVE D'INVASION ET DYNAMIQUES ADAPTATIVES DANS DES MODELES ECOLOGIQUES SPATIAUX

Régis Ferrière

Jean-François Le Galliard

RESUME

Une mesure appropriée de la valeur sélective est nécessaire pour décortiquer les processus proximaux et ultimes agissant sur la dispersion et évaluer leurs effets respectifs. Cependant, il y a eu relativement peu de tentatives théoriques pour définir avec cohérence la valeur sélective à partir des principes de base de la démographie, quand l'adaptation de traits à dimension spatiale, comme la dispersion, est envisagée. Dans ce chapitre, nous présentons le système des dynamiques adaptatives et nous proposons que la valeur sélective d'invasion fournit un concept robuste pour prendre en compte les processus écologiques agissant à l'échelle individuelle. La construction de la valeur sélective d'invasion pour un scénario écologique à dimension spatiale est présentée. La valeur sélective d'invasion inclut les effets des voisins sur un individu focal, médiés par des coefficients analogues aux coefficients d'apparentement de la génétique des populations. La valeur sélective d'invasion peut être utilisée pour analyser l'évolution conjointe de la dispersion et de l'altruisme, deux traits qui ont une influence directe sur la distribution spatiale des individus, et dont l'évolution dépend de la distribution spatiale des individus. Nos prédictions déterministes de l'évolution de la dispersion et de l'altruisme basées sur la valeur sélective d'invasion sont en accord avec des simulations stochastiques du processus de mutation-sélection agissant sur ces traits.

Chapitre 5 du livre « Dispersal » édité par J. Clobert, E. Danchin, A.A. Dhondt and J.D. Nichols avec des modifications incluses.

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Mots-clés : dynamiques adaptatives, altruisme, dispersion, valeur sélective d'invasion, modèles de réseau.

INVASION FITNESS AND ADAPTIVE DYNAMICS IN SPATIAL POPULATION

MODELS

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ABSTRACT

Disentangling proximate and ultimate factors of dispersal, and assessing their relative effects require an appropriate measure of fitness. Yet there have been few theoretical attempts to coherently define fitness from demographic ‘first principles’, when space-related traits like dispersal are adaptive. In this chapter, we present the framework of adaptive dynamics and argue that invasion fitness is a robust concept accounting for ecological processes that operate at the individual level. The derivation of invasion fitness for spatial ecological scenarios is presented. Spatial invasion fitness involves the effect of neighbors on a focal individual, mediated by coefficients analogous to relatedness coefficients of population genetics. Spatial invasion fitness can be used to investigate the joint evolution of dispersal and altruism, two traits that both have a direct influence on, and whose evolution is strongly responsive to, the spatial distribution of individuals. Our deterministic predictions of dispersal and altruism evolution based on spatial invasion fitness are in good agreement with stochastic individual-based simulations of the mutation-selection process acting on these traits.

Chapter 5 of « Dispersal » book edited by J. Clobert, E. Danchin, A.A. Dhondt and J.D. Nichols with modifications included.

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Key-words : Adaptive dynamics, altruism, dispersal, invasion fitness, lattice models.

INTRODUCTION

Even in homogeneous habitats, *spatial fluctuations* of population size arise inevitably as a result of demographic stochasticity, and *spatial correlations* build up from the imperfect mixing of individuals induced by the limited range of dispersal (Tilman and Kareiva, 1998 ; Dieckmann *et al.*, 2000). As a consequence, selective forces acting on the life-history traits of individuals are neither uniform nor independent across space. Dispersal propensity (in the broad sense of natal dispersal and breeding dispersal) is therefore a pivotal component of the individuals' phenotype, for it is both a target of selection and a primary factor of spatial fluctuations and correlations in the selective regime (Ferrière *et al.*, 2000).

Since the seminal work of Hamilton and May (1977) we know that the avoidance of competition with related individuals is an important factor in explaining the evolution of dispersal. It has been recently argued that dispersal probabilities evolving under the sole effect of kin competition provide a null model against which to assess the relative importance of alternative selective forces, as predicted by more elaborated kin selection models (Ronce, 1999). In kin selection theory based on diallelic, haploid genetics, the commonly used measure of fitness is *invasion fitness*, that is, the *per capita* growth rate of a mutant when rare. For pairwise interactions involving an 'actor' and a 'recipient', the definition of invasion fitness involves the *relatedness* of the recipient to the actor (Grafen 1979), for which the correct definition is the probability that the recipient is a mutant (Day and Taylor, 1998). However, this assumes that the altered phenotype of a mutant has no effect on that probability and therefore does not change relatedness. Obviously this does not hold true when phenotypic traits under consideration, like dispersal, modify the distribution of individuals across space. Furthermore, how to model mutants' initial rarity require some care in spatial models (Rousset and Billiard, 2000) : for the population size is everywhere locally finite, the initial number of mutants may not be regarded as locally infinitesimal.

The purpose of this chapter is to provide a modeling framework that allows to investigate the evolutionary dynamics of adaptive, continuous traits, while accounting explicitly for both the reciprocal effects of these traits on the spatial distribution of individuals, and for the effects of the spatial heterogeneity of selective pressures on the traits' evolutionary dynamics. In section 2, we provide a general argument that the notion of invasion fitness is appropriate to capture 'first' demographic principles operating at the level of individuals, and to describe the long-term evolutionary dynamics of adaptive life-history traits (Metz *et al.*, 1992, 1996 ; Dieckmann and Law, 1996 ; Geritz *et al.*, 1997, 1998). We then present in section 3 van Baalen and Rand's (1998) extension of the notion of invasion fitness to spatially heterogeneous populations. *Spatial invasion fitness* is derived from first demographic and behavioral principles operating at the levels of individuals and their nearby neighbors. In non-spatial populations where individuals are assumed to be constantly

well-mixed and interactions occur at random between them, invasion fitness can be obtained as the Malthusian growth rate of a simple birth-and-death process (Ferrière and Clobert, 1992 ; Metz *et al.*, 1992 ; Ferrière and Gatto, 1995). In contrast, when interactions develop locally and dispersal is limited to neighborhoods, the process of mutant growth should be modeled by keeping track of spatial statistics that describe local population structures beyond global densities. The theory of *correlation equations* (Matsuda *et al.*, 1992 ; Morris, 1997 ; Rand, 1999) provides the appropriate mathematical tools. Under certain assumptions about habitat structure and the model's mathematical properties, invasion fitness can then be obtained as the dominant eigenvalue of a matrix (van Baalen and Rand, 1998), just as one would recover the population growth rate of a simple Leslie model (Caswell, 1989). In the spatial setting, the matrix involved contains demographic parameters that depend upon the local, spatial structure of the population.

In section 4 we operate this framework to investigate the evolution of dispersal jointly with altruistic behavior. The evolution of dispersal and the evolution of altruism have been the focus of two rather independent lines of research that trace back to the seminal work of Hamilton (1964). Yet there are serious reasons for trying to merge these lines. With limited dispersal, individuals are likely to interact with relatives, and kin selection models would then predict altruism to evolve. Yet neighbors not only interact socially : they compete with each other as well. Thus, clustering of relatives may not be sufficient for sociality to evolve. A dose of dispersal is needed, so that a locally successful strategy can be exported throughout the resident population. Co-adaptive changes of dispersal and social behavior may thus be expected (Le Galliard *et al.*, *in prep.*).

ADAPTIVE DYNAMICS AND THE CONCEPT OF INVASION FITNESS

We will first introduce the basics of a general and coherent mathematical theory of Darwinian evolution which aims at describing the evolutionary dynamics of adaptive, continuous traits. This *adaptive dynamics theory* (founding papers are Metz *et al.*, 1992, 1996 ; Dieckmann and Law, 1996 ; Geritz *et al.*, 1997) satisfies three important requirements :

- Adaptive dynamics are modeled as a macroscopic description derived from microscopic mechanisms. Selective pressures are set by ecological mechanisms operating at the 'microscopic' level of individuals.
- Adaptive dynamics incorporate the stochastic elements of evolutionary processes, arising from the random process of mutation, and from the extinction risk of initially small mutant populations in the process of selection.
- Adaptive dynamics describe evolution as a dynamical process, identifying potential evolutionary endpoints and among them those which indeed are attractors for the traits dynamics.

In this section we present a brief overview of the principles of adaptive dynamics modeling to show that a consistent measure of fitness arises naturally from the description of microscopic

processes underlying ecological interactions. The reader should refer to Marrow *et al.* (1992), Metz *et al.* (1992) and Dieckmann and Law (1996) for a thorougher treatment. In the following sections, we shall see how to derive this fitness measure for a class of spatial population models where the individual probability of dispersal is one of the adaptive traits under consideration.

The canonical equation of adaptive dynamics

We consider a closed population of a single species. Individuals are characterized by a suite of adaptive, quantitative traits which define their *phenotype*. They reproduce and die at rates that depend upon their phenotype and their environment, including external factors as well as their own congeners population. Haploid inheritance is assumed, and there is a non-zero probability for a birth event to produce a mutant offspring, that is, an individual that differs from its parent in one of the traits. Individuals interact with each other, and the process of selection determines changes in the abundance of each phenotype through time. Direct individual-based models accounting for the stochasticity of birth, death and mutation events could be run to study how the distribution of phenotypes present in the population evolves through time. The theory of adaptive dynamics was developed as an alternative to intensive computer calculations, to provide a handy, deterministic description of the stochastic processes of mutation and selection.

Adaptive dynamics models rest on two basic principles (Metz *et al.*, 1996) : mutual exclusion, « in general two phenotypes x and x' differing only slightly cannot coexist indefinitely in the population » ; and timescale separation, « the timescale of selection is much faster than that of mutation ». Thus one may regard the adaptive dynamics as a trait substitution sequence. Each step occurs at a rate equal to the probability $w(x'|x)$ per unit time for a specific phenotype substitution, say x' substituted to x . The so-called canonical equation of adaptive dynamics then describes how the mean of the probability distribution of trait values in the evolving population changes through time. If we keep using x to denote this mean, the canonical equation reads (Dieckmann and Law, 1996) :

$$\frac{d}{dt}x = \int (x' - x) \cdot w(x'|x) dx' \quad (2.1)$$

where the integral sum is taken over the whole range of feasible phenotypes.

Following on the traditional view of the evolutionary process as a hill-climbing walk on an adaptive landscape (Wright, 1931), we seek to recast the canonical equation into the form

$$\frac{d}{dt}x = \eta(x) \cdot \left. \frac{\partial}{\partial x'} W(x', x) \right|_{x'=x} \quad (2.2)$$

where the coefficient $\eta(x)$ would scale the rate of evolutionary change, and $W(x', x)$ would rigorously define the measure of fitness of individuals with trait value x' in the environment set by the bearers of trait value x .

Mutant invasion rate as a measure of fitness

To recast the canonical equation (2.1) in the form of equation (2.2), we first expand $w(x'|x)$ as the product of a mutation term and a selection term. To keep notations simple, we shall restrict ourselves to the case where phenotypes are characterized by a single trait. The mutation term is the probability per unit time that the mutant enters the population. It involves four multiplicative components : the *per capita* birth rate $b(x)$ of phenotype x , the fraction $\mu(x)$ of births affected by mutations, the equilibrium population size \hat{n}_x of phenotype x , and the probability of a mutation step size $x' - x$ from phenotype x . The selection term is the probability that the initially rare mutant goes to fixation. Under the assumption that the population is *well mixed*, we can neglect the effects of the mutant density on the demographic rates of the mutant and resident populations. Let us denote the *per capita* birth and death rates of the rare mutant in a resident population of phenotype x by $b(x', x)$ and $d(x', x)$. Then the difference $b(x', x) - d(x', x)$ measures the mutant invasion rate, that is, the *per capita* growth rate of initially rare mutants, hereafter denoted by $s(x', x)$. The theory of stochastic birth-and-death processes (e.g. pp. 39-41 in Renshaw, 1991) shows that the probability that the mutant population escapes initial extinction starting from size 1 is zero if $s(x', x) < 0$, and is approximately equal to $s(x', x)/b(x', x)$ otherwise.

Altogether we obtain

$$w(x'|x) = \mu(x) \cdot b(x) \cdot \hat{n}_x \cdot M(x, x'-x) \cdot \frac{[s(x', x)]_+}{b(x', x)} \quad (2.3)$$

The quantity $[s(x', x)]_+$ is equal to $s(x', x)$ if $s(x', x) > 0$ and to zero otherwise ; this means that only advantageous mutants, with positive invasion rate, have a non-zero chance of getting established. Up to first order in the mutation step size $x' - x$ we further have

$$\frac{s(x', x)}{b(x', x)} \approx \frac{1}{b(x)} \cdot (x' - x) \cdot \left. \frac{\partial s}{\partial x'} \right|_{x'=x}, \quad (2.4)$$

where we have used $s(x, x) = 0$ since the population of phenotype x is at demographic equilibrium. If we assume the mutation process to be symmetric, and denote the variance of the mutation distribution by $\sigma^2(x)$, we can insert equation (2.3) together with equation (2.4) into equation (2.1) and compute the integral to obtain (Dieckmann and Law, 1996)

$$\frac{d}{dt} x = \left[\mu(x) \cdot \frac{\sigma^2(x)}{2} \cdot \hat{n}_x \right] \cdot \left. \frac{\partial s}{\partial x'} \right|_{x'=x} \quad (2.5)$$

which precisely conforms to equation (2.2). According to this deterministic approximation of adaptive dynamics, the evolutionary rate $\eta(x)$ of equation (2.2) is given by the bracketed product which encapsulates the influence of mutation. Most importantly, this derivation identifies the mutant invasion

rate $s(x', x)$ as the appropriate measure of fitness denoted by $W(x', x)$ in equation (2.2). Therefore we call $s(x', x)$ the mutant *invasion fitness*.

Invasion fitness, ESS, CSS, and evolutionary branching

The selection derivative (Marrow *et al.*, 1992), $\partial s / \partial x' \big|_{x'=x}$, determines the direction of adaptive change. When the selection derivative is positive (negative), an increase (a decrease) of the trait value x will be advantageous in the vicinity of the resident trait value. Phenotypes that nullify the selection derivative are called *evolutionary singularities* and represent potential end-points for the evolutionary process. Yet careful inspection of stability properties of evolutionary singularities is required before conclusions can be drawn about the adaptive dynamics in their vicinity (Geritz *et al.*, 1998) :

- If invasion fitness presents a local maximum at an evolutionary singularity, then this singularity is an *evolutionarily stable strategy* (ESS), in the classical terminology of evolutionary biology.
- An ESS needs not be attainable : if the selection derivative increases near the ESS, any evolutionary trajectory starting nearby will actually be repelled away from the ESS. In this case, the ESS also is an *evolutionary repeller*.
- Conversely, a singularity may attract evolutionary trajectories and yet correspond to a fitness minimum. In this perhaps most remarkable case, selection is initially stabilizing and drives the population to a point where ecological interactions turn the selective regime into a disruptive one, and dimorphism evolves. This phenomenon is known as *evolutionary branching*. The canonical equation for adaptive dynamics provides an approximate models for evolutionary trajectories heading to a branching phenotype, but obviously fails to capture the population's further evolutionary dynamics.

SPATIAL INVASION FITNESS IN HOMOGENEOUS HABITATS

One conclusion to be drawn from the previous section is that the derivation of invasion fitness must be underpinned on an ecological model for the population dynamics. The definition of a fitness measure as a function of space-related traits therefore requires that spatial structure and local interactions are incorporated in the underlying ecological model.

Spatial population models

Spatial models fall into two main categories, depending on the continuous versus discrete structure of the habitat. Traditional models for continuous space (*reaction-diffusion* models ; see Okubo, 1980) run into serious biological inconsistencies, like the assumption that infinitely many 'nano-individuals' may live on arbitrarily small areas. It is only recently that two new types of mathematically sound and biologically consistent models were derived. *Hydrodynamics limit* models are spatially explicit ; akin to reaction-diffusion equations, they involve correction terms that account

for local interactions and dispersal (Durrett and Levin, 1994). *Moment equations* are spatially implicit ; they describe the dynamics of the statistical moments of the distribution of individuals in space (Bolker and Pacala, 1999 ; Dieckmann and Law, 2000). To model spatial population processes over discrete space, there is a long tradition of *metapopulation models* (Levins, 1969 ; Hanski and Gilpin, 1997 ; Hanski, 1999, and references therein). Classical models of metapopulations are not truly spatial in the sense that they do not involve the notion of neighborhood ; dispersal is global, and all dispersing individuals are mixed in a common pool before being redistributed in patches irrespective to their location¹. *Stepping-stone* models (Kendall, 1948 ; Kingman, 1969 ; Renshaw, 1986) assume that a set of finite populations is distributed on a regular lattice of patches. Dispersal takes place between neighboring patches. In the field of population genetics, stepping-stone models usually assume that all patches are saturated at their carrying capacity (Malécot, 1948, 1975 ; Kimura, 1953). *Lattice models* (Matsuda *et al.*, 1992 ; Morris, 1997 ; Rand, 1999) have been developed recently as another tool to modeling population dynamics in discrete space. Lattice models prescribe the possible locations of individuals on a network of sites, each site hosting at most one individual. There is no saturation assumption : all sites need not be occupied. Local interactions and local dispersal occur between any site and its neighborhood of connected sites. Like moment equations, lattice models are spatially implicit, and they aim at describing neighbor-range spatial correlations.

When it comes to deriving a measure of invasion fitness from these ecological models, operational results are scant. So far no invasion criterion could be established rigorously for models of hydrodynamics limits or moments. Invasion fitness in metapopulations has been worked out by Olivieri *et al.* (1995) and in greater generality by Metz and Gyllenberg (2000). However, as we already pointed out, such models do not account for limited dispersal and therefore address spatial processes in a rather special way. The study of interacting populations on stepping-stone models remains very limited. Only lattice models have led to a rigorous mathematical definition of invasion fitness in space (van Baalen and Rand 1998), and it is this type of models that we shall consider further in the rest of this chapter.

Modeling the spatial dynamics of population lattices

The population is distributed over an infinite network, or lattice, of connected sites (Fig. 1). A site contains at most one individual. Connections have two meanings : interactions (social, competitive, parasitic, etc.) may occur only between individuals that inhabit connected sites, and movement may occur only from a given site to a connected site. This has the important consequence

¹ For the sake of completeness, we should mention the so-called two-patch or n-patch models frequently used (possibly overused) to describe local population regulation by means of simple nonlinear density-dependence (like the Ricker map). For examples and corresponding references, see chapter 3 in Hanski (1999). Unfortunately, as they treat the densities of local populations as continuous variables, they have to rely on the rather unsatisfactory premise that local population size is infinite.

that the spatial scale is the same for dispersal and interactions. For simplicity, we shall assume that each site is connected to the same number (n) of neighboring sites (e.g. a regular lattice). Each site is in one of several, finitely many possible states : empty, or occupied by an individual of one out of N possible types. The configuration of the whole lattice is given by the states of all sites. The lattice configuration changes as a result of two types of events potentially affecting any site during any short time interval : birth or immigration of an individual from a neighboring site, and death or emigration of the individual occupying a site. In general, dispersal (emigration-immigration) is not restricted to the newborn class.

We aim to describe the temporal dynamics of the frequencies of sites that are empty and sites that are occupied by any given phenotype (Matsuda *et al.*, 1992 ; Rand, 1999). The probability that the state of a site changes depends not only on its current state but also on the state of neighboring sites, for two different reasons. On the one hand, dispersal and birth are local events whose realization is conditional to the availability of empty sites in the neighborhood. The likelihood that an individual in a given site moves or exports its offspring is proportional to the frequency of empty sites in her neighborhood. On the other hand, local interactions with neighbors will affect the birth rate and death rate of any focal individual. For example, individuals might negatively affect each other's birth rate through local competition for food. In this case, the birth rate could be seen as a decreasing function of the number of neighbors.

Therefore the *frequency of sites in state i* among all sites of the lattice, p_i , must depend on the neighborhood structure as described by a second-order statistic for the distribution of the configurations of all pairs of nearest-neighbor sites. The dynamics of pair configurations depends in turn on the state of triplets including the pairs' neighbors, and so on. A full description of the lattice

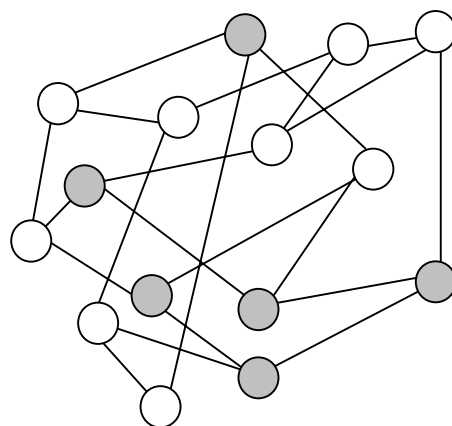


Figure 1. Example of a small random lattice. Each site is randomly linked to a fixed number n of other sites. Here $n = 3$. Dark circles are occupied sites, open circles are empty sites.

dynamics eventually requires an infinite hierarchy of statistics, each one describing the spatial structure on a particular scale (sites, pairs, triplets and so on) in relation to the immediately subsequent one (Morris, 1997). To make a model tractable, one has to choose a particular scale of description, and make appropriate approximations to close the exact, infinite system at that scale. This means that the frequencies of configurations beyond the chosen spatial scale are estimated from the frequencies of configurations up to that scale. No mathematical procedure is currently available to systematically identify the scale at which the system should be closed, and the closure that should be applied in order to obtain the best approximation of the dynamics of the infinite-dimensional model. This will depend on the particular model under consideration and of the biological motivation guiding the analysis (Morris, 1997 ; Dieckmann and Law, 2000).

Our aim is to describe the dynamics of lattices at the most local scale, that of pairs of nearest neighbors. Pair-dynamics models can account for the effect of spatial correlations which arise at a local scale and vanish quickly, although they are not concerned with the development of large-scale spatial structures. It should be noticed that, at least for regular lattices, one may straightforwardly recover the frequencies of sites in the various states (i.e., the p_i values) simply by adding the appropriate pair frequencies. Pair-dynamics models offer a handy compromise between the need to incorporate and describe some of the spatial complexity of the population dynamics, and the aim of deriving useful analytical results on population equilibrium and invasion conditions. The pair-dynamics approach has been used to construct appropriate correlation equations for plant dynamics models (Harada and Iwasa, 1994; Satō and Konno, 1995), spatial games (Morris, 1997 ; Nakamaru *et al.*, 1997), social interactions (Matsuda *et al.*, 1992 ; Harada *et al.*, 1995 ; van Baalen and Rand, 1998) and epidemic models (Keeling, 1996 ; Morris, 1997). In the case of a spatial game on a regular lattice, however, Morris (1997) showed that the pair-dynamics description could fail dramatically. Then moving up to the triplet dynamics is often sufficient to obtain a substantial improvement in the closure accuracy.

From individuals to pair dynamics and correlation equations

We define p_{ij} as the frequency of pairs of nearest-neighbor sites, one being in state i , and the other in state j . Such a pair is denoted by (i, j) , and the frequency p_{ij} is calculated over all pairs² in the lattice. We shall take four heuristic steps in order to derive the so-called correlation equations ; that is, a set of nonlinear differential equations that describe the lattice dynamics at the spatial scale of pairs. The four steps are :

- (1) Write the rates of local events for anchored pairs. We call *anchored pair* one that contains a given site z occupied by an individual in a specified state i . By definition, *local pair events* affect

² Note that the pairs are symmetric, which implies $(i, j) = (j, i)$.

anchored pair, and are triggered by a site event at the anchored site z (see Fig. 2). Four local events have to be considered.

- (2) Average the rates of local events for anchored pairs calculated at Step 1 over all sites z in state i .
- (3) Calculate the rate of change of the frequency of all (i, j) pairs by bookkeeping all possible transitions of anchored pairs that may create or destroy an (i, j) pair.
- (4) Apply an appropriate closure procedure designed to approximate all statistics involving triplets in terms of statistics for pairs.

Notations are introduced in Table 1. (See Morris, 1997, and Rand, 1999, for a rigorous account of all mathematical details involved).

Table 1. Variables and parameters of the lattice model

N	Set of all phenotypes present in the population
z	Generic notation for the location of a site in the graph
i, j, k	Generic notations for different site states
p_i	Frequency of sites in state i among all sites (<i>site frequency</i>)
p_{ij}	Frequency of (i, j) pairs among all pairs of sites (<i>pair frequency</i>)
$q_{i,j}$	Probability that next to a site in state j , there is a site in state i (<i>aggregation coefficient</i>)
$q_{i,jk}$	Probability that next to a site in state j in a (j, k) pair, there is a site in state i
n	Number of neighboring sites to any given site (constant)
$n_{k:ij}(z)$	Number of sites in state k in the neighborhood of a type i at site z in a (i, j) pair
ϕ	Probability to draw a connection at random uniformly among all connections to any given site ($\phi = 1/n$)
$b_i(z)$	Intrinsic <i>per capita</i> birth rate at location z
$d_i(z)$	Intrinsic <i>per capita</i> death rate at location z
$m_i(z)$	Intrinsic <i>per capita</i> dispersal rate of type i at location z
$E_{ij}^b(z)$	Additive effect (competition, cooperation) on the per capita birth rate of a type i individual located at z induced by interaction with a type j individual located in the neighborhood
$E_{ij}^d(z)$	Additive effect on the per capita death rate of a type i individual located at z induced by interaction with a type j individual located in the neighborhood
$C_i^b(z)$	Cost of type i strategy impacting the birth rate of a type i individual located at z
$C_i^d(z)$	Cost of type i strategy impacting the death rate of a type i individual located at z

Step 1. Transition rates for anchored pairs. We define the anchored pair ($i \in z; j \in z'$) to be the pair spanning the sites located at z and z' , and hosting a type i individual in site z while site z' is in

state j . We consider the four local events that can affect such a pair as a result of an individual event occurring at z (Fig. 2) : a birth event at z when j is the empty state; two mortality events affecting the i individual at z , differing in the presence or absence of an individual at z' ; a dispersal event from z to z' , assuming z' to be empty. The individual birth rate, death rate, and dispersal rate involve three additive components : an intrinsic, baseline rate that may depend on the individual's phenotype, an interaction term that measures the effect of neighbors, and a cost term that depends on the individual's phenotype. To calculate the rate of local events we must introduce the number $n_{k:ij}(z)$ of neighboring sites in state k next to the z site of an anchored pair ($i \in z; j \in z'$). We simply add the contributions to the event rate affecting the i individual at z resulting from all possible configurations of the neighborhood of site z . The per-capita rate of the birth and dispersal local events should be scaled by ϕ , the inverse neighborhood size. This reflects the fact that a birth or dispersal event affecting at a given rate a focal individual that belong to n pairs, will affect any of these pairs at a rate n times slower ; in contrast, a death event at z will concomitantly affect all n pairs containing z . Altogether this yields the following rates for each of the transitions depicted in Fig. 2 :

$$\phi \tilde{b}_i(z) = \phi \left(b_i(z) + \sum_{k \in N} E_{ik}^b(z) n_{k:io}(z) - C_i^b(z) \right) \quad (3.1a)$$

$$\tilde{d}_{ij}(z) = d_i(z) + E_{ij}^d(z) + \sum_{k \in N} E_{ik}^d(z) n_{k:ij}(z) + C_i^d(z) \quad (3.1b)$$

$$\tilde{d}_{io}(z) = d_i(z) + \sum_{k \in N} E_{ik}^d(z) n_{k:io}(z) + C_i^d(z) \quad (3.1c)$$

$$\phi \tilde{m}_i(z) = \phi m_i \quad (3.1d)$$

Notice that for the sake of simplicity, we have assumed that the intrinsic dispersal rate $m_i(z)$ of any focal individual was merely equal to the intrinsic dispersal rate. There is no conceptual predicament, however, to extend the model and make dispersal conditional on the neighborhood composition (Rand, 1999).

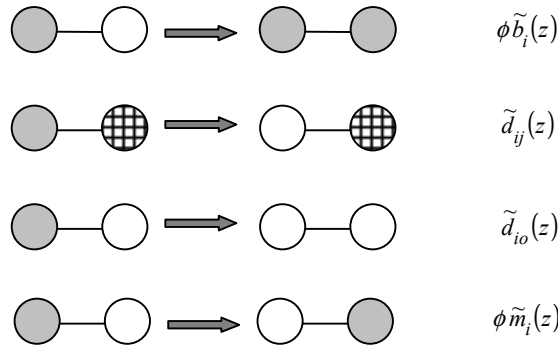


Figure 2. The four local pair events and their rate. Open circles are empty sites. Each dark circle is occupied by a type i individual. Hatched circles are in state j . See text for notations and explanations.

Step 2. Averaging transition rates for anchored pairs over the lattice. Assuming that the lattice is homogeneous, we can take the intrinsic rates, the interaction effects and the costs of interaction to be independent of the location z of any focal individual, and set $b(z) \equiv b$, $d(z) \equiv d$, $m(z) \equiv m$, $E_{ij}^b(z) \equiv E_{ij}^b$, $E_{ij}^d(z) \equiv E_{ij}^d$, $C_i^b(z) \equiv C_i^b$ and $C_i^d(z) \equiv C_i^d$. Transition rates for anchored pairs given by equations (3.1) are still influenced by the local configurations of the lattice, through the neighborhood-structure terms $n_{k:ij}(z)$ which depend on the location z . *Local fluctuations* caused by demographic stochasticity induce spatial variations in the neighborhood structure. If we would know at any time the state of every site z , then we could calculate each $n_{k:ij}(z)$ and obtain all transition probabilities for each anchored pair. However, the large number of sites makes this endeavor hopeless. Instead we aim at deriving average transition rates for anchored pairs across the lattice. We first compute an average measure of the neighborhood structure, $\bar{n}_{k:ij} = \sum n_{k:ij}(z) / |i|$, calculated as the total number $|i|$ of sites in state i is very large; the sum is taken over all sites z that hosts a type i individual belonging to a (i, j) pair. Likewise we define $q_{k:ij}$ as the average proportion of sites in state k in the neighborhood of a site in state i within a (i, j) pair; in other words, $q_{k:ij}$ is the conditional probability of having a site in state k in the vicinity of a site in state i , given that one of the latter's neighboring site is in state j . Since a focal site in an anchored pair is connected to $(n-1)$ sites outside that pair, we have $\bar{n}_{k:ij} = (n-1)q_{k:ij}$. This averaging procedure applied to all local pair-events rates, equations (3.1), eventually yields the following average rates :

$$\phi \bar{b}_i = \phi \left(b_i + \sum_{k \in N} E_{ik}^b (n-1) q_{k:io} - C_i^b \right) \quad (3.2a)$$

$$\bar{d}_{ij} = d_i + E_{ij}^d + \sum_{k \in N} E_{ik}^d (n-1) q_{k:ij} + C_i^d \quad (3.2b)$$

$$\bar{d}_{io} = d_i + \sum_{k \in N} E_{ik}^d (n-1) q_{k:io} + C_i^d \quad (3.2c)$$

$$\phi \bar{m}_i = \phi m_i \quad (3.2d)$$

Step 3. Pair transition rates and equations for pair dynamics. To compute the transition rates for all possible pairs, we have to complete the bookkeeping of all local pair events that may create or destroy any given pair, and use the average rates given by equations (3.2). This is done in Box 1 for one particular type of pair, in the case of a lattice where there are three possible states for a site : empty, or occupied by one of two types. Once all pair transition rates are available, it is straightforward to assemble a system of differential equations that govern the temporal dynamics of pair frequencies. It turns out that the combinations of rates that enter these equations can be simplified by making use of the following composite rates (van Baalen and Rand, 1998) :

$$\alpha_{ij} = (1 - \phi) (\bar{b}_i + \bar{m}_i) q_{i:oj} \text{ is the rate at which type } i \text{ enters a pair } (o, j) \text{ with } j \neq i,$$

Box 1 . Derivation of pair dynamics

We consider a dimorphic population with two types of individuals, x and y . We do the bookkeeping of all possible transitions and their rates that may create or destroy (x, o) pairs. The frequency of this pair is affected by six potential events which can be grasped easily by mere graphical depiction (Fig. B1 ; also see van Baalen and Rand, 1998). The rate of each transition is computed by summing the appropriate average rates of local pair events.

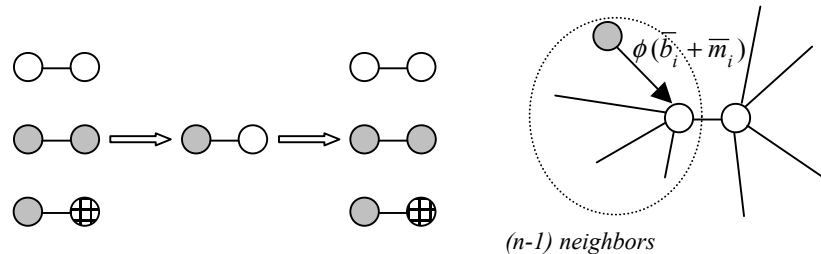


Figure B1. How local pair events affect the pair (x, o) . (a) All possible transitions that may create and destroy the focal pair (in the middle). (b) An example of a local pair event showing how (x, o) can be created from a pair (o, o) : reproduction or dispersal occurs in an anchored pair that belongs to the neighborhood of one of the empty sites of the focal pair.

Pairs (x, o) are created by :

- the transition from (o, o) , as illustrated in Fig. B1. There is on average $(n-1)q_{x,oo}$ anchored pairs (x, o) whose empty site belongs also to a pair (o, o) ; the empty pair (o, o) will be turned into an (x, o) pair by reproduction at the local pair-event rate $\phi \bar{b}_x$; and by dispersal at the rate $\phi \bar{m}_x$.
- the transition from (x, x) either due to death at rate \bar{d}_{xx} , or to movement towards a neighboring site. In the latter case there are $(n-1)q_{o,xx}$ anchored pairs that may undergo the corresponding transition, each at an average local pair-event rate $\phi \bar{m}_x$.
- and the transition from (x, y) , which is calculated in a similar way.

Pairs (x, o) are destroyed by :

- the transition to (o, o) due to death at rate \bar{d}_{xo} , or to dispersal. Again we calculate the number of anchored pairs where this transition may take place to be $(n-1)q_{o,ox}$, and for each of them the transition occurs at the rate $\phi \bar{m}_x$.
- the transition to (x, x) due to reproduction within this pair at rate $\phi \bar{b}_x$, or due to a reproduction or dispersal event involving an x neighbor. The latter transition involves $(n-1)q_{x,ox}$ (x, o) anchored pairs which are affected by a local birth event at rate $\phi \bar{b}_x$ and by a local dispersal event at rate $\phi \bar{m}_x$.
- likewise, the transition to (x, y) involves $(n-1)q_{y,ox}$ anchored pairs (y, o) , undergoing local birth at rate $\phi \bar{b}_y$ and local dispersal at rate $\phi \bar{m}_y$.

Collecting all these transition rates together, and using the notation $\bar{\phi} = (n-1)\phi$, we finally obtain the following rate of change for the pair frequency p_{xo} :

$$\begin{aligned} \frac{dp_{xo}}{dt} = & (\bar{b}_x + \bar{m}_x) \bar{\phi} q_{x,oo} p_{oo} + (\bar{d}_{xx} + \bar{\phi} \bar{m}_x q_{o,xx}) p_{xx} + (\bar{d}_{yx} + \bar{\phi} \bar{m}_y q_{o,yx}) p_{xy} \\ & - (\phi \bar{b}_x + \bar{d}_{xo} + \bar{\phi} \bar{m}_x q_{o,xo} + \bar{\phi} (\bar{b}_x + \bar{m}_x) q_{x,ox} + \bar{\phi} (\bar{b}_y + \bar{m}_y) q_{y,ox}) \end{aligned} \quad (\text{B1.1})$$

$\beta_i = \phi \bar{b}_i + (1 - \phi)(\bar{b}_i + \bar{m}_i) q_{i:oi}$ is the rate at which type i enters a pair (o, i) ,

$\delta_{ij} = \bar{d}_{ij} + (1 - \phi)\bar{m}_i q_{oij}$ is the rate of loss of type i from (i, j) pairs.

We shall refer to these equalities as equations (3.3a), (3.3b), and (3.3c), respectively. It is also convenient to introduce the auxiliary parameter $\alpha'_{ij} = (1 - \phi)(\bar{b}_i + \bar{m}_i)$.

Step 4. Closing the system. The equations for pair frequencies obtained at Step 3 involve the conditional probabilities $q_{k:ij}$. This implies that the system is not closed : the frequencies of pairs depend on the frequencies of triplets, and to avoid a cascade of dependency on even more complex configurations, the frequencies of configurations involved beyond pairs have to be approximated from the pairs. Finding an accurate approximation amounts to solving the « closure problem » posed by the dynamical system under concern.

The general form of such a pair approximation can be written as $q_{k:ij}$, the probability that there is a site in state k next to a site in state i , plus an error term capturing an estimation bias due to local fluctuations (Morris, 1997). Different pair approximations have been developed, reflecting different ways of correcting for the neighborhood structure (Matsuda *et al.*, 1992; Van Baalen, 2000), the lattice regularity (Morris, 1997), and the distribution of local fluctuations (Morris, 1997). Ad hoc corrections accounting for the population clustering pattern have also been proposed (Satō *et al.*, 1994). In general, we can safely assume that an infinite random lattice, or a more regular lattice with weak aggregation, will produce a small bias. The standard pair-approximation (Matsuda *et al.*, 1992) precisely equals the bias to zero and therefore reads $q_{k:ij} \cong q_{k:i}$. It has been confronted to individual-based simulations in a number of models corresponding to various biological situations (Matsuda *et al.*, 1992 ; Harada and Iwasa, 1994 ; Satō and Konno, 1995 ; Kubo *et al.*, 1996 ; Nakamaru *et al.*, 1997 ; Iwasa, 2000). The match is often very good, but sometimes devastatingly bad. In such cases, moving up the description level to the spatial scale of triplets can suffice to improve matters substantially (Morris, 1997). Satō *et al.* (1994), Harada *et al.* (1995), Ellner *et al.* (1998), Morris (1997) and van Baalen (2000) have investigated the alternative path of deriving better pair approximations.

Here we shall content ourselves with the standard pair approximation and apply it to equations (3.2) and (3.3). This yields

$$\phi \bar{b}_i = \phi \left(b_i + \sum_{k \in N} E_{ik}^b (n-1) q_{k:i} - C_i^b \right) \quad (3.4a)$$

$$\bar{d}_{ij} = d_i + E_{ij}^d + \sum_{k \in N} E_{ik}^d (n-1) q_{k:ij} + C_i^d \quad (3.4b)$$

$$\bar{d}_{io} = d_i + \sum_{k \in N} E_{ik}^d (n-1) q_{k:i} + C_i^d, \quad (3.4c)$$

and

$$\alpha_{ij} = (1 - \phi)(\bar{b}_i + \bar{m}_i)q_{i:o} = \alpha_i \quad (3.5a)$$

$$\beta_i = \phi\bar{b}_i + (1 - \phi)(\bar{b}_i + \bar{m}_i)q_{i:o} \quad (3.5b)$$

$$\delta_{ij} = \bar{d}_{ij} + (1 - \phi)\bar{m}_i q_{o:i} \quad (3.5c)$$

One can insert these approximate expressions into the system of differential equations for pair frequencies written with exact pair transition rates (see equation (B1.1)). If there is a single phenotype x in the population (resident phenotype), the dynamics of pairs obey the following system of so-called correlation equations (Rand 1999) :

$$\begin{pmatrix} dp_{ox}/dt \\ dp_{xx}/dt \end{pmatrix} = \begin{pmatrix} \alpha'_{xo} q_{o:o} - (\beta_x + \delta_{xo}) & \delta_{xx} \\ 2\beta_x & -2\delta_{xx} \end{pmatrix} \begin{pmatrix} p_{ox} \\ p_{xx} \end{pmatrix} \quad (3.6)$$

The equilibrium state of the population, fully characterized by $q_{o:x}$ and $q_{o:o}$, may then be found by solving the system $dp_{ox}/dt = 0$ and $dp_{xx}/dt = 0$.

Spatial invasion fitness

We now have the modeling machinery in place to tackle the calculation of invasion fitness, that is, a measure of the population growth rate of a mutant (phenotype y) introduced at low frequency in the resident population where only phenotype x is present. When two strategies x and y are represented in the population, there are six possible types of pairs. A simple bookkeeping procedure is applied to all possible transitions of these pairs, and the rates defined by equations. (3.3) are used to construct a system of correlation equations (3.7) :

$$\begin{pmatrix} dp_{ox}/dt \\ dp_{xx}/dt \\ dp_{oy}/dt \\ dp_{yx}/dt \\ dp_{yy}/dt \end{pmatrix} = \begin{pmatrix} \alpha'_{xo} q_{o:o} - (\beta_x + \alpha_y + \delta_{xo}) & \delta_{xx} & 0 & \delta_{yx} & 0 \\ 2\beta_x & -2\delta_{xx} & 0 & 0 & 0 \\ 0 & 0 & \alpha'_y q_{o:o} - (\beta_y + \alpha'_y q_{y:o} + \delta_{xo}) & \delta_{xy} & \delta_{yy} \\ 0 & 0 & \alpha_x + \alpha'_y q_{x:o} & -(\delta_{xy} + \delta_{yx}) & 0 \\ 0 & 0 & 2\beta_y & 0 & -2\delta_{yy} \end{pmatrix} \begin{pmatrix} p_{ox} \\ p_{xx} \\ p_{oy} \\ p_{xy} \\ p_{yy} \end{pmatrix}$$

The mutant rate of growth, denoted by $s(y, x)$, can be obtained by summing up the last three equations of system (3.5) :

$$\frac{dp_y}{dt} = \frac{dp_{oy}}{dt} + \frac{dp_{xy}}{dt} + \frac{dp_{yy}}{dt} = s(y, x)p_y \quad (3.8)$$

which after some algebra simplifies into :

$$s(y, x) = \bar{b}_y q_{o:y} - \bar{d}_y, \quad (3.9)$$

where

$$\bar{b}_y = b_y + (n-1)E_{yx}^b q_{x:y} + (n-1)E_{yy}^b q_{y:y} - C_y^b \quad (3.10)$$

$$\bar{d}_y = d_y + nE_{yx}^d q_{x:y} + nE_{yy}^d q_{y:y} + C_y^d. \quad (3.11)$$

Rearranging terms, we obtain the final expression :

$$s(y,x) = \left[(b_y - C_y^b) q_{o:y} - d_y - C_y^d \right] + \left[(n-1) E_{yx}^b q_{o:y} - n E_{yx}^d \right] q_{x:y} + \left[(n-1) E_{yy}^b q_{o:y} - n E_{yy}^d \right] q_{y:y} \quad (3.12)$$

This expression bears an interesting relationship to the notion of *direct* or *neighbor-modulated fitness* (Hamilton, 1970 ; Frank, 1998). Direct fitness is defined by summing the fitness effects on an individual caused by all the phenotypes of neighbors (including the individual itself). Likewise, spatial invasion fitness is obtained by adding the effects on a focal mutant of a resident or mutant neighbor weighted by the probability that the focal individual is neighbored by a resident or a mutant individual.

Further analysis based on spatial invasion fitness as defined by (3.12) requires that we solve equation (3.7) for $q_{y:y}$, $q_{x:y}$, and $q_{o:y}$. This can be done numerically by following the algorithmic recipe outlined in Box 2, or even analytically in the simplest cases (Matsuda *et al.*, 1992).

Box 2. A numerical recipe to compute spatial invasion fitness in lattice models

The expression of mutant population growth rate depends on the spatial statistics $q_{o:y}$, $q_{x:y}$ and $q_{y:y}$, which a priori vary over time. Yet the so-called *relaxation property* of the system entails that the statistics $q_{o:y}$, $q_{x:y}$ and $q_{y:y}$ converge very fast to equilibrium values, compared to the slow growth or decline of the system variables p_{oy} , p_{xy} , p_{yy} (Matsuda *et al.* 1992, our simulations). Therefore, to obtain a measure of spatial invasion fitness we may write an auxiliary system of differential equations for the variables $q_{o:y}$, $q_{x:y}$, $q_{y:y}$ only, solve it for equilibrium, and insert the result into equation (4.1).

The numerical derivation of this auxiliary system relies on the initial rarity of the mutant in the resident population. This, by definition, means : $q_{y:o} = 0$. This property allows us to write a closed model for the mutant pair dynamics, using the 3×3 lower-right block M of the transition matrix which appears in equation (3.5) :

$$\frac{d\vec{p}_y}{dt} = \mathbf{M}(\vec{q}_y) \vec{p}_y \quad \text{with} \quad \vec{p}_y = (p_{oy}, p_{xy}, p_{yy}) \quad (B2-1)$$

Using the relations $dp_y/dt = s(y,x)p_y$ and $\vec{p}_y = p_y \vec{q}_y$, we can further transform this system into

$$\frac{d\vec{q}_y}{dt} = [\mathbf{M}(\vec{q}_y) - s(y,x) \mathbf{I}] \vec{q}_y \quad (B2-2)$$

(I is the 3×3 identity matrix). At equilibrium, $d\vec{q}_y/dt = 0$ and the spatial statistics \vec{q}_y are obtained by solving (numerically or analytically in the simplest cases) the nonlinear system $\mathbf{M}(\vec{q}_y) \vec{q}_y = \lambda \vec{q}_y$, which involves four unknowns ($q_{o:y}$, $q_{x:y}$, $q_{y:y}$, and the corresponding eigenvalue λ) and three equations, along with the constraint $q_{o:y} = 1 - q_{x:y} - q_{y:y}$. Solving for λ at the same time yields the numerical value of the spatial invasion fitness $s(y,x)$ (4.1).

APPLICATION : COADAPTATION OF DISPERSAL AND ALTRUISM

Empirical work has stressed the importance of spatial structure and spatial processes for the evolution of dispersal (Hanski, *this volume* ; Ims and Hjermann, *id.* ; Ronce *et al.*, *ibid.*). Coadaptation of other life history components is also expected to have a decisive influence on the evolution of dispersal, because of physiological and/or genetic correlations (Ronce *et al.*, *this volume* ; Roff and Fairbairn, *id.*) or behavioral alternatives (see Lambin *et al.*, *this volume*, for a discussion of the joint adaptation of dispersal, competition and cooperation). There is an urgent need for theory to incorporate these empirical facts.

The purpose of this section is to take a step forward in that direction. We make use of the framework of lattice population models to investigate the joint evolution of dispersal and social behavior while accounting explicitly for local interaction and dispersal processes. More specifically, our main objectives are (i) to identify selective pressures acting on these traits, (ii) to make predictions on their relative effects on the direction of evolution, and (iii) to relate them quantitatively to basic individual and interaction traits. The material presented here provides a short review of analyses expounded in Le Galliard (1999), Le Galliard *et al.* (*in prep.*), and Ferrière and Le Galliard (*in prep.*).

Model assumptions

We focus on two adaptive components of the individual's phenotype: dispersal and altruism (Table 2). The former trait is measured by the dispersal rate m . The altruistic trait is measured by the total investment in altruism u and the amount u/n of help an actor individual may distribute over its neighborhood. This amount affects any recipient's intrinsic birth rate additively. Note that this is a simplified description of altruism because individuals will have a total potential amount u to give and will always give the same amount of help per neighbor, whatever the number of receivers. In the biological realm, this would mean the absence of any kind of strategical distribution of altruism.

Both traits are costly to the bearer. A linear model for the cost of dispersal m is assumed, whereas the cost of altruism scales algebraically with the amount of total investment u (Table 2). The total cost is subtracted from the intrinsic birth rate. The costs of dispersal and altruism are paid unconditionally, irrespective to the movement actually performed by the individual and the average amount of help actually given to the neighborhood. A representative biological instance would be an organism where both dispersal and altruism imply an initial ontogenetic shift towards a fixed physiological or morphological state that would determine the lifetime level of dispersal and altruism. This state would permanently impact the birth rate. This might be the case of a dispersal structure (O'Riain *et al.*, 1996).

Starting from the general model presented in section 3, we make two simplifying assumptions on our way to derive the measure of spatial invasion fitness : the intrinsic birth and death rates are independent of the phenotype, and costs and benefits impact the birth rate only. Referring to

notations introduced in Table 1, this means : $b_i \equiv b$, $d_i \equiv d$, $E_{ij}^d \equiv 0$, $C_i^d \equiv 0$. We use the notation $C(u, m)$ to designate the total cost associated with altruism u and dispersal rate m , $C(u, m) = \kappa u^\gamma + \nu m$ (Table 2). Parameters κ and ν measure the sensitivity of the cost to altruism and dispersal. The parameter γ further indicates how the sensitivity of the cost to altruism varies with altruism. A high value of γ means that the cost of altruism increases slowly with altruism when altruism is low, and becomes more sensitive to altruism as altruism increases.

Table 2. Specific variables and parameters of the model

b	Intrinsic per capita birth rate ($b=2$)
d	Intrinsic per capita death rate ($d=1$)
m	Intrinsic per capita dispersal rate (<i>adaptive trait</i>)
u	Intrinsic per capita altruism rate (<i>adaptive trait</i>)
κu^γ	Cost of altruism impacting the birth rate
νm	Cost of dispersal impacting the birth rate

Adaptive dynamics of dispersal and altruism

Spatial invasion fitness s follows from the general model equation (3.10) and is given here by

$$s \equiv \left(b + u(1 - \phi)q_{x,y} + u'(1 - \phi)q_{y,y} - C(u', m') \right) q_{o,y} - d \quad (4.1)$$

where $x = (u, m)$ denotes the resident phenotype, $y = (u', m')$, the mutant phenotype. The canonical equation (2.5) reads

$$\frac{d}{dt} \begin{pmatrix} u \\ m \end{pmatrix} = \begin{pmatrix} \eta \cdot \frac{\sigma^2}{2} \cdot p_x \cdot \left. \frac{\partial s}{\partial u'} \right|_{u'=u} \\ \eta \cdot \frac{\sigma^2}{2} \cdot p_x \cdot \left. \frac{\partial s}{\partial m'} \right|_{m'=m} \end{pmatrix} \quad (4.2)$$

where η and σ^2 respectively denote the mutation rate and the mutation step variance, that we assume to be the same for both traits and independent of the current phenotypic mean. By making use of the facts that the resident population is at equilibrium and that the mutant is little different from the resident, a first-order approximation of spatial invasion fitness reads :

$$s/q_{o,y} \approx d \left(1/q_{o,x} - 1/q_{o,y} \right) + (1 - \phi)q_{y,y} (u' - u) - [C(u', m') - C(u, m)] \quad (4.3)$$

(see Le Galliard *et al.*, *in prep.*, for details). This expression clearly identifies three components of selection operating on dispersal and altruism. The first term in the right-hand side of equation (4.3) quantifies the pressure for reducing local competition for space. This pressure increases with the intrinsic death rate d : when mortality is low, there is little selective advantage to be gained from opening space by reducing altruism or increasing dispersal. The second term in equation (4.3)

expresses the pressure for increased altruism under aggregated conditions ; the third term measures the pressure for reducing the direct costs of dispersal and altruism. By following the numerical recipe for the calculation of aggregation coefficients and spatial invasion fitness (Box 2), one can obtain explicit analytical expressions for $q_{y,y}$ and $q_{o,y}$. It is thus possible to write each component of selection as a function of individual parameters.

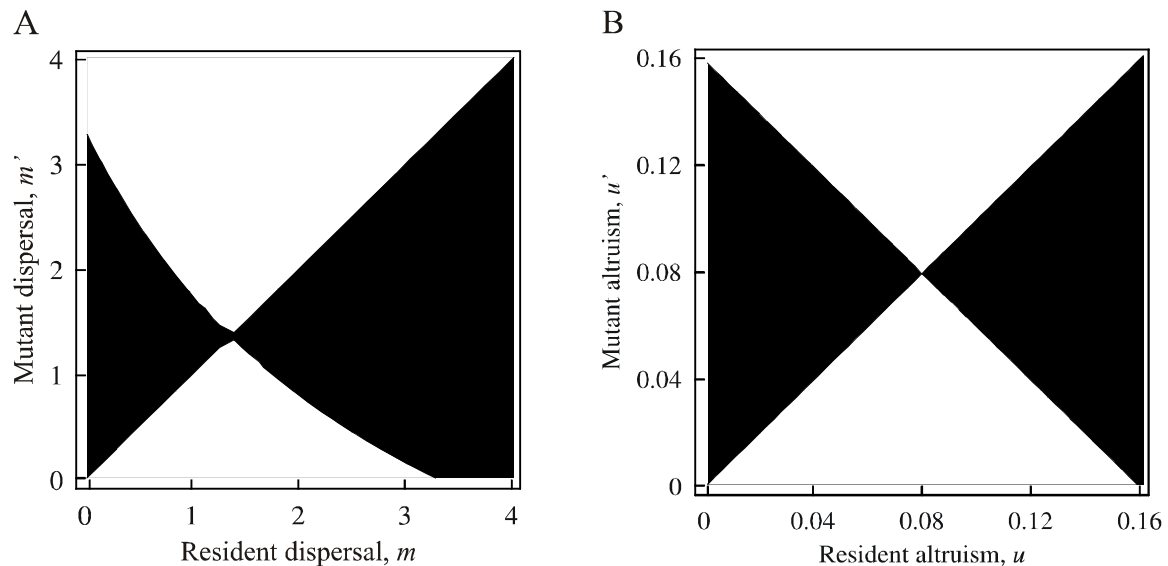


Figure 3. Pairwise invasibility plots when either the altruism trait or the dispersal trait is fixed. Spatial invasion fitness (see equation (4.1)) is positive in the dark region. A, Evolution of dispersal for fixed altruism ($u = 0.1$). B, Evolution of altruism for fixed dispersal ($m = 0.5$). In both cases, there is a single evolutionary singularity, which is attracting and evolutionarily stable. Parameter values : $n = 4$, $b = 2.0$, $d = 1.0$, $\gamma = 2.0$, $\kappa = 1.0$, $\nu = 0.1$.

In general, when the evolution of one trait alone is considered, the adaptive dynamics of the trait are monotonous and converge to a point attractor. This attractive point corresponds to a singularity of the adaptive dynamic, e.g. a point where the selection derivative vanishes. A mutant appearing around this phenotype value is actually counterselected and cannot invade (Fig. 3). The pattern of stabilizing selection is well explained by the relative effects of conflicting pressures. Focusing on the case of dispersal, we can see that at low dispersal, the predominant selective pressure is induced by local competition for space ; reduced aggregation is favored, and this selects for higher dispersal rates. As dispersal increases the intensity of the opposed selective pressure induced by the cost of dispersal also raises. An intermediate equilibrium value is reached at which both pressures exactly compensate each other. Numerical analysis of the dispersal rate at this attractor suggest that its value is mainly sensitive to the parameter ν , which scales the cost of dispersal.

We now consider the coadaptive dynamics of dispersal and altruism. The selective gradient respective to either trait vanishes along the corresponding isocline (Fig. 4), which is the set of evolutionary singularities obtained for this trait, for each possible value of the other trait. Both

isoclines cross at the singularity of the coadaptive dynamics, denoted by (m^*, u^*) . When the cost of altruism is high and very sensitive to a change in the degree of altruism, the singularity is always a stable node (Le Galliard *et al.*, in prep.). The dispersal rate still converges monotonically to the singularity, but explaining the adaptive dynamics in the two dimensional trait space now requires that we consider how the three selective pressures interplay. This can be done by identifying the sign of each selection component locally in the direction of adaptation (Fig. 5). For example one can interpret the four trajectories (1-4) depicted in Fig. 4 in this way. (1) Starting from low dispersal and low altruism, mutants that invest more in altruism and dispersal are initially favored (selection components I and II are positive) ; being more altruistic is advantageous because the level of aggregation is high ; being slightly more mobile is also beneficial for it reduces local competition for space. In a second phase of the dynamics, mutants dispersing more are selected for (selective component I is positive) ; this reduces spatial aggregation and therefore promotes invasion by less altruistic phenotypes. (2) Initially dispersal is low and altruism is high. Only the first phase of the adaptive dynamics differs : here the adaptive dynamics begins with the reduction of the cost of altruism and the reduction of local competition for space (components III and I are positive). (3) Starting with a high dispersal-low altruism phenotype, selection favors an increase of altruism and a decrease of dispersal : at low altruism, mutants with lower dispersal rate pay a significantly reduced cost (component III is positive), and the benefit of more altruism in a population that develops more aggregation dominates the cost of increased local competition (component II is positive). (4) Finally, when ancestral dispersal and altruism are high, the selective pressure for reduced costs dominates (component III is positive) and drives the system all the way down to the singularity where both traits stabilize.

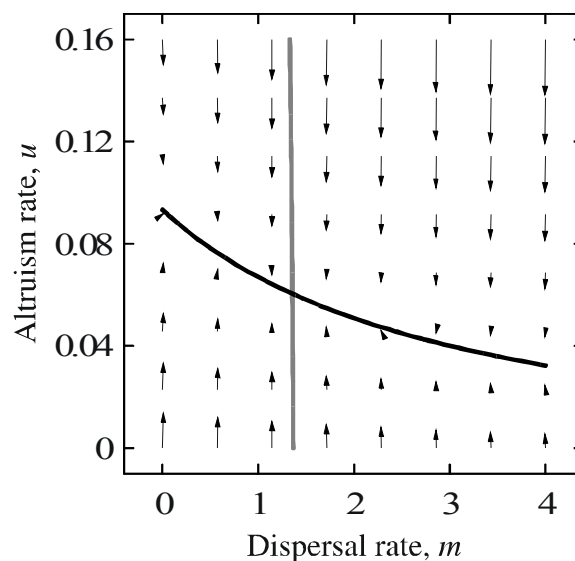


Figure 4. Co-adaptive dynamics of dispersal and altruism. Predictions from the canonical equation (4.2). Vector field : canonical equation of adaptative dynamics. Thin lines : evolutionary isoclines of altruism (black) and dispersal (gray). The crossing point of the isoclines gives the singularity, which is attracting and evolutionarily stable. Parameter values : same as in Fig. 3.

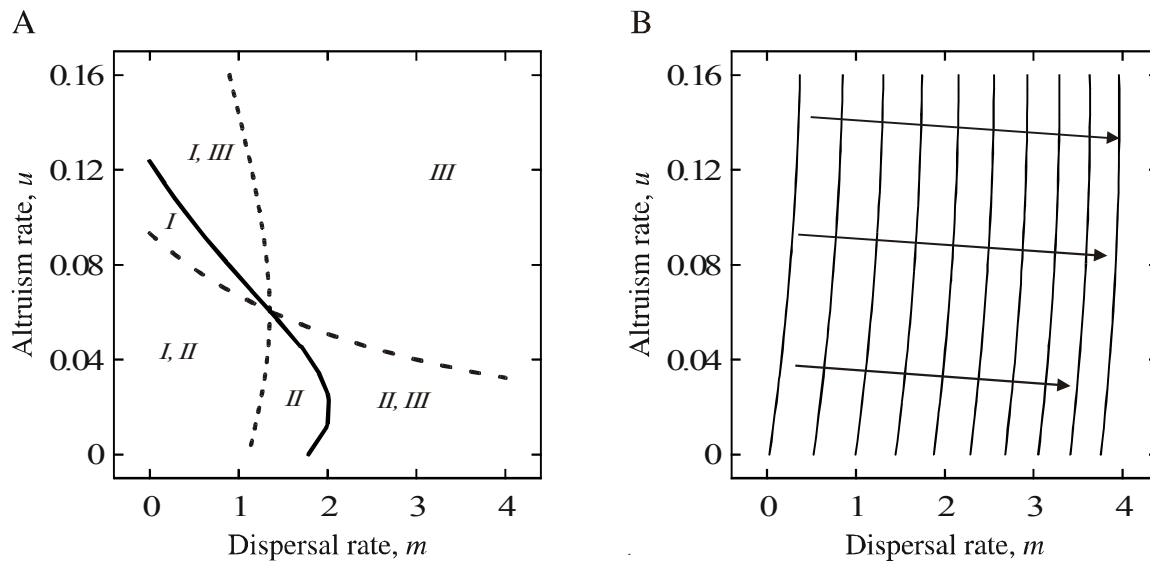


Figure 5. A, Zero-contour lines of the components of selection along adaptive trajectories. In each of the six delineated regions, positive pressures are indicated. Component I (dotted curve) : pressure for reducing local competition for space ; component II (dashed curve): pressure for increased altruism under aggregated conditions ; component III (continuous curve) : pressure for reducing the direct costs of dispersal and altruism. B, Spatial aggregation, shown as a contour plot of the aggregation coefficient q_{xx} for a pure population of phenotype x . Arrows indicate a decreasing aggregation coefficient. Parameter values : same as in Fig. 3.

Revisiting the Hamilton's rule

Hamilton (1964) formulated his famous rule according to which if an actor expresses a behavior that costs him C offspring and increases by B the number of individuals related to the actor, this behavior is selected for if $B r > C$. There has been much debate over the interpretation of the fitness costs C , benefits B , and of the *relatedness* r which make Hamilton's rule work, and by which this rule can be generalized for more complex ecological scenarios.

Defining and measuring relatedness in spatially structured populations is a longstanding problem of population genetics (Malécot, 1948 ; Rousset and Billiard, 2000). The spatial invasion condition provides a natural definition of relatedness as a measure of phenotypic correlation between neighbors (Frank, 1998 ; van Baalen and Rand, 1998). When altruistic and selfish individuals are identical in their basic demographic rates (b , d , and m), altruists with phenotype $y = (u', m)$ can invade non-altruists with phenotype $x = (0, m)$ if

$$u'(1 - \phi) \cdot q_{y,y} > \kappa \cdot u'^{\gamma} \quad (4.4)$$

that is, we have recovered a variant of Hamilton's rule in which $B \equiv u'$, $C = \kappa \cdot u'^{\gamma}$, and the coefficient of relatedness r is given by

$$r = (1 - \phi) \cdot q_{y,y} \quad (4.5)$$

As already mentioned, $q_{y,y}$, and therefore r , can be computed from the invasion matrix (Box 2). This coefficient r estimates how much of an altruist's environment consists of other altruists, an interpretation that is consistent with Day and Taylor (1998). The precise interpretation of B , C , and r in Hamilton's rule, however, is dependent of the details of demographic processes operating in the population. For example, van Baalen and Rand (1998) note that if the cost of altruism is incurred as an increased mortality rate instead of a decreased birth rate, for zero dispersal the invasion condition of altruists in a selfish population becomes

$$u'(1-\phi) \cdot q_{y,y} > (b/d) \cdot \kappa \cdot u'^{\gamma}. \quad (4.6)$$

This provides another version of the Hamilton's rule where the cost C is recovered as the cost of altruism corrected for intrinsic birth and death rates. Other variants of the spatial Hamilton's rule, where relatedness similarly depends on local demographic processes, have been established by Ferrière and Michod (1995, 1996) for the invasion of cooperation in a spatial iterated Prisoner's Dilemma.

How kin selection models handle relatedness is usually problematic (Day and Taylor, 1998 ; Rousset and Billiard, *manuscript*). This is not to mean that kin selection is not the ultimate cause of the evolution of altruism in viscous populations, as Hamilton originally asserted (1964), but that measure of inclusive fitness may not correctly predict the evolutionary dynamics of social traits when selection is density dependent. Using spatial invasion fitness, Hamilton's principle is recovered as an emergent property of the model. This backs up Nunney's (1985) statement that kin selection is the only form of group selection that is able to maintain altruism.

Does spatial invasion fitness rightly predict evolutionary dynamics ?

Although our coevolutionary model of dispersal and altruism incorporates salient features of the ecological and evolutionary processes (including density-dependence, demographic stochasticity and evolutionary feedbacks), it remains underpinned on several critical simplifications. We assume an infinite lattice size, and describe the dynamics of local densities by making use of the pair-approximation (Morris, 1997). The derivation of the fitness measure relies on the small frequency of mutants as they originate and on the relaxation assumption that they instantaneously build up a characteristic cluster that may serve as a vehicle for the potential invasion process (Dieckmann and Law, 2000). Furthermore, the deterministic description of the adaptive dynamics gives an approximation for the mean path of the stochastic mutation selection-process (Dieckmann and Law, 1996), which itself already represents averaging over an infinite number of realizations.

Notwithstanding all this, the properties of stochastic simulations are remarkably well captured by the deterministic predictions (Fig. 6 ; see Le Galliard *et al.*, *in prep.*, for a thorougher comparison). The position of isoclines and the attracting singularity (m^*, u^*) remain nearly unchanged. Overall trends of stochastic trajectories are correctly predicted by the deterministic model. Wilder fluctuations

in trait values, involving the repeated rise and fall of altruism, are observed nearer to the singularity, as the selection gradient tends to weaken there. In our case, these complex regimes in the altruism level, which have received some attention elsewhere (Doebeli and Knowlton, 1999), are best explained by genetic drift in regions of low selection pressure across the phenotypic space.

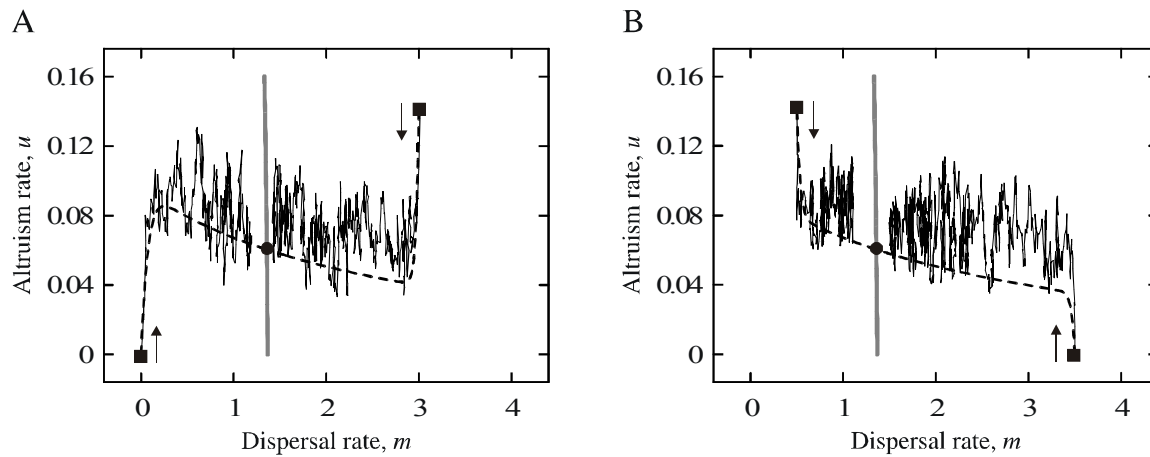


Figure 6. Mean trajectory of ten individual-based simulations of dispersal and altruism evolutionary dynamics. Grey line is the mobility isoclines predicted by the canonical equation (4.2) (see Fig. 4), black squares indicate initial states, dashed curves are predictions from the canonical equation and black dot is the singularity. A, Simulations of two trajectories starting at $(m,u)=(0,0)$ and $(m,u)=(3,0.15)$ respectively. B, Simulations of two trajectories starting at $(m,u)=(0.5,0.15)$ and $(m,u)=(3.5,0)$ respectively. The stochastic trajectories, although rather jerky near the convergence state at the isoclines intercept, hit rather close to it after following closely the deterministic path predicted by spatial invasion fitness. For both traits, the mutation rate is 10^{-2} and the mutation variance is 10^{-2} . Lattice size : 900 sites.

CONCLUDING REMARKS

Defining invasion fitness for spatial ecologies is no trivial matter. Starting from demographic and behavioral processes operating at the individual level and locally between close neighbors, the invasion exponent of a simple system of correlation equations for a mutant population dynamics provides a tractable solution to this problem. The notion of spatial invasion fitness allows one to *derive*, rather than postulate, an explicit relationship between distinct components of selection on the one hand, and the characteristics of the individuals and their interactions on the other. Numerical simulations of individual-based models confirm that the resulting spatial invasion fitness correctly predicts the dynamics of the stochastic mutation-selection process. On the empirical side, Rainey and Travisano's (1998), in their experiments on the evolution of polymorphism in bacteria, have shown that invasion fitness measured in spatially heterogeneous populations successfully predicts the maintenance of morphs diversity. In contrast, the destruction of local structures developed in the

course of population growth alters the phenotypes' invasion fitnesses and modifies the eventual phenotypic composition of the population.

The mathematical derivation of spatial invasion fitness proceeds by averaging over space the transition rates of pairs. This amounts to look at the local structure of the mutant population as homogeneously replicated across the whole (infinite) lattice. The non-homogeneous distribution of the pairs containing mutants, induced by the finite size of the mutant population and the non-typical clustering pattern that may develop at the earliest stage on invasion, may also require to bring corrections to the measure of spatial invasion fitness. There may be an interesting parallel to be drawn with the theory of evolutionary games in continuous space. In this context the initial clustering of mutants entails that fitness should be defined not from space averages of individual traits, but as the speed at which the front of a mutant cluster moves forward and propagates mutants through space (Hutson and Vickers, 1992 ; Ferrière and Michod, 1995, 1996 ; Ellner *et al.* 1998).

We have used the notion of spatial invasion fitness to model the joint adaptive dynamics of dispersal and altruism. Even without further corrections for more subtle spatial effects, spatial invasion fitness appears to predict very well how these two behavioral traits coevolve. The analysis of this particular model underlines three important and general achievements of adaptive dynamics based on the notion of spatial invasion fitness. First, it unravels the interplay of the ecological (spatial) dynamics of a population and the evolutionary dynamics of the individual traits. The spatial structure shapes the selective pressures, which in return may alter the aggregation pattern. Here we have seen that a high degree of spatial aggregation is not a prerequisite for, but rather a consequence of the joint evolution of altruism and dispersal. Second, this analysis underlines important transient effects. A state of high dispersal or high altruism may be maintained transitorily, up to the point where the direction of selection changes or even reverts. In general, this means that variations, under the same environmental conditions and for the same species, of adaptive traits may be explained by different ancestral states and the observation of populations at different points in time in their evolutionary history. Finally, this approach allows to separate out distinct components of the selective regime and to express these components in terms of individual traits and characteristics of the population aggregation structure. In practice, there is potential here to predict how the selective pressures should equilibrate to produce patterns observed empirically, and how dispersal-related traits may respond to the experimental manipulation of each component of the selective regime.

Acknowledgements. Initially the chapter was planned to be co-authored with Denis Couvet, whose expertise in population genetics would have been critical to achieve a complete reinterpretation of traditional kin selection models in a spatially explicit context. Obviously the shot is longer than we thought, and we are still far away from the big integration of spatial ecology and population genetics. Yet discussions with Denis were most useful to delineate the critical issues and pitfalls in this enterprise. We ought to acknowledge him very gratefully. We also owe many thanks to Ulf Dieckmann who kindly wrote the C code which was used to produce the individual-

based simulations presented in Section 4, and is contributing substantially to our ongoing research project on the coadaptive dynamics of altruism and dispersal. Many thanks also to Mats Gyllenberg, Laurent Lehman, Nicolas Perrin, François Rousset and Minus van Baalen for stimulating discussions and invaluable comments on a previous draft of this chapter, and to the Editors of this volume for their constant support and patience. Part of this work has been supported by the Adaptive Dynamic Network (IIASA, Laxenburg, Austria).

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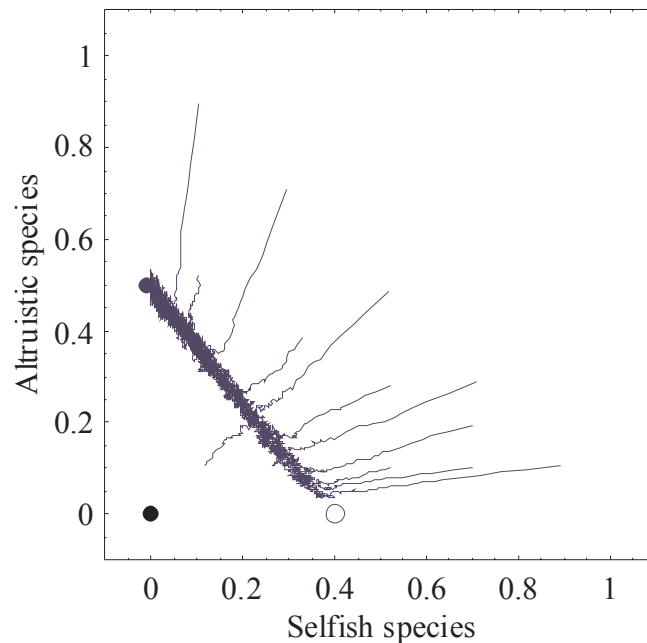
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CHAPITRE 2 – ÉVOLUTION DE L'ALTRUISME



“With many natural populations it must happen that an individual form the center of an actual local concentration of his relatives which is due to a general inability or disinclination of the organisms to move far from their place of birth. In such a population, which we may provisionally term ‘viscous’, [kin selection] may apply fairly well to genes which affect vagrancy, [and we] would expect to find [cooperation] commonest and most highly developed in the species with the most viscous populations whereas uninhibited competition should characterize species with the most freely mixing populations.” W. D. Hamilton dans *The genetical evolution of social behaviour*. 1964.

LES DYNAMIQUES ADAPTIVES DE L'ALTRUISME DANS UNE POPULATION HETEROGENE DANS L'ESPACE

Jean-François Le Galliard, Régis Ferrière & Ulf Dieckmann

RESUME

Nous étudions les dynamiques adaptatives d'un trait continu qui mesure l'investissement dans l'altruisme. Notre étude repose sur un modèle écologique d'une population hétérogène dans l'espace à partir duquel nous dérivons une mesure appropriée de la valeur sélective. L'analyse de cette mesure de valeur sélective met en évidence trois processus sélectifs contrôlant l'évolution de l'altruisme: le coût physiologique direct, les bénéfices génétiques indirects de la coopération, et les coûts génétiques indirects de la compétition pour l'espace. En contraste avec les suggestions des études précédentes, nous trouvons que le coût génétique indirect de la compétition pour l'espace exerce une pression négligeable contre l'évolution de l'altruisme. Par ailleurs, notre étude fournit une classification des états adaptatifs de l'altruisme en fonction de la forme des coûts physiologiques de l'altruisme (avec une dépendance décélérante, linéaire ou accélérante à l'investissement altruiste). L'invasion de l'altruisme est aisée chez une espèce égoïste avec des coûts de type accélérant, mais des mutations à effets larges sont nécessaires chez des espèces à coûts de type décélérant. L'égoïsme stricte n'est maintenu que sous des conditions restreintes. Chez les espèces à coûts accélérant rapidement, l'adaptation conduit à un taux d'investissement altruiste évolutivement stable qui décroît continûment avec le niveau de mobilité de l'espèce. Un régime adaptatif différent émerge chez les espèces à coûts accélérant lentement : un altruisme fort évolue pour une mobilité faible de l'espèce, alors qu'un état quasi-égoïste est sélectionné pour une mobilité forte de l'espèce. Le niveau d'altruisme fort peut être prédit sur la base des paramètres caractérisant la connectivité de l'habitat et les coûts physiologiques de l'altruisme. Nous montrons aussi que des changements environnementaux qui favoriseraient une augmentation de la mobilité chez des espèces fortement altruistes peuvent provoquer l'auto-extinction de l'espèce par un processus de suicide adaptatif. Ceci pourrait contribuer à la rareté des espèces sociales.

Référence : Le Galliard, J.-F., Ferrière, R. et U. Dieckmann. 2003. « The adaptive dynamics of altruism in spatially heterogeneous populations ». *Evolution* 57(1): 1-17.

THE ADAPTIVE DYNAMICS OF ALTRUISM IN SPATIALLY HETEROGENEOUS POPULATIONS

Jean-François Le Galliard, Régis Ferrière & Ulf Dieckmann

ABSTRACT

We study the spatial adaptive dynamics of a continuous trait that measures individual investment in altruism. Our study is based on an ecological model of a spatially heterogeneous population from which we derive an appropriate measure of fitness. The analysis of this fitness measure uncovers three different selective processes controlling the evolution of altruism: the direct physiological cost, the indirect genetic benefits of cooperative interactions, and the indirect genetic costs of competition for space. In contrast with earliest suggestions, we find that the cost of competing for space with relatives exerts a negligible selective pressure against altruism. Our study yields a classification of adaptive patterns of altruism according to the shape the of costs of altruism (with decelerating, linear, or accelerating dependence on the investment in altruism). The invasion of altruism occurs readily in species with accelerating costs, but large mutations are critical for altruism to evolve in selfish species with decelerating costs. Strict selfishness is maintained by natural selection only under very restricted conditions. In species with rapidly accelerating costs, adaptation leads to an evolutionarily stable rate of investment in altruism that decreases smoothly with the level of mobility. A rather different adaptive pattern emerges in species with slowly accelerating costs: high altruism evolves at low mobility, whereas a quasi-selfish state is promoted in more mobile species. The high adaptive level of altruism can be predicted solely from habitat connectedness and physiological parameters that characterize the pattern of cost. We also show that environmental changes that cause increased mobility in those highly altruistic species can beget selection driven self-extinction, which may contribute to the rarity of social species.

Reference : [Le Galliard, J.-F., Ferrière, R. and U. Dieckmann. 2003. « The adaptive dynamics of altruism in spatially heterogeneous populations ». *Evolution* 57\(1\): 1-17.](#)

Key-words : Adaptive dynamics, altruism, mobility, spatial heterogeneity, relatedness, kin competition, kin selection.

Altruism is a cooperative behavior by which a donor individual increases a recipient's fitness at the cost of its own fitness. Major progress in the study of the evolution of altruism has been made over the last decade on both theoretical and empirical sides. On the theoretical side, models have gained a significant dose of realism from the explicit inclusion of spatial factors and the consideration of conditional behavior (Nowak and May 1992; Ferrière and Michod 1995; Roberts and Sherratt 1998). On the empirical side, ecological and genetic determinants of altruistic behavior have started to be identified, and physiological costs and benefits have been measured (Crespi 1996; Bourke 1997; Cockburn 1998; Heinsohn and Legge 1999). However, the merging between theory and facts has led to conflicting interpretations of processes and patterns in the evolution of altruism.

Two main processes have been put forward to explain the evolution and maintenance of altruism: kin selection (Hamilton 1964) and reciprocity (Trivers 1971; Axelrod and Hamilton 1981). Kin selection initially met with great success in explaining empirical observations (for example in social insects). However, recent theoretical developments, based on spatially implicit models, have pointed out a critical issue in this framework: the deleterious effects of kin competition should cancel out the indirect benefits of an altruistic behavior, thereby preventing the evolution of altruism (Taylor 1992a, 1992b; Wilson et al. 1992; Queller 1992, 1994). In contrast, game-theoretic spatial models involving conditional reciprocity have shown that reciprocal altruism evolves readily in spatially heterogeneous populations (Nakamaru et al. 1997, 1998). These theoretical findings are altogether in sharp contrast with empirical advances. On the one hand, unequivocal evidence is lacking for the expectedly widespread occurrence of reciprocal altruism, and reciprocity involves already fairly elaborate behavioral mechanisms (e.g., memory of past interactions) that are unlikely to be relevant to our understanding of the evolution of primitive forms of altruism (Pusey and Packer 1997). On the other hand, kin selection is still regarded as essential to explain the transition from selfish to cooperative units at all levels of biological organization (Maynard-Smith and Szathmary 1995), and many empirical examples of the specific transition from solitary to social life in animals seem indeed to fall under the scope of kin selection (Bourke 1997; Emlen 1997).

Widely different patterns of altruistic behavior have been described in a large array of taxa spread across bacteria, slime moulds, arachnids, insects and vertebrates. Levels of altruism, as described by the qualitative and quantitative natures of the investment by donors and benefit to recipients, have been found to vary between different species (Edwards and Naeem 1993; Crespi 1996) or within the same lineage across evolutionary time (Jarvis et al. 1994; Wcislo and Danforth 1997), between different populations within the same species (Spinks et al. 2000) and between groups of individuals within the same population (Cockburn 1998; Velicer et al. 2000; Strassmann et al. 2000). Most models have aimed at understanding how altruism can evolve in a selfish world, and how altruists can persist in the face of cheaters that reap the benefits of altruism while providing less or no help. Yet little theory is currently available to probe the adaptive significance of such variation in patterns of altruism and to identify physiological, ecological and genetic determinants.

This study offers a theoretical framework to address these tensions. We consider a population of asexual organisms that live in a spatially homogeneous, temporally constant habitat where competition and cooperation take place between kin and non-kin neighbors (van Baalen and Rand 1998). First, we address the robustness of previous investigations that questioned the role of kin selection for the evolution of altruism. To this end, we relax two of their critical assumptions. A dose of movement may help export the local benefits of altruism. Thus, we expect the conclusion that kin competition cancels kin cooperation to be sensitive to the inclusion and intensity of individual mobility (Queller 1992). We therefore relax the “pure viscosity” hypothesis according to which individuals (except offspring) are sessile (Hamilton 1964; Taylor 1992a,b). In our model, offspring are born locally, but in contrast with most viscous population models, individuals move during their lifetime (van Baalen and Rand 1998). Also, most kin selection models assume that the population is saturated and constantly maintained at carrying capacity. This lack of environmental “elasticity” might prevent the spread of altruism (Queller 1992, Mitteldorf and Wilson 2000). To overcome this restriction, we assume that population regulation arises locally from the limited empty space being available for offspring. In our model, the habitat is not saturated, because occupied sites coexist with empty sites generated by demographic stochasticity (Ferrière and Le Galliard 2001).

Second, we want to understand adaptive variation in altruism from basic physiological, ecological and genetic properties that could be documented in natural populations. This is achieved by assuming that altruism is not an all-or-nothing behavior and is better modeled as a quantitative trait that measures the amount of time, energy or resources invested in the altruistic function (Doebeli and Knowlton 1998; Roberts and Sherratt 1998; Koella 2000). At the physiological level, populations or species may differ according to the pattern of energy allocation to altruism versus other costly functions (Heinsohn and Legge 1999). We therefore assume that the physiological cost of altruism relates quantitatively to the actual altruistic investment. However, in contrast with previous models (Doebeli and Knowlton 1998; Roberts and Sherratt 1998), we envision three alternative costs patterns: a decelerating, a linear and an accelerating dependence of costs on investment in altruism. At the level of ecology, populations or species may also differ with respect to interaction structure. Two determinants of this structure are habitat connectedness and individual mobility (Ferrière and Michod 1995, 1996; Nakamaru et al. 1997; Frank 1998). Introducing specific parameters for these two factors allows us to investigate their effect on the adaptive evolution of altruism. At the level of the genetic processes, mutation rates and mutational effects determine the population phenotypic diversity upon which selection operates. Our study addresses to what extent variations in these basic genetic features can contribute to variations in adaptive patterns of altruism.

From a methodological point of view, we develop a model of population dynamics based on spatial correlation equations (Matsuda et al. 1992; van Baalen and Rand 1998; Rand 1999; Ferrière and Le Galliard 2001) to study the evolutionary dynamics of altruism in the framework of adaptive dynamics theory (Metz et al. 1996; Dieckmann and Law 1996). The central notion is that selective

pressures acting on mutant phenotypes are generated by the background population dynamics of resident phenotypes. After identifying selective pressures and incorporating them in a deterministic model of adaptive dynamics, we provide a classification of adaptive patterns of altruism according to the shape of physiological costs, the levels of individual mobility and the degree of habitat connectivity. The stability of the evolutionary endpoints and the effect of large mutations are investigated to gain insight into how variation in the mutation process may determine the adaptive outcome. Finally, the robustness of the salient conclusions drawn from our analytical study is tested against stochastic, individual-based simulations.

MODEL ASSUMPTIONS

We consider a population of haploid individuals that inhabit a network of homogeneous sites, modeled as an infinite lattice (Appendix 1). Each site may be empty, or occupied by one individual. Each site is randomly connected to a set of sites that defines a neighborhood (Appendix 1). We assume that every site is connected to the same number of sites, denoted by n . Thus, the neighborhood size n provides a measure of the habitat's connectedness.

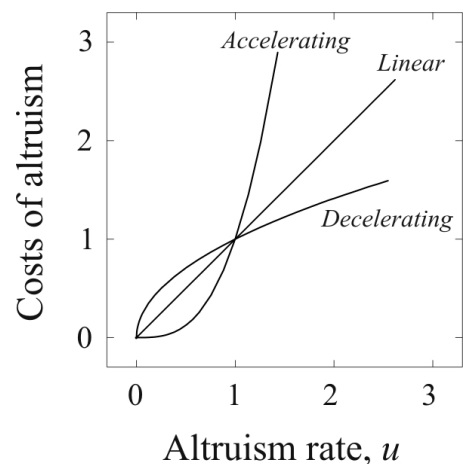
Mobility and interaction are defined locally, at the neighborhood scale. During any small time interval, an individual may move to an empty site within its neighborhood, reproduce by putting an offspring into an empty neighboring site, or die. The per capita mobility rate m and death rate d are unaffected by local interactions. Mobility is assumed to be costly to the individual, with a permanent negative effect on the individual's birth rate. This is expected in organisms where a stronger ability to move, resulting from specific structures (e.g., gliding flagella or muscles), imposes a developmental or maintenance cost. For example, the dispersive morph in the naked mole rat diverts more energy into growth and fat storage to compensate for the risks of moving in inhospitable habitats (O'Riain et al. 1996). The cost of mobility is assumed to impact linearly on the intrinsic birth rate such that the net per capita birth rate (in the absence of interaction) is given by $b(m) = b - \nu m$, where b measures the intrinsic per capita birth rate in sessile organisms that do not invest energy into mobility, and ν measures the sensitivity of the cost to mobility.

We assume that two types of local density-dependent factors affect movement and reproduction (Appendix 1). First, both movement and reproduction are conditional on the availability of empty sites within the neighborhood. Thus, local crowding negatively affects the rates of mobility and birth. Second, reproduction is enhanced by altruistic interactions with neighboring individuals, which induces a positive effect of local crowding. Here we assume that an altruistic interaction improves the quality of neighboring sites. This may involve storage of resources, habitat engineering, or signaling. The altruistic phenotype is defined by the per capita rate of investment u into the altruistic function. The altruistic behavior is directed evenly toward all neighboring sites, regardless of the presence or phenotypes of neighbors. In effect, every neighbor of a focal individual that invests at rate u into

altruism receives a birth rate increment equal to u/n (Wilson et al. 1992). Therefore, altruism is only effective in practice provided some recipients are present in the neighborhood of the donor and some space is available in the neighborhood of the recipient for its offspring. We use the terms selfishness to describe a phenotype that does not invest in altruism ($u = 0$) and quasi-selfishness to refer to a phenotype that hardly invests in altruism ($u \approx 0$).

We further assume that altruism involves a physiological cost on the donor's reproduction, and we distinguish three patterns of dependence of costs on the investment in altruism: accelerating, linear, and decelerating (Fig. 1). With accelerating costs, the increase of the cost resulting from an increased altruistic investment becomes disproportionately larger as the initial investment increases. For example, in the cooperative bird *Corcorax melanorhamphos* physiological costs are detected only among individuals that invest strongly in altruism (Heinsohn and Cockburn 1994). Conversely, a decelerating pattern yields a disproportionate increase of costs at lower investment. This would apply to organisms in which the initiation of altruism from a selfish state would be very costly. In the limiting case of a linear pattern, the cost sensitivity is independent of the level of investment. The physiological cost of altruism $C(u)$ is modeled as a simple, allometric function that encapsulates the three patterns of decelerating, linear, and accelerating costs: $C(u) = \kappa u^\gamma$, where κ scales the sensitivity of the cost to the investment ($\kappa > 0$), and γ determines whether costs are accelerating ($\gamma > 1$), linear ($\gamma = 1$) or decelerating ($\gamma < 1$).

Figure 1. Costs of altruism as a function of the individual investment in altruism (u). This function is given by $C(u) = \kappa u^\gamma$ (with $\kappa = 1$ in this display). Decelerating costs, $\gamma < 1$: the cost increases with the rate of altruism first steeply and then more slowly. This pattern makes the origin of altruism from selfishness harder. Accelerating costs, $\gamma > 1$: the cost increases with the rate of altruism first slowly and then steeply. This pattern turns out to influence the long-term adaptive level of altruism. Linear costs, $\gamma = 1$: the rate of increase of the cost is independent of the level of altruism.



Mutations cause the altruistic phenotypes of offspring to differ from those of their parents. Mutations occur with a fixed probability per birth event, denoted by k . The mutant phenotype is obtained by adding the mutation effect to the progenitor phenotype. Mutation effects are drawn randomly from a normal probability distribution, with zero mean and a mutational variance σ^2 . The

resulting polymorphic, stochastic process can be simulated on a finite lattice (Appendix 1). Table 1 summarizes the used notation.

Table 1. Notation used in this paper.

<i>Model parameters</i>	
n	Neighborhood size
ϕ	Probability to draw a site at random in the neighborhood ($\phi = 1/n$)
b	Intrinsic birth rate
d	Intrinsic death rate
m	Intrinsic mobility rate
u_i	Intrinsic investment rate in altruism of a phenotype i (<i>adaptive trait</i>)
$C(u_i)$	Cost of altruism, impacting the birth rate of a phenotype i
κ	Cost sensitivity with respect to the level of investment in altruism
γ	Cost acceleration with respect to the level of investment in altruism
k	Mutation probability per birth event
σ^2	Mutational step variance
<i>Model variables</i>	
p_i	Global frequency of sites i
$q_{i j}$	Local frequency of sites i neighboring a j site
\bar{p}_x	Equilibrium global frequency of a resident x
$\bar{q}_{i x}$	Equilibrium local frequency of sites i neighboring a resident x
$\tilde{q}_{i y}$	Pseudo-equilibrium frequency of sites i neighboring a rare mutant y

SPATIAL POPULATION DYNAMICS OF RESIDENTS

Selective pressures acting on a mutant phenotype result from the interaction between the initially scarce mutant population and the background population. The finite size of the interaction neighborhood and the finite range and rate of dispersal and fecundity cause spatial fluctuations and spatial correlations to develop in population density (Dieckmann and Law 2000). Thus, spatial population heterogeneity develops in a spatially homogeneous habitat. We use the framework of correlation equations to derive an analytical model describing the spatial dynamics of such a background population (Appendix 2). Assuming that mutation occurs rarely, the background population may be considered as monomorphic (Dieckmann and Law 1996; Metz et al. 1996). In this section we apply the polymorphic, ecological model to the specific case of a monomorphic population. This will provide the basic ingredients needed in the next section to model the dynamics of a mutant phenotype against this resident population.

Let us consider a single phenotype x which invests in altruism at rate u_x . The temporal dynamics of a population of x can be described by tracking over time t the frequency $p_x(t)$ of occupied sites. These dynamics depend on the neighborhood composition, described by the local frequencies $q_{i|x}$, i.e. the probabilities that an occupied site is neighbored by at least one site in the state i (Matsuda et al. 1992). The frequency p_x obeys the ordinary differential equation

$$\frac{dp_x(t)}{dt} = \left[\left(b(m) + (1 - \phi) \cdot u_x \cdot q_{x|x}(t) - C(u_x) \right) \cdot q_{0|x}(t) - d \right] \cdot p_x(t), \quad (1)$$

involving the local frequencies $q_{x|x}(t)$ and $q_{0|x}(t)$ of occupied and empty sites next to an occupied site at time t , and $\phi = 1/n$. A closed system of correlation equations for the dynamics of local frequencies is constructed in Appendix 2 by making use of the standard pair approximation (Matsuda et al. 1992; Rand 1999; Iwasa 2000; van Baalen 2000).

At equilibrium, the spatial structure of a monomorphic population depends on the mobility rate and the altruistic investment (Appendix 3). The spatial structure is characterized by some degree of aggregation (Fig. 2). The spatial structure vanishes at high mobility rates, and for large birth rates, because birth is associated with offspring dispersal. More aggregation is found in organisms with low mobility, and also in organisms with very high mobility that consequently incur a severe reduction of their birth rate (due to the cost of mobility). The relationship between altruism and aggregation depends on the pattern of cost. In species with linear and decelerating costs, strongest aggregation is observed at low altruistic investment (Figs. 2B to D). In species with accelerating costs, strongest aggregation is observed in organisms with low altruism, or with high altruism, when the birth rate is drastically reduced by the cost of altruism (Fig. 2F).

For some parameter combinations, extinction is the only stable population equilibrium (Fig. 2). Extinction results from the total cost of mobility and altruism not being compensated. High mobility causes extinction because it implies a large direct cost that depresses the intrinsic birth rate $b(m)$, along with the reduction of the indirect benefits of altruism due to the loss of local aggregation. Species with accelerating costs can also undergo extinction at high investment in altruism (Fig. 2F). In all other cases, the altruistic population is viable and two types of population dynamics can be distinguished (Fig. 2). Borrowing terminology from the field of mutualism studies, we call the corresponding phenotypes facultative versus obligate. Thus, altruism is said to be facultative when the population growth rate in the limit of very low population density, $b(m) - d - C(u_x)$, is positive. The population is then characterized by a single, globally stable, and positive equilibrium $(\bar{p}_x, \bar{q}_{x|x})$ (Fig. 2A). Altruism is said to be obligate when the limit growth rate is negative and the population dynamics thus shows bistability. In this latter case, the positive equilibrium is locally stable and coexists with the extinction equilibrium, which is also locally stable. A population of obligate altruists

may attain the viable equilibrium state only if its initial density lies above a critical threshold (Fig. 2A). This phenotypic state is therefore associated with low colonization ability and an elevated risk of extinction since a viable population can neither be established from an initially low density nor be maintained below a critical density threshold.

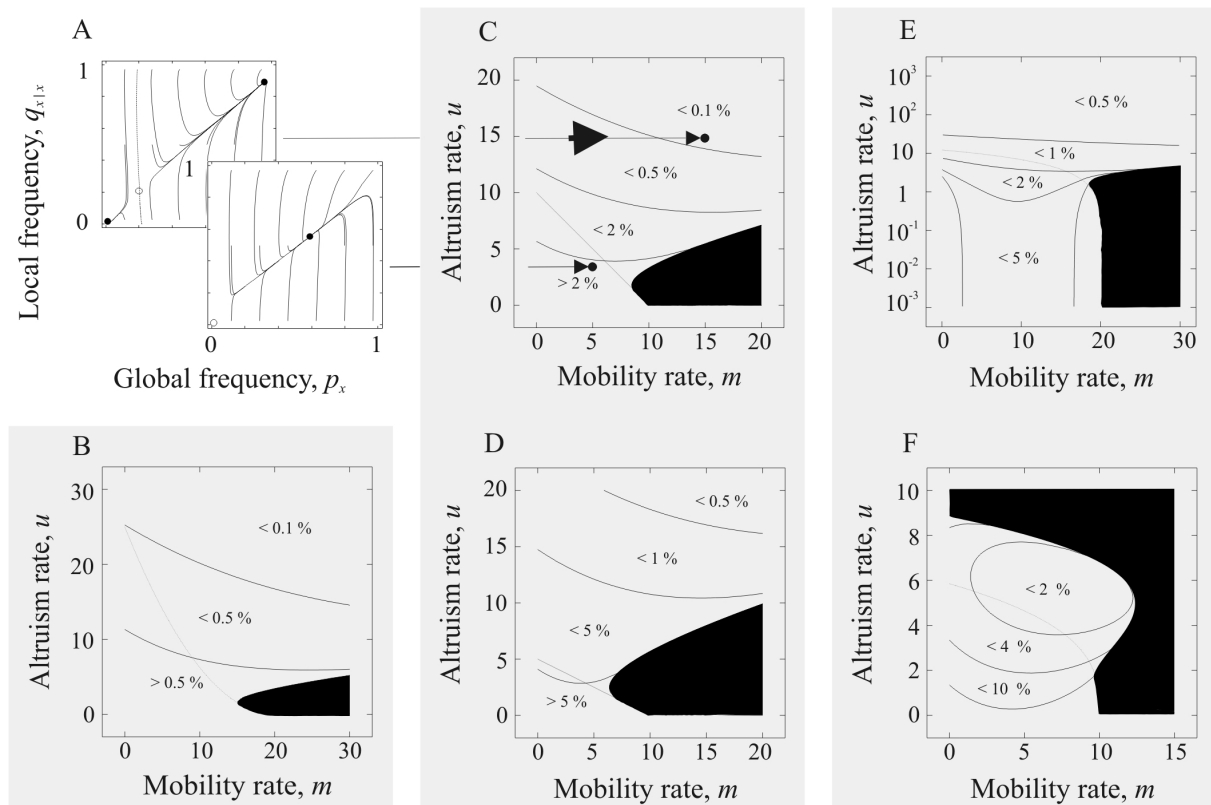


Figure 2. Monomorphic population dynamics. A, Population trajectories of global and local frequencies, as predicted by Equations (A4) and (A10). Starting from any initially rare state, the local frequency converges fast toward a one-dimension manifold along which most of the global frequency dynamics take place. The upper panel shows a case of obligate altruism ($m = 15, u_x = 20$): a positive equilibrium and the extinction equilibrium are both locally stable (filled circles) and coexist with a saddle point (open circle). The dotted curve separates the basins of attraction of the two stable equilibria. The lower panel shows a case of facultative altruism ($m = 5, u_x = 3$): there is a globally stable equilibrium (filled circle); the extinction equilibrium (open circle) is unstable. Parameters: $\gamma = 1, \kappa = 0.1$, and $\nu = 0.1$. B-F, Parameter regions of facultative altruism (below dashed curve), obligate altruism (above dashed curve) and population extinction (black area). Black curves are contours of the relative percent of deviation of spatial structure from mean-field equilibrium. B, Species with decelerating costs ($\gamma = 0.5, \kappa = 0.2$, and $\nu = 0.05$). C, Species with weak linear costs (parameter values as in A). D, Species with strong linear costs ($\gamma = 1, \kappa = 0.2$, and $\nu = 0.1$). E, Species with slowly accelerating costs ($\gamma = 1.2, \kappa = 0.05$, and $\nu = 0.05$); extinction also occurs at higher values of altruistic investment (not shown). F, Species with rapidly accelerating costs ($\gamma = 3, \kappa = 0.005$, and $\nu = 0.1$). Life-history and connectedness parameters are $b = 2, d = 1$ and $n = 4$, here as well as in all other figures.

SPATIAL INVASION FITNESS OF MUTANTS

The invasion fitness of a mutant is defined by its per capita growth rate while being rare in a resident population at ecological equilibrium (Metz et al. 1992). In the present section, we analyze the growth of such a small mutant population in the resident population described in the previous section (Appendix 4).

The invasion dynamics of a rare phenotype involves three phases (van Baalen 2000; Fig. 3). In a first, short phase, the small mutant population locally spreads from a single mutant individual up to the point where the mutant population attains a pseudo-equilibrium correlation structure. The build-up of this structure is highly stochastic but occurs with certainty on a finite time scale (Matsuda et al. 1992). Indeed, the cost of altruism dooms any single altruistic mutant in an established population of selfish individuals. Drift is first needed to drive the mutant population to its pseudo-equilibrium spatial structure. Also, the initial spread of the mutant depends on the local spatial structure of the resident population. For example, an altruistic mutant that arises in a neighborhood where selfish residents are more frequent than expected on average will face an increased risk of extinction. Denoting the mutant by y , we use the pseudo-equilibrium local frequencies $\tilde{q}_{0|y}$, $\tilde{q}_{x|y}$ and $\tilde{q}_{y|y}$ of (respectively) empty, resident and mutant sites around a focal mutant site to describe this transient structure. These statistics are calculated in Appendix 5. Conditional on non-extinction during this first phase, the mutant dynamics then enter the second phase during which the mutant population expands or contracts while its population keeps its pseudo-equilibrium structure and the resident population remains close to its own equilibrium (Fig. 3). Spatial invasion fitness can be defined as the mutant population growth rate during this second phase (van Baalen and Rand 1998). A positive fitness implies that the invasion process enters a third phase during which the mutant phenotype displaces the resident (Fig. 3), while a negative fitness implies mutant population extinction.

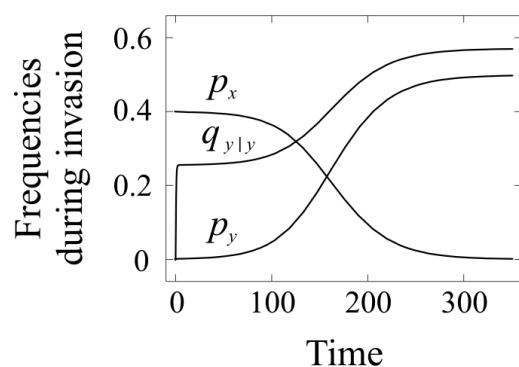


Figure 3. Successful invasion of an initially rare, altruistic mutant ($u_y = 1$) into a selfish resident population at equilibrium. Dynamics of the resident global frequency (p_x) and of the mutant global (p_y) and local frequency ($q_{y|y}$), as predicted by the deterministic system of correlation equations (A13). The three phases of invasion apparent in the dynamics of $q_{y|y}$ are discussed in the text. Parameter values: $\gamma = 2$ (accelerating costs), $\kappa = 0.1$, $\nu = 0.1$, and $m = 0$.

The spatial invasion fitness $s_x(y)$ can be expressed as a function of the pseudo-equilibrium statistics of the mutant population. Combining the population growth rate (1) with the expression of the mutant pseudo-equilibrium local frequencies, $s_x(y)$ is given by

$$s_x(y) = \left[(b(m) - C(u_y)) \tilde{q}_{0|y} - d \right] + (n-1)\phi u_x \tilde{q}_{0|y} \tilde{q}_{x|y} + (n-1)\phi u_y \tilde{q}_{0|y} \tilde{q}_{y|y}. \quad (2)$$

Notice that the benefit of altruism (second and third terms) is measured conditionally on the presence of at least one empty site for breeding and depends upon the amount of help received from $n-1$ (not n) neighboring sites and the local frequency of empty sites $\tilde{q}_{0|y}$.

This expression bears an interesting relationship to the notion of direct or neighbor-modulated fitness of additive behavioral effects (Frank 1998). Direct fitness is derived by summing the effects on a focal individual's fitness of all phenotypes present in the neighborhood (including the focal individual itself). Likewise, the spatial invasion fitness of a focal mutant is obtained by adding to the mutant neighbor-independent fitness (first term) the effects of a resident neighbor (second term) and that of a mutant neighbor (third term), weighed by the probabilities of occurrence of such neighbors.

SELECTIVE PRESSURES

We now derive a simplified version of the spatial invasion fitness to analyze the selective pressures acting on the altruistic trait under small mutational steps. This will be the basis for studying the evolutionary dynamics of altruism. By using the fact that the resident's fitness in its own environment is always zero, $s_x(x) = 0$, the selection derivative can be derived from a first-order approximation of the spatial invasion fitness, and equals

$$\left. \frac{\partial s_x(y)}{\partial y} \right|_{y=x} = \bar{q}_{0|x} \left((1-\phi) \bar{q}_{y|y} - a \left((1-\phi) u_x - \frac{d}{\bar{q}_{0|x}^2} \right) - \left. \frac{\partial C(u_y)}{\partial u_y} \right|_{y=x} \right), \quad (3)$$

where a measures the gain (or loss) of open space in a mutant's pseudo-equilibrium neighborhood relative to the resident's at equilibrium (see Appendix 5 for details). This expression exhibits three selective pressures driving the evolution of altruism. The first term on the right-hand side of Equation (3) quantifies the pressure for increased investment in altruism. The second term measures the pressure for opening free space in an individual's neighborhood. The last term measures the pressure for reducing the physiological cost of investing in altruism.

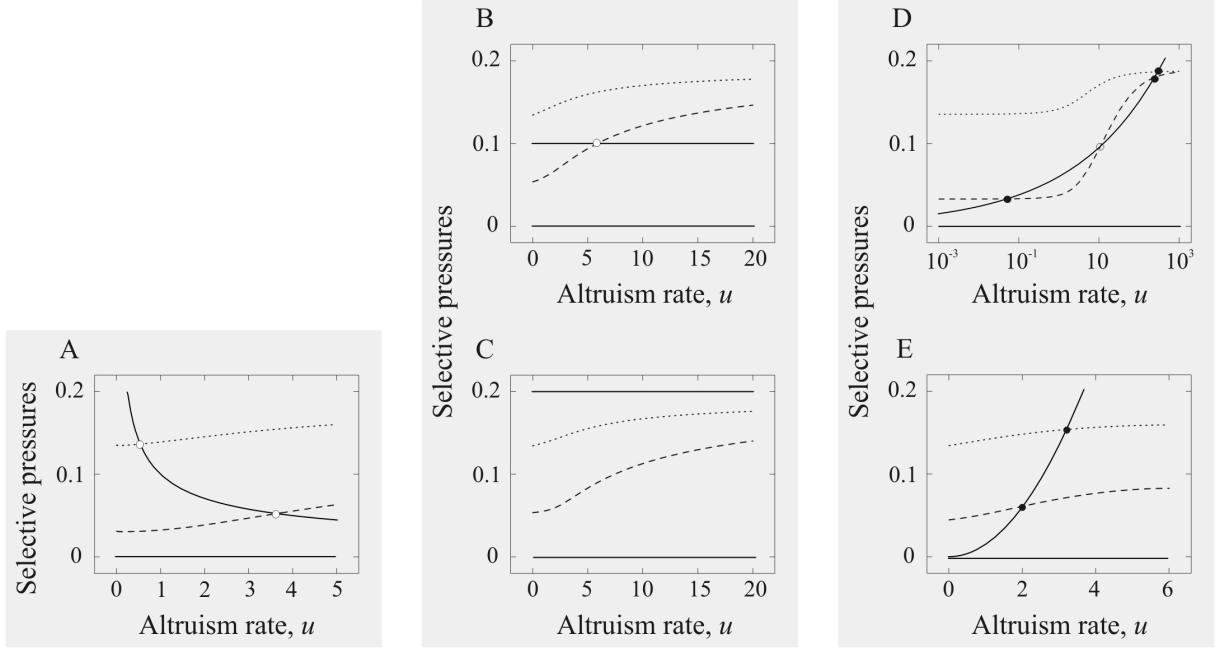


Figure 4. Selective pressures acting on altruism under small mutational steps calculated by following the recipe described in Appendix 5. Broken curves: positive pressure for increasing altruism, $(1-\phi) \bar{q}_{y|y}$, evaluated at low ($m=1$, dotted curves) and high mobility ($m=10$, dashed curves). Continuous curve: negative pressure for reducing the cost of altruism. Lower continuous line: negative, negligible selective pressure for decreasing local competition. Within the range of altruism where a broken curve is below (above) the continuous curve, selection favors the increase (decrease) of altruism. Circles indicate singular points where selective pressures exactly balance each other. Filled circles: attracting evolutionary singularities. Open circles: repelling evolutionary singularities. Parameter values in A to E are the same, respectively, as in Fig. 2B to F.

Extensive computations suggested that the pressure for opening space, albeit not vanishing, is negligible compared to the two other selective components (Fig. 4). This implies that $\bar{q}_{0|x} \approx \tilde{q}_{0|y}$, hence $a \approx 0$ in the Equation (3) (see Appendix 5). This also implies that as long as the mutant phenotype stays rare, the resident correlation structure is redistributed over the pairings of mutants with their own type and the resident type: $\bar{q}_{0|x} = \tilde{q}_{y|y} + \tilde{q}_{x|y}$. Thus, the mutant is less aggregated than expected when common, and therefore rare mutants are less likely to interact among themselves during the initial phases of invasion (Fig. 3). Globally, the evolution of altruism is not limited by competition for empty sites within the invasion structure, and the condition for an adaptive increase in altruism, $\partial s_x(y)/\partial y > 0$, is equivalent to

$$(1-\phi) \tilde{q}_{y|y} > \left. \frac{\partial C(u_y)}{\partial u_y} \right|_{y=x}. \quad (4)$$

This condition is a spatial form of Hamilton's rule (see also Ferrière and Michod 1995, 1996; Frank 1998; van Baalen and Rand 1998). The right-hand side is the marginal cost of altruism. The left-hand side measures the marginal benefit of altruism, weighed by the average frequency $\tilde{q}_{y|y}$ of recipient neighbors that are phenotypically identical to the focal mutant individual. For a haploid mutant population descended from a single mutation event, the identity in phenotype is equivalent to the identity by descent, and $\tilde{q}_{y|y}$ provides a measure of relatedness (Day and Taylor 1998).

The mutant relatedness can be expressed as a function of the resident population structure (Appendix 5), hence in terms of the basic demographic, mobility and lattice parameters, according to the following equality

$$\tilde{q}_{y|y} = \frac{d\phi}{d + (1 - \phi)m\bar{q}_{0|x}}. \quad (5)$$

Thus relatedness is higher in a population with lower $\bar{q}_{0|x}$, which promotes the invasion of even more altruistic phenotypes. Insofar as the local frequency $\bar{q}_{0|x}$ correlates negatively with the investment u_x , this relation establishes a positive ecological feedback on the evolution of altruism: a negative effect of altruism investment on the local frequency $\bar{q}_{0|x}$ increases the relatedness of mutants, thereby enhancing the selective pressure for increased altruism. Also, Equation (5) shows that there is a direct negative effect of mobility on mutant relatedness, and an indirect effect through $\bar{q}_{0|x}$. Both effects add up to decrease mutant relatedness and weaken the selective pressure that favors altruism. Finally, increasing the neighborhood size n decreases $\tilde{q}_{y|y}$: a larger neighborhood size hampers the evolution of altruism.

CANONICAL EQUATION OF ADAPTIVE DYNAMICS

We use the results of the previous section to develop a deterministic model of adaptive dynamics under small mutations. This allows us to identify general patterns in the adaptive dynamics of altruism, to characterize the evolutionary endpoints and to study transient evolutionary dynamics. In a large population where mutations are rare and mutational steps are small, the stochastic mutation-selection process can be approximated by a deterministic process whose trajectories are the solution of the so-called canonical equation of adaptive dynamics (Dieckmann and Law 1996):

$$\frac{du_x}{dt} = \left[k \cdot \frac{\sigma^2}{2} \cdot \bar{p}_x \right] \cdot \left. \frac{\partial s_x(y)}{\partial y} \right|_{y=x}. \quad (6)$$

The bracketed term captures the effect of mutations, involving the mutation probability k , the mutational variance σ^2 , and the equilibrium population frequency \bar{p}_x of a monomorphic population of

Le Galliard J.-F. Dynamiques adaptives de l'altruisme dans une population hétérogène dans l'espace phenotype u_x . The local direction of phenotypic change is given by the selection derivative (Marrow et al. 1992) that we approximate according to Equation (4) by

$$\left. \frac{\partial s_x(y)}{\partial y} \right|_{y=x} = \bar{q}_{o;x} \left[(1-\phi) \bar{q}_{y|y} - \left. \frac{\partial C(u)}{\partial u} \right|_{u=u_x} \right]. \quad (7)$$

The resting points that satisfy $du_x/dt = 0$ are called evolutionary singularities and correspond to phenotypic states where the selection derivative vanishes (Marrow et al. 1992). Thus, at an evolutionary singularity, the marginal cost of altruism balances exactly the marginal benefit weighted by mutant relatedness. A singularity u^* can be locally evolutionarily attractive (“convergence stable”), or acts as an evolutionarily repeller.

Classification of Adaptive Dynamics

We develop a classification of the adaptive dynamics of altruism depending on the cost pattern specified by parameters κ and γ . To this end, we perform a numerical bifurcation analysis of the evolutionary singularities generated by (6) and (7) with respect to the mobility rate. We obtain five generic bifurcation diagrams as parameters κ and γ are varied (Fig. 5A).

For a decelerating cost of altruism, there is a single positive singularity that is unstable for any mobility rate (Fig. 5B). For linear costs, two cases can be distinguished. Either the selfish state undergoes a transcritical bifurcation as mobility increases, turning from unstable to stable and then coexisting with an unstable positive singularity. This is characteristic of “weak linear costs” (Fig. 5C). Alternatively the selfish singularity remains stable irrespective of the mobility rate, which characterizes “strong linear costs” (Fig. 5D). For accelerating costs, there are also two distinct patterns. For low values of κ and γ , there is a range of intermediate mobility rates over which the adaptive dynamics of altruism possess one unstable and two stable singularities. As mobility decreases, the lower stable equilibrium and the unstable one collide, leaving the upper stable singularity alone. Such combinations of γ and κ values define “slowly accelerating costs” (Fig. 5E). For higher values of κ and γ , characterizing “rapidly accelerating costs”, there is a single stable positive equilibrium for every mobility rate (Fig. 5F).

Generically, natural selection favors altruism in species characterized by a large intrinsic birth rate b and a small death rate d . Also, altruism is selected against in species characterized by a large mobility rate. Selection against the altruistic trait may even lead to the “evolutionary suicide” of the population, if the adaptive dynamics start from an intermediate level of altruism and a high level of mobility (Figs. 5C to F). Although highly mobile organisms could persist on the ecological timescale provided that they behave sufficiently altruistically, the adaptive process would drive their altruistic investment down to the point where the population becomes non-viable. Increasing the size of the

neighborhood selects strongly against altruism. The whole patterns are not sensitive to variations in the mobility cost parameter ν .

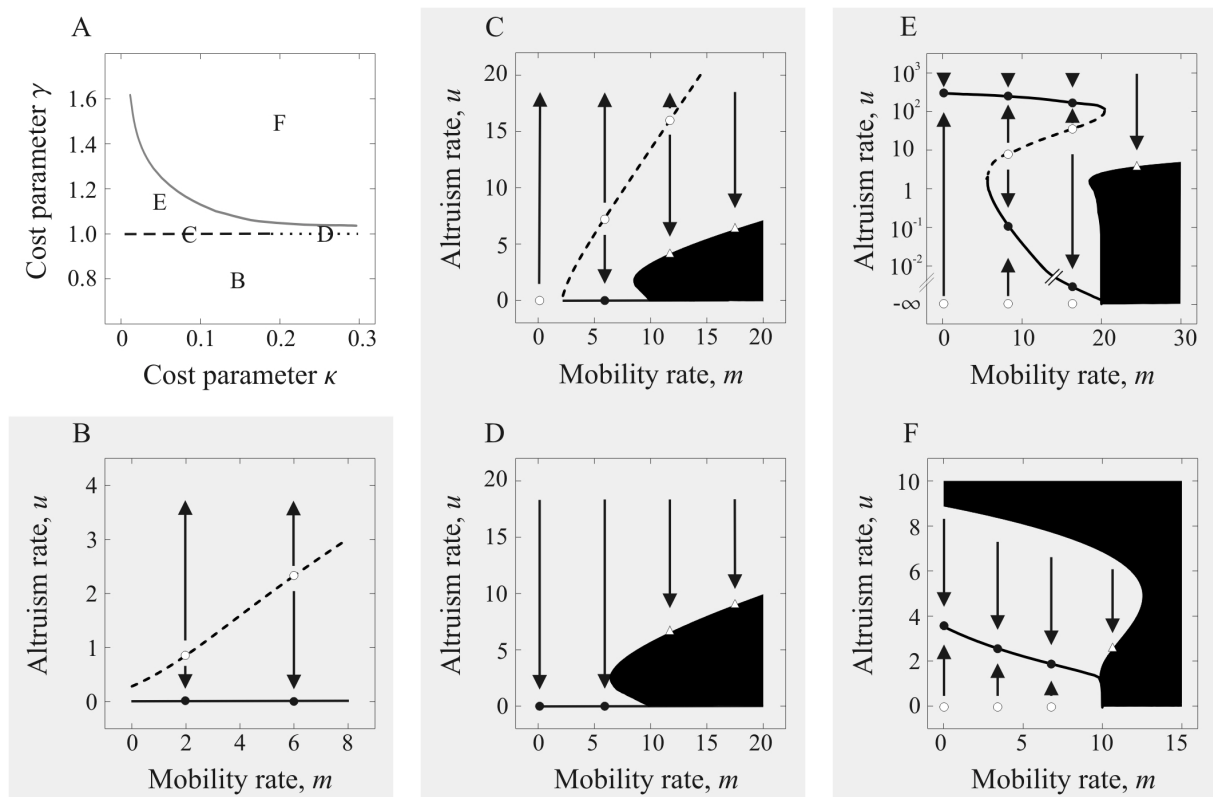


Figure 5. Adaptive dynamics of altruism. A, Classification of adaptive dynamics according to cost parameters γ and κ . Lettering refers to panels B to F showing bifurcation diagrams of the evolutionary singularities with respect to the mobility rate. In B-F, plain black curves are sets of convergence stable (attracting) singularities; dashed black curves are sets of convergence unstable (repelling) singularities. Population extinction occurs in black regions. Arrows indicate the direction of selective pressures at particular values of the mobility rate. Filled circles: attracting evolutionary singularity; open circles: repelling evolutionary singularity; triangles: evolutionary self-extinction. B, Species with decelerating costs. Inner singularities are repelling, resulting in bistable adaptive dynamics. C, Species with weak linear costs. Below a mobility threshold, altruism invades a purely selfish population and increases monotonically; above the threshold, the adaptive dynamics are bistable. D, Species with strong linear costs. Pure selfishness is globally attractive. E, Species with slowly accelerating costs. High altruistic investments are selected at low mobility. At higher mobility, an unstable singularity separates the basins of attraction of two locally attracting singularities that differ dramatically in their level of altruism (high altruistic investment versus quasiselfishness). F, Species with rapidly accelerating costs. The adaptive dynamics typically converge to a globally stable singularity. In all cases (not shown in B), the adaptive process can hit a region of extinction when the population originates from an ancestral state characterized by high mobility and intermediate or high altruism. Values of parameters κ and γ in B to F are the same, respectively, as in Fig. 2B to F. In all panels $\nu = 0.1$.

Decelerating Costs

With decelerating costs, there is a single, repelling evolutionary singularity for any mobility rate, and adaptive dynamics exhibit bistability (Fig. 5B). At the evolutionary singularity, the positive selective pressure on altruism resulting from mutant relatedness and the negative pressure exerted by the physiological cost balance exactly. The evolutionary singularity increases with the mobility rate, which is due to the effect of increased mobility on mutant relatedness as described by Equation (5).

Since the cost pattern is decelerating, a slight increase of altruism within the range below the singularity is counter-selected by a cost disproportionately larger than the gain. As a result, the adaptive dynamics ought to converge to selfishness (Fig. 4A). If the ancestral population state is sufficiently altruistic, the adaptive process will result in ever-increasing altruism. This is because, with decelerating costs, the cost of altruism increases more slowly than the benefits of altruism resulting from increased relatedness (Fig. 4A). In real systems, the adaptive increase of altruism should be limited by physiological or functional constraints, and the evolutionary process is expected to halt at such a limiting trait value.

Linear Costs

The adaptive dynamics of altruism in species with linear costs can be classified in two categories according to the cost parameter κ (Fig. 5A). For species with low κ , costs are said to be “weak linear” and the adaptive dynamics depend on the mobility rate (Fig. 5C). For low mobility, the selfish state is invadable by altruism and the adaptive process leads to the maximum physiologically feasible investment in altruism. Above a threshold on mobility, there exists a positive, repelling singularity and the adaptive process behaves as in the case of decelerating costs. If the initial investment in altruism lies below the singularity, the marginal benefit is too low to compensate for the marginal cost, and decreased altruism evolves. Above the singularity, the adaptive process causes the rise of altruism up to the physiological bound. For species with high κ (“strong linear” costs), the selfish state is evolutionarily attractive at any value of the mobility rate (Fig. 5D).

This pattern can be understood by comparing selective pressures (Figs. 4B, C). In the case of species with linear costs, the marginal benefit of altruism, $(1-\phi) \cdot \tilde{q}_{y|y}$, increases monotonously towards $\phi \cdot (1-\phi)$ as the altruistic investment becomes larger. If κ is larger than this value, the marginal costs of altruism always oppose the evolution of altruism (Fig. 4C). Otherwise, in species with low mobility marginal benefits are sufficiently high in the selfish state to select for altruism (Fig. 4B); in species with high mobility, marginal benefits exceed marginal costs only at high investment in altruism, and selfishness is locally attractive. The mobility threshold, where the stability of selfishness switches from global repulsion to local attraction, is given by the mobility rate m_l of a selfish population at which marginal benefits $(1-\phi) \cdot \tilde{q}_{y|y}$ and marginal costs κ equalize:

$$m_l = b \frac{\phi \cdot (1 - \phi) - \kappa}{v(\phi \cdot (1 - \phi) - \kappa) + \kappa \cdot (1 - \phi)}. \quad (8)$$

This relation shows that among slowly reproducing organisms (small b), altruism may evolve only in species that exhibit little mobility. In species with very weak linear costs, the mobility threshold may not be observed, for it may exceed the critical value $(b - d)/v$ above which the population becomes non-viable (Appendix 3, $\kappa < 0.05$ in Fig. 5A). As a consequence, selfishness is invaded by altruism at any mobility rate smaller than this critical value, whereas at higher mobility, the evolution of decreasing altruism always drives the population to extinction (not shown).

Accelerating Costs

With accelerating costs, the cost of altruism is negligible compared to the benefits as long as the investment in altruism is not too high, and the selfish state is always invadable. This is in sharp contrast with predictions from well-mixed populations, in which selfishness is uninvadable even by only slightly altruistic mutants as soon as altruistic individuals incur a non-zero cost (Equation (A14) in Appendix 4). As altruistic phenotypes gain a foothold in the population, there are two possible outcomes depending on the combination of cost parameters.

Under a pattern of “slowly accelerating cost” (Fig. 5E), altruism rises toward a high evolutionary singularity in species with low mobility. With higher mobility the adaptive dynamics regime is bistable: the adaptive process converges to a high or a low singularity depending on the ancestral state. Extensive numerical explorations show that the altruism is always obligate (facultative) at the high (low) singularity. Under a pattern of “rapidly accelerating cost” (Fig. 5F), the adaptive dynamics converge monotonously to a low altruistic investment, whatever the ancestral state (including selfishness). The selected altruistic trait is found to correlate negatively with mobility. The evolved altruistic interactions shift from facultative to obligate as the cost parameters γ and/or κ increase.

The analysis of selective pressures helps us to understand these results (Figs. 4D, E). With slowly accelerating costs, when mobility is low, the marginal benefits start high and increase slowly (Fig. 4D). Then mutant relatedness easily opposes the initially low but faster-growing marginal cost. The selective force that favors altruism keeps dominating as the investment in altruism increases, until the marginal costs and benefits of altruism balance each other, which occurs at a high value of altruism. At higher mobility rates, the initial level of relatedness is lower, yet it remains sufficient for altruism to invade (Fig. 4D). The increase of relatedness with altruism is slower, which causes the selective pressures to balance at a low-altruism singularity. Beyond this point, the negative pressure exerted by the cost grows smoothly, while the positive pressure catches up rapidly across a range of intermediate investments (Fig. 4D). This generates a second unstable singularity, above which the net selective pressure turns positive again and favors the increase of altruism until a third, attractive

singularity is reached at high altruistic investment. With rapidly accelerating costs, the selective pressures balance at a low-altruism singularity (Fig. 4E). Above the singularity, the net selective pressure against altruism increases, whereas the positive ecological feedback through relatedness remains weak.

Although in general there is no analytical expression for the singularities, the selected altruistic trait reaches a maximum value in the limit where mobility becomes very low, which is given explicitly by

$$u_{\max}^* = \left[\frac{\phi(1-\phi)}{\kappa\gamma} \right]^{\frac{1}{\gamma-1}}. \quad (9)$$

This maximum is independent of the organism's birth and death rates, and it decreases as the neighborhood size n increases. In species that experience rapidly accelerating costs, the singularity smoothly rises toward u_{\max}^* as mobility decreases. In contrast, species with slowly accelerating costs fall into two main categories: quasi-selfish species, and obligatory altruistic species. In these obligatory altruistic species, the level of altruism is approximately equal to u_{\max}^* , and thus primarily depends on cost parameters and habitat connectedness.

EVOLUTIONARY STABILITY AND LARGE MUTATIONS

The previous analysis based on the canonical equation assumes small mutational steps and does not yet address the potential invasibility of attractive states. A locally attractive singularity would give rise to evolutionary branching if it is invadable (Metz et al. 1996). Evolutionary stability is probed by inspecting pairwise invasibility plots (PIPs; Geritz et al. 1998) that display the sign of $s_x(y)$ as u_x and u_y vary throughout the trait space (Fig. 6). Mutation effects are actually small but not infinitesimal, and even large mutations may occur, albeit rarely. The PIPs also describe the invasion potential of mutants that may differ substantially from their resident progenitors.

For species with decelerating costs, the PIPs show that selfishness is locally uninvadable: a slightly altruistic phenotype may not thrive in a primeval egoistic world. However, large mutations can move the population out of the basin of attraction of the selfish state, thus allowing for the adaptive increase of altruism (Fig. 6A). Even starting from a purely selfish population, rare mutations of large effect, together with random drift in a finite size population, makes this occur with certainty, although the waiting time can be long. The case of species with linear costs is radically different: even very large mutations may not move the population out of the basin of attraction of the selfish state, which is thus globally evolutionary stable (Figs. 6B, C).

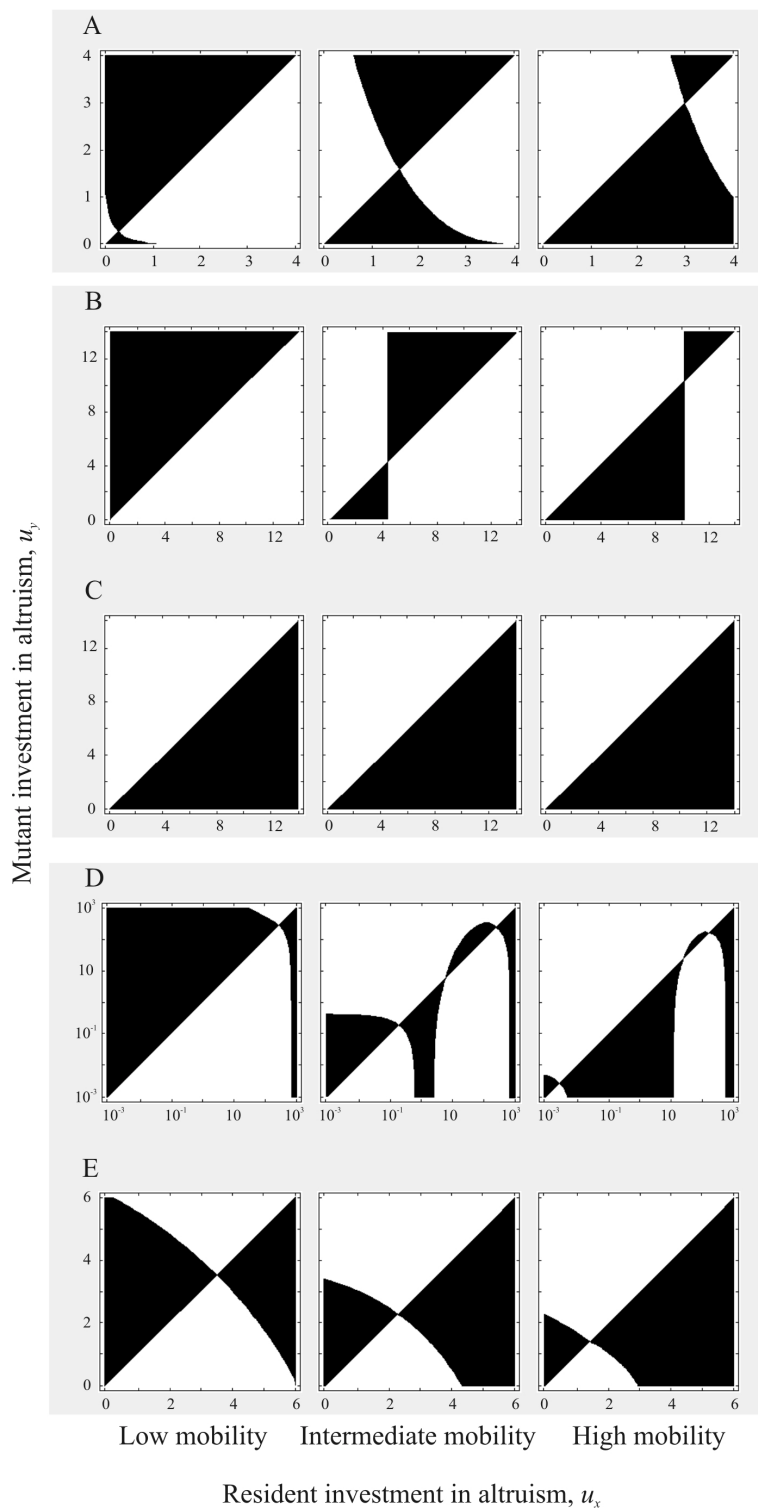


Figure 6. Invasibility of altruism phenotypes at different mobility rates. Each ‘pairwise invasibility plot’ represents the sign and zero contour of spatial invasion fitness as a function of the resident (horizontal axis) and mutant (vertical axis) trait values. Black (white) areas indicate combinations of resident altruism and mutant phenotypes for which spatial invasion fitness $s_x(y)$ is positive (negative). Singularities lie at the intersection of the diagonal line $s_x(x)=0$ and non-trivial zero contour $s_x(y)=0$ with $y \neq x$. A singularity x^* is locally uninvadable if for any y in the vicinity of x^* $s_{x^*}(y)$ is negative. A singularity x^* is attracting if the spatial invasion fitness is positive above the diagonal on the left of x^* and below the diagonal on the right of x^* . A, Decelerating costs, with $m=0$, $m=4$ and $m=8$ from left to right. The singularity is attracting. B, Weak linear costs with $m=0$, $m=4$ and $m=8$ from left to right. At low mobility, the increase of altruism is always favored. At high mobility, there is one repelling singularity. C, Strong linear costs with $m=0$, $m=3$ and $m=6$ from left to right. Selfishness is attracting, and also locally and globally evolutionarily stable. D, Slowly accelerating costs with $m=0$, $m=7.5$ and $m=15$ from left to right. At low mobility, altruism converges to a high singularity that is uninvadable. For higher mobility, two evolutionary attracting singularities are separated by a repelling singularity. E, Rapidly accelerating costs with $m=0$, $m=4.5$ and $m=9$ from left to right. The singularity is evolutionarily attracting and uninvadable by mutations of any size. All unspecified parameters in panels A to E are as in Fig. 2B to F, respectively.

In species with accelerating costs, the PIPs indicate that the attractive singularities are uninvadable (Figs. 6D, E). Starting from any viable trait value, altruism gradually evolves toward the singularity, which is robust against invasion by any alternative mutant. Large mutations may fail to invade even if they occur in the direction of adaptation predicted by the selection derivative (Figs. 6D, E). This will cause the adaptive process to slow down, all the more as it approaches the singularity. The non-trivial zero contour of fitness flattens in response to increased mobility, indicating that this “evolutionary slowing down” (Dieckmann and Law 1996) should be more pronounced in more mobile species. Overall, the inspection of many generic pairwise invasibility plots conclude that in our model the continuous evolution of altruism never undergoes evolutionary branching.

POLYMORPHIC SIMULATIONS

Although our analytical investigation of the evolution of altruism incorporates salient features of the ecological and evolutionary processes, it also involves several important simplifications. We assume an infinite lattice size, and describe the ecological dynamics with the standard pair approximation (Appendix 2). The derivation of the fitness measure relies on the small frequency of mutants as they originate and on the assumption that the build up of the mutant’s pseudo-equilibrium correlation structure can be regarded as instantaneous (Fig. 3). Furthermore, the deterministic description of the adaptive dynamics is an approximation for the mean path of a stochastic mutation selection-process (Dieckmann and Law 1996). Individual-based simulations that track the fate of each individual in the population (Appendix 1) provides a natural way to circumvent these limitations and can be used to test the robustness of our main findings.

Patterns of invasion can be probed by running a large number of stochastic simulations in which a single individual mutant arises in a stable, resident population (Fig. 7A). We observe a sharp increase of the mutant local frequency $q_{y|y}$ at low values of p_y which corresponds to the rapid phase of convergence towards the pseudo-equilibrium of the mutant correlation structure (i.e., $\tilde{q}_{y|y}$) predicted by the pair approximation (Fig. 3).

The evolutionary patterns predicted by the canonical equation can be tested by running individual-based simulations of the mutation-selection process in which the assumption that mutants arise one at a time is relaxed, and averaging over a set of simulations (Figs. 7B to F). In species with decelerating costs, we predict that selfishness is invaded by altruistic phenotypes after a potentially long waiting time. Individual-based simulations confirm this prediction and show that the adaptive increase of altruism starts earlier when mutational effects are larger (Fig. 7B). Possibly, for very small mutational effects, the corresponding waiting time may be too long for being observed in simulations of feasible duration. Keeping mutational variance constant but increasing mobility or decreasing mutation rate causes a similar increase of the waiting time for altruism to take off. In species with weak linear costs, individual-based simulations confirm both the adaptive increase of altruism at low

mobility and the evolutionary stability of selfishness at high mobility, even when very large mutations are feasible (Fig. 7C). In species with strong linear costs, convergence to selfishness or evolutionary suicide, depending on mobility, occurs as predicted by the canonical equation (Fig. 7D). Species with slowly accelerating costs are characterized by two clear-cut patterns, namely quasi-selfishness versus high altruism. At intermediate mobility, the adaptive dynamics bistability is confirmed by individual-based simulations run from different ancestral conditions (Fig. 7E). This implies that alternative adaptive investments can be reached for identical life-history profiles, due to different ancestral states or to contingent events during evolutionary history. Notice also that quasi-selfish states are practically indistinguishable from the stable selfish state of a stochastic mutation-selection process. In species characterized by rapidly accelerating costs the individual-based simulations closely match the predictions (Fig. 7F). The negative correlation between selected altruism and mobility expected in this case is confirmed. Overall, the agreement between stochastic simulations and the deterministic approximation is satisfactory. In general, the deterministic approximation converges slower than the stochastic process and underestimates the adaptive altruistic investment. This may be due to small systematic errors introduced by the standard pair approximation.

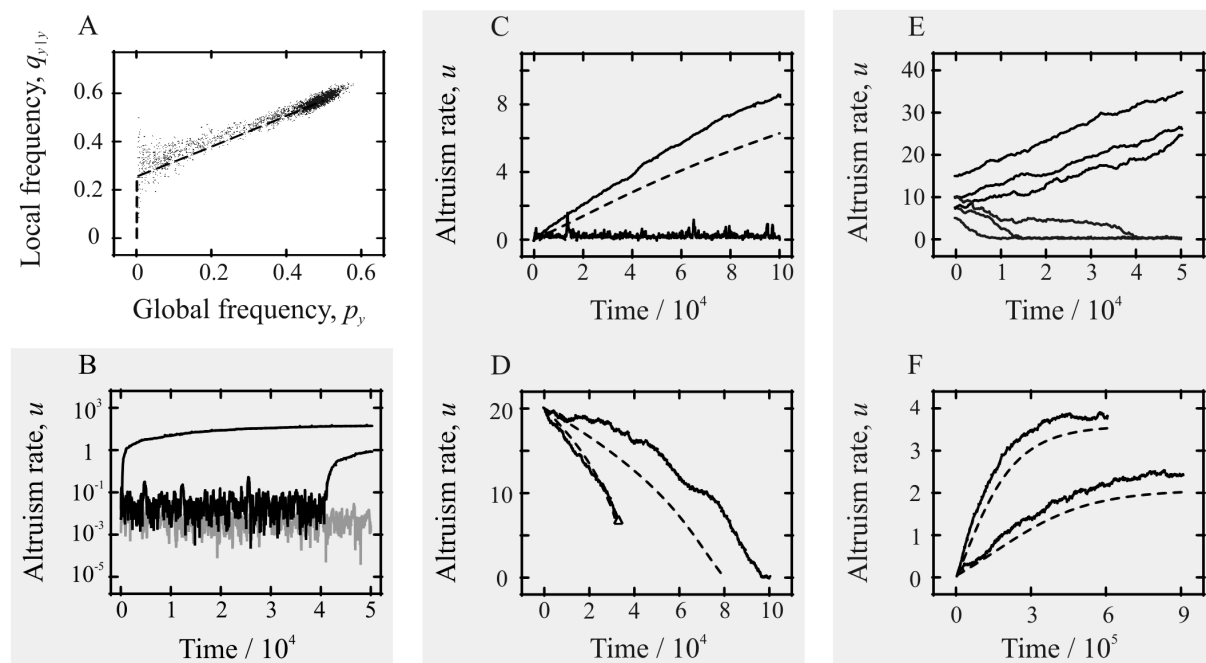


Figure 7. Individual-based simulations. A, Invasion dynamics. Deterministic dynamics (dashed curve) paralleled the stochastic simulations (continuous curve, mean of 1500 runs). Each dot gives the altruist local frequency $q_{y|y}$ and the altruist frequency p_y value at one point in time. Parameter values as in Fig. 2. B-F, Adaptive dynamics. B, Species with decelerating costs. Adaptive dynamics with large ($\sigma=0.5$, first rising black trajectory), intermediate ($\sigma=0.1$, second rising black trajectory) and low mutational variance ($\sigma=0.01$, gray trajectory). Mobility: $m=0$. Mutation rate: $k=0.01$. C, Species with weak linear costs. Average of 10

independent stochastic trajectories (continuous upper curve) against the deterministic prediction computed from Equation (7) (dashed curve) at low mobility ($m=0$, $k=0.1$, $\sigma=0.1$). Stochastic adaptive dynamics at high mobility with large mutation effects (lower trajectory, $m=6$, $k=0.05$, $\sigma=0.1$). D, Species with strong linear costs. Average of 10 independent stochastic trajectories (continuous trajectories) compared to the deterministic prediction computed from Equation (7) (dashed curves) at low mobility (right-hand side of panel; $m=0$, $k=0.1$, $\sigma=0.02$) and at high mobility (left-hand side of panel; $m=10$, $k=0.1$, $\sigma=0.02$). Triangle indicates population extinction. E, Species with slowly accelerating costs and intermediate mobility. Adaptive dynamics starting from a low ancestral altruistic investment $u_x=5$ or a high ancestral state at $u_x=15$ diverge. Starting from the same ancestral state, $u_x=8$ or $u_x=10$, stochastic trajectories either rise to a high singularity or decline toward quasi-selfishness. Average from ten stochastic runs per starting condition. Parameter values: $m=15$, $k=0.05$, $\sigma=0.1$. F, Rapidly accelerating cost. Average of 10 independent stochastic trajectories (continuous curves) compared to the deterministic prediction (dashed curves), at low mobility ($m=0$, upper curves, simulations run over 600,000 time units) and high mobility ($m=6$, lower curves, simulation run over 900,000 time units). Mutation parameters: $k=0.01$, $\sigma=0.01$. Unspecified parameters as in Fig. 2B to F, respectively.

Random lattices (featuring randomly assigned connections between sites) have been proposed for the purpose of modeling social networks (Rand 1999). The alternative of a regular habitat geometry, where interactions are limited to the geographically closest sites, compromises the use of the standard pair approximation to derive correlation equations for the population dynamics (van Baalen 2000). Individual-based simulations involving a regular square lattice indicate that our main findings are not altered qualitatively whereas selected trait values tend to be higher (results not shown).

DISCUSSION

We study the adaptive dynamics of a quantitative trait that measures the individual investment in altruism. The habitat is constant and homogeneous, but selective pressures arise from the phenotypic heterogeneity of the population. Altruism evolves from selfishness under a gradual kin selection process. This pattern is similar to the continuous evolution of cooperative investment observed in a spatial evolutionary game (Killingback et al. 1999). However, our model is not restricted to accelerating costs and pure viscosity, which would make up the most favorable case for the rise of altruism in a selfish population. In fact, we show that the qualitative and quantitative features of the adaptive evolution of altruism depend on the patterns of the cost and their interactions with mutation, individual mobility and habitat structure. Even when an accelerating cost pattern allows altruism to evolve easily from selfishness (Killingback et al. 1999), the adaptive increase of altruism appears to be often halted at very low levels. In contrast, when the cost pattern is decelerating, the selfish state will usually be displaced upon to the occurrence of rare mutations of large effects.

Kin Selection, Cooperation and Competition

The conceptual path followed here to define and measure fitness differs from the usual approach of kin selection theory (Frank 1998; Michod 1999 for reviews), although the results from both angles can be formulated in similar terms. Starting from demographic and behavioral processes operating at the level of individuals and their neighbors, we follow on from van Baalen and Rand (1998) to define fitness as the invasion exponent of a system of correlation equations for the spatial dynamics of a mutant population. This notion extends the concept of invasion fitness defined for well-mixed populations (Metz et al. 1992; Rand et al. 1994; Ferrière and Gatto 1995). In our model, invasion fitness is found to compound the per capita intrinsic growth rate and the per capita “neighbor-modulated” growth rate (Frank 1998) that accounts for the respective effects of competitive and cooperative interactions between a mutant focal individual and mutant *versus* resident neighbors.

In the terminology of kin selection, this invasion fitness is analogous to a “direct fitness function” from which one can derive a direct fitness gradient and decipher the selective pressures that operate on the trait under consideration (Frank 1998). We identify three selective pressures acting on altruism: the direct physiological cost to the individual, the indirect beneficial effect of altruistic interactions, and the indirect negative effect of competition for space. According to the analysis of Taylor (1992a, 1992b) and Queller (1994), spatial kin selection models raise a critical difficulty for the evolution of cooperation, because costs of competing for space with relatives exactly cancel out the benefits of altruism. Similarly, Wilson et al. (1992) concluded “local population regulation often, if not always, cancels the effects of relatedness”. We arrive to the conclusion that the effect of competition with relatives can become negligible in organisms with a continuous life cycle, which reemphasizes that kin selection is effective at explaining the evolution of unconditional altruism (also see Taylor and Irwin 2000). This result holds independently of the level of individual mobility; and therefore cannot be attributed to relaxing the “pure viscosity” hypothesis of traditional kin selection models, according to which only offspring are dispersed (Hamilton 1964). Thus, why is the indirect cost of kin competition so low in our model? Help is processed by any recipient to produce offspring in sites that are unlikely to be located in the donor’s neighborhood because of the random structure of the habitat. Even with more regular habitat structure, the availability of free sites to host any donor’s offspring is made likely by individual mortality that keeps reopening sites irrespective to social interactions between neighbors.

One key feature of our model therefore lies in the fact that the habitat offers empty sites for the local spread of altruistic mutants. This occurs because the stochastic death process keeps reopening space in the neighborhood of any helping individual. Consequently, the population does not reach a steady state of saturation, and the selective pressure generated by kin competition remains negligible. Such a dominant effect of the availability of free space on the evolution of altruism was anticipated by Taylor (1992b) and Queller (1992, 1994) who introduced the notion of “population elasticity” to refer

to it. In a recent study of a contest of selfishness versus altruism, Mitteldorf and Wilson (2000) included a similar effect as generated by environmental stochasticity, and came to the same conclusion. However, these authors assumed an initial mixture of egoists and altruists instead of a single mutant in a resident background population, which does not address the crucial phase of the invasion process.

Whether it is demographic stochasticity or environmental stochasticity that underlies the site-opening process is unlikely to make much difference as long as there is no feedback of the adaptive trait dynamics on that stochastic process. This is the case both in our model and in the study by Mitteldorf and Wilson (2000) because the process of site opening amounts to a form of individual mortality whereas the altruistic trait affects fecundity. In a different setting where altruism would impact on the individual mortality rate, such a feedback could exist depending on whether sites are opened by demographic or environmental stochasticity. The adaptive increase of altruism would reduce the death rate, hence the rate of site opening by demographic stochasticity. As a consequence, the selective pressure of local competition against altruism would be enhanced, as can be demonstrated by an extension of our analysis (results not shown) and by the studies of Nakamaru et al. (1997, 1998) and Taylor and Irwin (2000). By contrast, the rate of site opening due to environmental stochasticity could remain independent of the adaptive change in altruism. Environmental stochasticity might then become critical for the evolution of altruism.

Because the selective pressure resulting from competition for open space turns out to be negligible, the criterion for mutant invasion amounts simply to comparing the marginal physiological cost of altruism to the marginal benefit withdrawn from interaction with the mutant's own kind. This is a variant of Hamilton's rule (Hamilton 1964) where the coefficient of relatedness is given by the local frequency of mutants neighboring a focal mutant during the invasion process. That the probability for the recipient of a focal mutant's act also to be a mutant is the appropriate definition of relatedness has already been shown in kin selection models involving pairwise interactions (Day and Taylor 1998, Frank 1998). However, such kin selection models assume that relatedness is constant and that the phenotype of a mutant has no effect on relatedness, which obviously cannot be true when invasion is a dynamical process and altruism impacts the distribution of individuals across space. The approach first advocated by van Baalen and Rand (1998) and followed up in this study shows that the same concept of relatedness holds nonetheless. In effect, relatedness is a dynamical variable for which the relevant equilibrium value can be expressed as a function of basic features of the organism's life cycle and behavior (also see Ferrière and Michod 1995, 1996; Hutson and Vickers 1995; van Baalen and Rand 1998).

Adaptive Patterns of Altruism

The pattern of physiological costs, individual mobility, the mutation process and habitat connectedness all interact to determine the adaptive dynamics of altruism (Table 2). The consideration

of decelerating costs is more relevant to study the rise of altruism from selfishness. In species with decelerating costs, altruism is under the most stringent conditions to evolve from selfishness. However, once altruism is established by the mutation-selection process, the population invariably evolves toward the physiologically maximum investment. In contrast, the assumption of accelerating costs is more relevant to study the determinants of adaptive variation in altruism. In species with accelerating costs, altruism evolves right away from selfishness (Killingback et al. 1999); but contrary to the case of decelerating costs, the evolutionary endpoint is predicted to vary according to the physiological and ecological parameters.

Table 2. Overview of the results derived in this paper.

<i>Physiological cost</i>	<i>Adaptive dynamics</i>	<i>Evolutionary outcome from a selfish ancestral state</i>
Decelerating costs	Bistability	<ul style="list-style-type: none"> • Selfishness always displaced if finite mutations occur • Waiting time for the adaptive rise of altruism increases as mutation rate or mutational variance decreases, or mobility increases • Evolution toward physiologically maximum investment in altruism
Weak linear costs	Monotonic increase at low mobility Bistability at high mobility	<ul style="list-style-type: none"> • Evolution toward physiologically maximum investment in altruism if mobility is low • Persistent selfishness if mobility is high
Strong linear costs	Monotonic decrease	<ul style="list-style-type: none"> • Persistent selfishness
Slowly accelerating costs	Monotonic convergence at low mobility Bistability at high mobility	<ul style="list-style-type: none"> • Evolution toward high altruistic investment if mobility is low • Evolution toward quasi-selfishness if mobility is high
Rapidly accelerating costs	Monotonic convergence	<ul style="list-style-type: none"> • Evolution toward low altruistic investment, correlating negatively with mobility

Following on from this dichotomy, an important result is that generically any ancestral selfish population will evolve some degree of altruism. In the case of accelerating costs, the evolution of altruism is not influenced by the mutation process. On the contrary, assuming that in the primeval selfish state the cost of altruism is decelerating, the adaptive initiation of altruism depends primarily on the mutation process. We found that higher mutation frequency and larger mutational steps decrease the waiting time for altruism to evolve. For a given mutation process, the waiting time also increases with mobility, as higher mobility carries a larger direct cost and lowers the indirect benefit of altruism. The study of a linear cost function, which can be interpreted as a degenerate case in between

decelerating and accelerating cost patterns, pinpoints the fallacious consequences that result from restricting attention to such a simple case (e.g., Roberts and Sherratt 1998). Incorporating a strong linear cost in the model completely hides the potential effect of the genetic process on the displacement of selfishness. The assumption of weak linear costs yields a type of bistable adaptive dynamics similar to the case of decelerating costs. However, large mutations have no effect in this case.

Mobility is expected to be an important factor of adaptive variation in altruism, as shown by the study of accelerating costs of altruism. First, mobility is found to impact on the speed of the adaptive process — the altruistic trait evolves at a slower pace among more mobile individuals. Second, mobility is a significant determinant of the evolutionary endpoint. In species with rapidly accelerating costs, the selected altruistic trait value correlates negatively with mobility. In species with slowly accelerating costs, mobility has a profound qualitative effect. High altruistic investments evolve in species with low mobility whereas quasi-selfishness evolves in species with high mobility. The finding of altruism being associated with low mobility is in line with previous insights into the evolution of cooperation in the Iterated Prisoner's Dilemma game (Dugatkin and Wilson 1991; Enquist and Leimar 1993; Hutson and Vickers 1995; Ferrière and Michod 1995, 1996), although the mechanisms involved are different. In these studies, mobility opposes the evolution of altruism by reducing the probability of repeated interactions between the same partners. On the empirical side, many independent studies have related the evolution of complex social systems with reduced mobility. For example, the emergence of cooperative breeding in birds may have been driven by delayed dispersal in a context of intense competition for space ("habitat saturation" hypothesis; Emlen 1982, 1997). Also, African mole-rat populations exhibit strong levels of philopatry, and the eusocial species of this mammal group occur in the harshest habitats, namely arid zones where benefits of group-living are high and dispersal is low (Jarvis et al. 1994; Spinks et al. 2000).

In species with slowly accelerating costs and low mobility, most variations of altruism between species are expected in response to differences in physiological costs and the degree of habitat connectedness. Our model outlines the importance of describing and measuring these parameters (Heinsohn and Legge 1999). Controlled experiments including the analysis of a broad range of levels of investment in altruism would enhance our knowledge of the shape and values of costs of altruism. In reality, the costs of cooperation may impact on different life history traits at different periods of the individual lifetime, and these experiments would require multivariate approaches and long-term studies.

In contrast, in species with slowly accelerating costs and high mobility, quasi-selfishness is expected to evolve. This state is eventually indistinguishable from a stable selfish population in which slightly altruistic phenotypes would chronically spread by mutation and drift. High altruistic investments could still be observed by the phylogenetic conservation of an ancestrally altruistic state while a slow environmental change favors an increase in mobility (Fig. 5E). High altruistic investment

would have evolved under the early low mobility, and be preserved throughout the subsequent environmental increase of mobility. In support of the role of phylogenetic conservation, recent comparative analyses of sociality have demonstrated a phylogenetic component of sociality in birds (Edwards and Naeem 1993) and different groups of arthropods (Crespi 1996; Weislo and Danforth 1997). High levels of investment in sociality seems to be maintained in more various ecological contexts once they evolve from cooperative ancestors. Possibly, a slow, gradual environmental change could even cause the loss of altruistic behavior at very high mobility through the catastrophic extinction of the population (Fig. 5E). An environmentally driven loss of sociality may provide another element of explanation for the uneven distribution of social species across taxa (Velicer et al. 1998).

Our analysis highlights the critical importance of mobility, which we modeled as a fixed parameter. This simplifying assumption may apply to species in which mobility is strongly constrained by the environment, the developmental program, or the genetic system. Otherwise, mobility and altruism should be entangled in a co-adaptive process, the dynamics of which will be investigated in a forthcoming paper.

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APPENDIXES

APPENDIX 1 - POLYMORPHIC INDIVIDUAL-BASED MODEL

Here we describe the stochastic, individual-based model of polymorphic population dynamics that forms the basis of our study. The habitat structure is generated by randomizing the edges of a regular, square lattice of 30×30 sites with Moore neighborhoods (which, locally, gives a so-called Cayley or Bethe lattice). The state of any site is either empty or occupied by a type i individual with a certain phenotype u_i . The demographic parameters at time t of such an individual located at z are the birth rate

$$b_i(z, t) = \left[b(m) + \sum_{k=1}^n \frac{u_k}{n} - C(u_i) \right] \frac{n_{0|i}(z, t)}{n}, \quad (\text{A1})$$

the intrinsic death rate d and the mobility rate

$$m_i(z, t) = m \frac{n_{0|i}(z, t)}{n}, \quad (\text{A2})$$

where k (varying from 1 to n) labels each neighboring site, u_k is the altruistic investment of a neighbor or zero if that site is empty at that moment, and $n_{0|i}(z, t)$ denotes the number of empty sites neighboring a type i individual located at z at time t . The local birth rate and movement rate are multiplied by the proportion of empty sites within the neighborhood.

The simulation starts by distributing individuals of an ancestral phenotype randomly over half of the lattice. Mutations generate variability with a probability k per birth event. The mutant phenotype is obtained by adding a mutation effect drawn randomly from a normal probability distribution, with zero mean and mutational variance σ^2 . When a negative investment in altruism is produced, the mutant phenotype is reset to selfishness. We use the minimal process method (Gillespie 1976) to simulate the time-continuous stochastic dynamics of the population. This means that the waiting time between two events is drawn from an exponential distribution with the inverse of its mean given by the total sum of event rates per unit time. Typically the completion of such a stochastic simulation requires around a day of computation on the fastest personal computer available at the time this work was conducted.

APPENDIX 2 - SPATIAL POPULATION DYNAMICS

Here, we derive an analytical model of the polymorphic population dynamics. The frequency of occupied sites varies through time along with the neighborhood configuration. The configuration of the neighborhood of a focal individual is given by the states of all pairs containing that individual, which themselves typically depend on the states of higher-order structures that contain those pairs

(triplets, quadruplets, and so on). This kind of dependence cascades through all orders and spatial scales. Therefore, a full description of the lattice dynamics requires an infinite hierarchy of dynamical equations, also called correlation equations (Dieckmann and Law 2000). The system, however, can be closed at any order of description by making use of appropriate approximations. We close the system at the order of pairs with the standard pair approximation (Matsuda et al. 1992, Ferrière and Le Galliard 2001). This is the simplest approximation as it assumes that third-order correlations just vanish, and it has been used to construct correlation equations for spatial games (Nakamaru et al. 1997) and social interactions (Matsuda et al. 1992).

We first describe the temporal dynamics of the frequency of occupied sites. We assume that a fixed number of phenotypes are present in the population initially. We use the indices i and j to label phenotypes, and more generally the indices k or l to designate the state of a site, including the empty state 0. We proceed by averaging the local birth rate (A1) over the lattice, which after some algebra yields the average birth rate of a type i individual at time t :

$$\bar{b}_i(t) = \left[b(m) + \sum_j u_j (1 - \phi) q_{j|i}(t) - C(u_i) \right] q_{0|i}(t), \quad (\text{A3})$$

where $q_{j|i}(t)$ is the local frequency of phenotype j around a focal i individual at time t , the sum is taken over all phenotypes in the population and $\phi = 1/n$. The mean change in the frequency of the i phenotype at time t during an infinitesimal time step dt then is

$$\frac{dp_i(t)}{dt} = (\bar{b}_i(t) - d) p_i(t) = \lambda_i(t) p_i(t). \quad (\text{A4})$$

We now describe the temporal dynamics of the local frequency of sites. As local frequencies are simply determined by pair frequencies according to

$$q_{k|i}(t) = p_{ki}(t) / p_i(t), \quad (\text{A5})$$

where $p_{ki}(t)$ designates the frequency of ki pairs at time t , it is enough to describe the dynamics of the frequencies of pairs involved in (A5) to obtain equations for the local frequencies involved in (A4). An inventory of all different events that may affect any type of pairs at time t yields three elementary fluxes (van Baalen and Rand 1998, Rand 1999). The first is the average per capita input rate of a type i into a $0j$ pair with $j \neq i$

$$\alpha_{ij}(t) = (1 - \phi)(\bar{b}_{i0}(t) + m) q_{i|0j}(t) = \alpha'_{ij}(t) q_{i|0j}(t). \quad (\text{A6})$$

The second flux corresponds to the average per capita input rate of a type i into an $0i$ pair:

$$\beta_i(t) = \phi \bar{b}_{i0}(t) + (1-\phi)(\bar{b}_{i0}(t) + m)q_{i|0i}(t) . \quad (\text{A7})$$

The third flux is the average per capita output rate of a type i from an ij pair:

$$\delta_{ij}(t) = d + (1-\phi)m q_{0|ij}(t) . \quad (\text{A8})$$

The term $\bar{b}_{i0}(t)$ involved in these fluxes is the average birth rate of a type i individual inside a $i0$ pair, given by

$$\bar{b}_{i0}(t) = (b(m) + \sum_j u_j (1-\phi)q_{j|i0}(t) - C(u_i)) . \quad (\text{A9})$$

From equations (A7), (A8) and (A9), we can obtain the dynamics of the frequencies for the three general types of pairs, $0j$, ij and jj . Unfortunately, the dynamics of these pair frequencies depend on higher-order configurations because $q_{k|il} = p_{kil}/p_{il}$. Using the standard pair approximation, we assume that $q_{k|il} = q_{k|i}$, which gives

$$\begin{aligned} \frac{dp_{0j}(t)}{dt} &= (\alpha'_j(t)q_{0|0}(t) - (\beta_j(t) + \delta_j(t)))p_{0j}(t) + \sum_{k \neq (0,j)} \delta_k(t)p_{kj}(t) + \delta_j(t)p_{jj}(t) \\ \frac{dp_{ij}(t)}{dt} &= (\alpha_i(t) + \alpha'_j(t)q_{0|0}(t))p_{0j}(t) - (\delta_j(t) + \delta_i(t))p_{ij}(t), \quad i \neq (0,j) \\ \frac{dp_{jj}(t)}{dt} &= 2\beta_j(t)p_{0j}(t) - 2\delta_j(t)p_{jj}(t) \end{aligned} \quad (\text{A10})$$

APPENDIX 3 - MONOMORPHIC POPULATION

A monomorphic version of the analytical model can be derived from (A4) and (A10). We assume there is only one phenotype and we denote by x the state of an occupied site. We are interested here in the feasible population equilibria. According to equation (A4), the non-trivial population equilibrium $\bar{q}_{0|x}$ must satisfy the quadratic equation

$$((b(m) + u_x(1-\phi)(1-\bar{q}_{0|x}) - C(u_x))\bar{q}_{0|x} - d = 0 . \quad (\text{A11})$$

The spatial population is also characterized by a second, independent statistic, $\bar{q}_{0|0}$. From (A10) $\bar{q}_{0|0}$ satisfies

$$\bar{q}_{0|0} = \delta_x / \alpha'_x . \quad (\text{A12})$$

We now analyze the viability and stability of the equilibria if b is sufficiently larger than d . The resident population is non-viable when no real solution exists for $\bar{q}_{0|x}$, which gives a first extinction boundary $\Delta = 0$ and the extinction domain $\Delta < 0$ (where Δ denotes the discriminant of the quadratic

Equation (A11)). In the area where $\Delta > 0$, there are two sub-domains. In the sub-domain defined by $b(m) - d - C(u_x) > 0$, the maximal root of (A11) corresponds to a viable equilibrium that is globally stable. In the disjunct sub-domain of obligate altruism, this solution is locally stable and coexists with the locally stable, trivial solution. A saddle point separates these two locally attractive solutions. The resident population goes extinct when the saddle point collides with the upper boundary, which leads to a second extinction domain adjacent to the first one.

APPENDIX 4 - DIMORPHIC POPULATION

Here we make use of the general polymorphic equations (A4) and (A10) to describe the population dynamics when there are only two phenotypes, indexed by x and y . Deriving a closed dynamical system requires equations for the two global frequencies p_x and p_y and for the three local frequencies $q_{x|x}$, $q_{x|y}$, and $q_{y|y}$. Using (A10) and (A5) for the dynamics of local frequencies and (A4) for the dynamics of global frequencies yields

$$\begin{aligned}
 \frac{dp_x(t)}{dt} &= \lambda_x(t) p_x(t) \\
 \frac{dp_y(t)}{dt} &= \lambda_y(t) p_y(t) \\
 \frac{dq_{x|x}(t)}{dt} &= 2\beta_x(t)q_{0|x}(t) - (2\delta_x(t) + \lambda_x(t))q_{x|x}(t) \\
 \frac{dq_{x|y}(t)}{dt} &= (\alpha_x(t) + \alpha'_y(t)q_{0|0}(t))q_{0|y}(t) - (\delta_y(t) + \delta_x(t) + \lambda_y(t))q_{x|y}(t) \\
 \frac{dq_{y|y}(t)}{dt} &= 2\beta_y(t)q_{0|y}(t) - (2\delta_y(t) + \lambda_y(t))q_{y|y}(t)
 \end{aligned} \tag{A13}$$

As pointed out by van Baalen and Rand (1998), the mean-field version of system (A13) with selfishness (x type) and altruism (y type) interacting on the lattice is given by

$$\begin{aligned}
 \frac{dp_x}{dt} &= \left((b(m) + u_y(1-\phi)p_y - C(0))p_0 - d \right) p_x \\
 \frac{dp_y}{dt} &= \left((b(m) + u_y(1-\phi)p_y - C(u_y))p_0 - d \right) p_y
 \end{aligned} \tag{A14}$$

This system readily shows that selfishness is uninvadable because it benefits from the same amount of altruism without paying the costs. This serves to highlight that spatial population heterogeneity is a key prerequisite for the invasion of altruism in a selfish world.

APPENDIX 5 – INVASION STRUCTURE AND FITNESS

Let $\tilde{q}_{0|y}$, $\tilde{q}_{x|y}$, and $\tilde{q}_{y|y}$ denote the pseudo-equilibrium local frequencies characterizing the mutant correlation structure during invasion. These terms are the steady states of (A13) when x is a resident type at ecological equilibrium and y is a mutant type at low frequency, or

$$\begin{aligned} \frac{dq_{x|y}(t)}{dt} &= (\bar{\alpha}_x + \tilde{\alpha}'_y \bar{q}_{0|0})\tilde{q}_{0|y} - (\tilde{\delta}_y + \bar{\delta}_x + \tilde{\lambda}_y)\tilde{q}_{x|y} = 0 \\ \frac{dq_{y|y}(t)}{dt} &= 2\tilde{\beta}_y \tilde{q}_{0|y} - (2\tilde{\delta}_y + \tilde{\lambda}_y)\tilde{q}_{y|y} = 0 \end{aligned} \quad (\text{A15})$$

Noting that $\tilde{q}_{y|0} = 0$ when the mutant is rare, the non-linear system involves three unknowns ($\tilde{q}_{0|y}$, $\tilde{q}_{x|y}$, and $\tilde{q}_{y|y}$) and two equations, along with the constraint $\tilde{q}_{0|y} = 1 - \tilde{q}_{x|y} - \tilde{q}_{y|y}$. The non-linear system (A15) can be used generically to evaluate numerically the spatial invasion fitness. However, one further analytical step can be taken by introducing the Taylor expansion of spatial invasion fitness up to the first order:

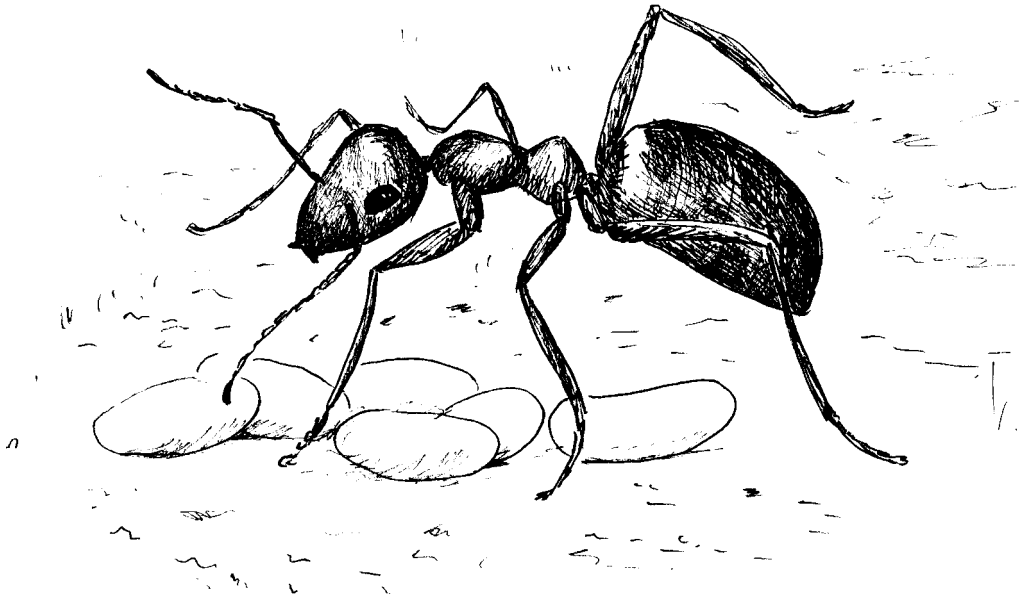
$$s_x(y) = s_x(x) + (y-x) \left. \frac{\partial s_x(y)}{\partial y} \right|_{y=x} + o(y-x). \quad (\text{A16})$$

For the degenerate mutant, $y = x$, we can solve analytically the non-linear system (A15) using symbolic resolution. This yields the solutions $\tilde{q}_{0|y} = \bar{q}_{0|x}$, $\tilde{q}_{y|y} = \bar{q}_{y|y}$ given as Equation (5) in the text, and $s_x(y) = s_x(x) = 0$. We now consider a slightly perturbed resident investment, i.e., $u_y = u_x + \varepsilon$, $\tilde{q}_{0|y} = \bar{q}_{0|x} + a\varepsilon$, and $\tilde{q}_{y|y} = \bar{q}_{y|y} + b\varepsilon$. The term a measures the marginal gain or loss of open space in a mutant's neighborhood relative to a resident. The term b measures the marginal gain or loss of relatives in a mutant's neighborhood relative to a resident. Plugging these approximations in the spatial invasion fitness defined by (1) yields after some algebra

$$s_x(y) = \varepsilon \bar{q}_{0|x} \left[(1-\phi)\bar{q}_{y|y} - a \left((1-\phi)u_x - \frac{d}{\bar{q}_{0|x}^2} \right) - \frac{C(u_y) - C(u_x)}{\varepsilon} \right], \quad (\text{A17})$$

from which we derive the selection derivative (3) at the limit where ε vanishes. Next, we use the non-linear system (A15) to solve for the a and b terms introduced before and to evaluate numerically the different components of (A17).

CHAPITRE 3 – ORIGINE ET EVOLUTION DES STRUCTURES SOCIALES



“What set species that form multigenerational families apart is the tendency for offspring to remain in association with their parent(s) beyond the age of sexual maturity and, commonly, throughout their lifetimes. The key to understanding the evolution of families is understanding delayed dispersal.” S. T. Emlen dans *Behavioural Ecology*. 1997.

“Aspects of genetics, phenotype, ecology, and demography interact in their influences on social systems. Thus, to explain the phylogenetic distribution of social systems, the effects of these variables should be considered jointly.” B. J. Crespi & J. C. Choe dans *Social behavior in insects and arachnids*. 1997.

ÉVOLUTION ADAPTATIVE DES TRAITS SOCIAUX: ORIGINE, HISTOIRE, ET PATRONS DE CORRELATION DE L'ALTRUISME ET DE LA MOBILITE

Jean-François Le Galliard, Régis Ferrière & Ulf Dieckmann

RESUME

Le comportement sociale implique un délai de la dispersion et une entraide locale — deux attributs individuels qui varient considérablement entre organismes. Cette étude analyse les facteurs ultimes de cette variation. L'évolution conjointe de l'altruisme et de la mobilité est influencée par les coûts physiologiques des deux traits, des rétroactions éco-évolutives, et une interaction sélective complexe entre les deux traits. La saturation de l'habitat, autour des individus (agrégation locale) ou autour des sites vides (concurrence locale), est un nœud critique du processus éco-évolutif. La promiscuité locale induit de la sélection de parentèle pour et est réciproquement augmentée par l'altruisme; la mobilité favorise l'invasion de mutants moins agrégés, et maximise la concurrence locale au cours de l'évolution unidimensionnelle. Quand les deux traits évoluent conjointement, l'agrégation locale est le filtre principal de l'interaction sélective et des effets indirects de la connectivité de l'habitat et des traits d'histoire de vie. Les dynamiques de la coévolution ont trois propriétés principales. (1) Le coût à la mobilité est la clef de l'origine de l'altruisme, en déterminant si l'égoïsme est envahissable, et l'échelle de temps de l'invasion. (2) Il existe deux voies typiques vers la socialité: l'évolution de la philopatrie, résultant en plus d'agrégation, peut avoir lieu avant ou après l'accroissement adaptatif d'altruisme. (3) A l'équilibre évolutif, une corrélation positive entre l'altruisme et la mobilité est attendue sous l'effet de changements dans les contraintes sur la mobilité, ou quand les traits d'histoire de vie varient conjointement.

Référence : Le Galliard, J.-F., Ferrière, R. et U. Dieckmann. 2003. « Adaptive evolution of social traits: origin, history, and correlation patterns of altruism and mobility ». *Manuscript en préparation pour soumission à The American Naturalist*.

Mots-clés : Dynamiques adaptatives, valeur sélective d'invasion, altruisme, mobilité, saturation de l'habitat, sélection de parentèle.

ADAPTIVE EVOLUTION OF SOCIAL TRAITS: ORIGIN, HISTORY, AND CORRELATION PATTERNS OF ALTRUISM AND MOBILITY

Jean-François Le Galliard, Régis Ferrière & Ulf Dieckmann

ABSTRACT

Social behavior involves “staying and helping”—two individual attributes that vary considerably among social organisms. This study investigates the ultimate factors of such variation. Altruism and mobility co-evolution is driven by physiological costs, eco-evolutionary feedbacks, and a complex selective interaction between the traits. Habitat saturation, around individuals (local aggregation) or around empty space (local contention), is a critical node of the co-evolutionary process. Local aggregation induces kin selection for, and is reciprocally enhanced by more altruism; mobility favors the spread of less aggregated mutants, and, as a single-evolving trait, maximizes local contention. When both traits co-evolve, local aggregation is the predominant mediator of the traits’ selective interaction, and of the indirect effects of habitat structure and life-history traits. Co-evolutionary dynamics display three general properties. (1) The cost of mobility is key to the origin of altruism, determining whether selfishness is invadable, and the timescale of invasion. (2) There are two archetypal routes to sociality: the evolution of less mobility, resulting in stronger aggregation, can occur either before or after the adaptive rise of altruism. (3) At evolutionary equilibrium, a positive correlation between altruism and mobility is expected as constraints on mobility change, or as life-history traits covary.

Référence : Le Galliard, J.-F., Ferrière, R. et U. Dieckmann. 2003. « Adaptive evolution of social traits: origin, history, and correlation patterns of altruism and mobility ». *Manuscript in preparation for submission to the American Naturalist*.

Key-words : Adaptive dynamics, spatial invasion fitness, altruism, mobility, habitat saturation, kin selection

INTRODUCTION

Sociality is an essential characteristic of life. Sociality involves specific individual behaviors that lead to collective properties, new levels of natural selection, and the adaptive complexification of living systems (Maynard Smith and Szathmary 1995; Michod 1999). One of the most intriguing feature of sociality is that it induces at least a two-fold cost to the individual. Sociality often requires some form of altruistic behavior whereby individuals sacrifice their own fitness to help others (Hamilton 1964a, 1964b), and some reduction in individual mobility that raises the risks of competition for local resources (Frank 1995; Perrin and Goudet 2001). Genes involved in such deleterious effects are expected to be eliminated by natural selection. Yet a wide diversity of social behaviors are observed in the wild (Choe and Crespi 1997; Crespi 2001; Wilson 1975), and one of the challenge for evolutionary theory is to explain the role that genetic adaptation can play in molding individual altruism along with population structure, and more generally the diversity of social systems (Crespi and Choe 1997).

The two-fold cost of sociality reflects only some of the selective pressures acting on social traits. Low individual mobility may increase local genetic relatedness between interacting individuals, thus promoting the evolution of helping behavior through kin selection (Frank 1998; Hamilton 1964b). Yet the enhancement of neighbors reproduction ensuing from helping may also generate habitat saturation and exacerbate competition among kin (Grafen 1984; Queller 1992; West et al. 2002). Increased competition between relatives for local resources can in turn reduce or even totally negate the indirect genetic benefits of altruism (Taylor 1992; Wilson et al. 1992). The extent to which kin competition resulting from low mobility fundamentally alters our understanding of kin selection on social traits has been demonstrated by recent comparative work on fig wasps. In these insects, strict philopatry of males competing for mates results in extremely strong local competition and completely cancels out any indirect genetic benefits of decreasing aggressiveness toward relatives (West et al. 2001). Substantial overlap between social and competitive neighborhoods may also occur in other species. In cooperatively breeding vertebrates, local offspring recruitment can result in competition among relatives for dominance and breeding opportunities within a group (Cockburn 1998; O'Riain and Braude 2001). Limited dispersal in some social insects can lead to competition between colonies founded by relatives (Thorne 1997). In general, the importance of kin competition for the evolution of altruism should depend upon the species' life history profile, the spatial scale over which cooperation and competition occur, and the structure of the habitat (Kelly 1992, 1994; Queller 1992).

In a recent study, Le Galliard et al. (2003) showed that fluctuations in local population size caused by demographic stochasticity suffices to turn local competition into a weak selective force against reproduction altruism (see also Mittleldorf and Wilson 2001). As a consequence, cooperation can almost always evolve from pure selfishness. However, the level of individual mobility has a

paramount influence on the evolutionary outcome: high altruism can only evolve in species with low mobility, and the evolutionary trajectory of highly mobile species is halted in a state of 'quasi-selfishness'. The underlying assumption that mobility can be treated as a constant trait may apply if mobility is strongly constrained by the environment, the developmental program, or the genetic system. Otherwise, mobility and altruism will be entangled in a co-adaptive process. The costs and benefits of altruism should depend on local spatial structures, which are shaped by the current levels of individual mobility and helping in the population (Ferrière and Michod 1996; Le Galliard et al. 2003). The costs and benefits of mobility should also depend upon local levels of competition and cooperation (Ferrière and Le Galliard 2001; Lambin et al. 2001). Understanding the origin and evolutionary diversification of social behaviors then raises the need to conduct a joint analysis of the intertwined adaptive dynamics of altruism and mobility (Emlen 1997; Helms Cahan et al. 2002). The purpose of this paper is to develop such a unifying approach.

By expanding the framework laid out by Le Galliard et al. (2003), we study the joint evolution of altruism and mobility in a spatially explicit model. In this model, individuals move and interact locally on a lattice of suitable sites (Matsuda et al. 1992; van Baalen 2000b). The study requires to define an appropriate measure of fitness; the notion of invasion fitness, that is, the per capita growth rate of a mutant when rare in the environment set by the wild-type population (Metz et al. 1992), appropriately extends to kin selection processes involving diallelic, haploid genetics (Frank 1998; Michod 1999). Following on from van Baalen and Rand (1998), we derive invasion fitness from a set of correlation equations describing the population's spatial heterogeneity (Ferrière and Le Galliard 2001; Le Galliard et al. 2003). We then use this measure of spatial invasion fitness to (i) identify the selective pressures acting on altruism and mobility traits, and relate these pressures to the model underlying parameters; (ii) analyze the course of evolution of both traits, and their interplay with the population spatial structure; and (iii) make predictions about the correlation patterns between altruism and mobility at evolutionary equilibrium—patterns which are expected to emerge across populations or species in response to variation of life-history traits or ecological constraints.

MODEL OF SOCIAL NETWORKS

We assume that interactions and mobility occur locally between neighbors. Altruism and mobility are continuous characters affecting individuals' demographic parameters. Demographic parameters and individual interactions mold the local population structure from which selective pressures on the individual traits arise.

The model takes the form of a lattice of sites over which individuals are distributed. Each site may be empty, or occupied by one individual, and is connected to a set of sites that defines a neighborhood. Connections are assigned randomly between sites and every site is connected to the same number of sites, denoted by n which defines a degree of 'habitat connectivity'. This

representation of a spatial habitat is appropriate to model social interactions, and may be typical of the social structure of some vertebrates which defend individual territories and disperse primarily among adjacent sites (e.g., Rand 1998).

Mobility and interaction are defined at the neighborhood scale. During any small time interval, an individual may move to an empty site within its neighborhood, reproduce by laying an offspring into an empty neighboring site, or die. The per capita mobility rate m and death rate d are unaffected by local interactions. Mobility is assumed to be costly to the individual, with a permanent negative effect on the individual's birth rate. This cost may result from differential allocation of resources between dispersal and fecundity (Cohen and Motro 1989). The cost of mobility is assumed to impact linearly the intrinsic birth rate such that the net per capita birth rate (in the absence of interaction) is given by $b(m) = b - \nu m$, where b measures the intrinsic per capita birth rate in sessile organisms that do not invest energy into mobility, and ν measures the sensitivity of the cost to mobility.

We assume that movement and reproduction are affected by two types of local density-dependent factors. First, movement and reproduction are conditional to the availability of a neighboring empty site, because of a prior-resident advantage. Thus, local crowding negatively affects the rates of mobility and birth. Second, reproduction is enhanced by altruistic interactions with neighbors, which implies a positive effect of local population size. Here we assume that an altruistic donor improves the quality of the neighboring sites at the expense of its own reproduction. For example, in cooperatively breeding vertebrates, helpers usually participate in alloparental care (Cockburn 1998). The altruistic phenotype is defined by the per capita rate of energetic investment u into the altruistic function. The altruistic behavior is directed evenly towards all neighboring sites, regardless of the presence or phenotypes of neighbors. In effect, every neighbor of a focal individual that invests at rate u into altruism sees her birth rate augmented by the amount u/n . We use the terms "selfishness" to describe a phenotype that does not invest in altruism ($u = 0$) and "quasi-selfishness" to refer to a phenotype that invests nearly zero in altruism ($u \approx 0$).

We further assume that altruism carries a physiological cost. This is known for example in the suricate *Suricata suricatta*: adults engaging in the altruistic activity of baby-sitting lose significant body weight (Clutton-Brock et al. 1998). We distinguish three patterns of dependence of costs on the amount of energy invested in altruism, that we call accelerating, linear, and decelerating. With accelerating costs, the increase of the cost resulting from an increased altruism rate becomes disproportionately larger as the initial investment increases. Conversely, a decelerating pattern yields a disproportionate increase of costs at lower investment. This would apply to organisms in which the initiation of altruism from a selfish state would be very costly. In the limiting case of a linear pattern, the cost sensitivity is independent of the level of investment. The physiological cost of altruism $C(u)$ encapsulates the three patterns of decelerating, linear, and accelerating costs: $C(u) = \kappa u^\gamma$, where κ

scales the sensitivity of the cost to altruism ($\kappa > 0$), and γ determines whether costs are accelerating ($\gamma > 1$), linear ($\gamma = 1$) or decelerating ($\gamma < 1$).

Mutations may cause the altruism or mobility phenotypes of offspring to differ from their parents'. Mutations occur with a fixed probability per birth event, denoted by k . The mutant phenotype is obtained by adding the mutation effect to the progenitor phenotype. Mutation effects are drawn randomly from a normal probability distribution, with zero mean and a mutation step variance σ . There are no genetic correlations between the altruism and mobility traits. The polymorphic, stochastic process can be simulated on a finite lattice (Appendix A). Symbols of the model are defined in Appendix E.

CANONICAL EQUATION OF ADAPTIVE EVOLUTION

In a large population where mutations are rare and mutational steps are small, the stochastic mutation-selection process can be approximated by a deterministic process whose trajectories are solution of the so-called canonical equation of adaptive dynamics (Dieckmann and Law 1996):

$$\frac{d}{dt} \begin{pmatrix} u_x \\ m_x \end{pmatrix} = k \frac{\sigma^2}{2} N_x \begin{pmatrix} \left. \frac{\partial s_x(y)}{\partial u_y} \right|_{u_y=u_x} \\ \left. \frac{\partial s_x(y)}{\partial m_y} \right|_{m_y=m_x} \end{pmatrix}, \quad (1)$$

where $x = (u_x, m_x)$ denotes a resident phenotype, and $y = (u_y, m_y)$, a mutant phenotype. Parameters k and σ are the mutation rate and the mutation step variance, which we assume to be the same for both traits. N_x is the resident population size at equilibrium, and $s_x(y)$ denotes the invasion fitness of a mutant phenotype y in a resident phenotype x . The three first terms of the right hand-side quantify the effects of mutation and population size on the evolutionary rate. The bracketed term is the selection gradient which defines the local direction of the adaptive process.

The resting states of the canonical equation (1) correspond to resident phenotypes where the selection gradient vanishes. A stability analysis of these singular points requires examining independently the evolutionary attractivity, or convergent stability, and the non-invasibility or evolutionary stability (Eshel 1983; Geritz et al. 1998). The local evolutionary attractivity of a singular state x^* means that trajectories starting in the vicinity of x^* converge to the singularity. Under the assumption of canonical equation (1), the convergence stability of x^* is characterized by the Jacobian matrix

$$\mathbf{J} = \begin{bmatrix} \frac{\partial^2 s_x(y)}{\partial^2 u_y} + \frac{\partial^2 s_x(y)}{\partial u_x \partial u_y} & \frac{\partial s_x(y)}{\partial m_x \partial u_y} \\ \frac{\partial s_x(y)}{\partial m_y \partial u_x} & \frac{\partial^2 s_x(y)}{\partial^2 m_y} + \frac{\partial^2 s_x(y)}{\partial m_x \partial m_y} \end{bmatrix}_{y=x=x^*} \quad (2)$$

For a singular point to be locally attractive, it is sufficient that the two eigenvalues of the Jacobian matrix have negative real part. The local non-invasibility of a singular point x^* means that a mutant with a phenotype close to the singular phenotype is unable to invade. Under the assumption of the canonical equation (1), the Hessian matrix characterizes the evolutionary stability of the singular point

$$\mathbf{H} = \begin{bmatrix} \frac{\partial^2 s_x(y)}{\partial^2 u_y} & \frac{\partial^2 s_x(y)}{\partial m_y \partial u_y} \\ \frac{\partial^2 s_x(y)}{\partial m_y \partial u_x} & \frac{\partial^2 s_x(y)}{\partial^2 m_y} \end{bmatrix}_{y=x=x^*} \quad (3)$$

(Leimar In press; Marrow et al. 1996). For the singular state x^* to be locally non-invadable, it is sufficient that the two eigenvalues of the Hessian matrix have negative real part (Leimar In press). Convergence and evolutionary stability can also be characterized globally by geometrical tools. Global evolutionary attractivity has been analyzed here by plotting adaptive trajectories in the trait plane, and global non-invasibility has been studied by the use of pairwise invasibility plots, that display the sign of the invasion fitness $s_x(y)$ with regard to x and y values (Geritz et al. 1998).

SPATIAL INVASION FITNESS

The spatial invasion fitness of a mutant (denoted by y) can be defined as the propensity of an initially rare mutant population to establish in a resident population at ecological equilibrium (Metz et al. 1992). The dynamics of a mutant phenotype y is derived by tracking its population size across time. Mutant dynamics depend on the resident population configuration and are affected by two types of density-dependent effects. Local competition affects the likelihood of movement and birth events. Birth and movement rates of mutant are proportional to the frequency of empty sites in the neighborhood of mutant sites. Altruistic interactions affect additively the birth rate of any focal individual. The benefits obtained from altruistic interactions are proportional to both the altruism rate and the frequency distribution of neighboring phenotypes.

The growth of the mutant population depend on the neighborhood structure, which involves the configuration of pairs of sites (Appendix B). This neighborhood structure can be described in terms of 'local frequencies', the average probabilities that a site is neighbored by a site in a given state (Matsuda et al. 1992). The dynamics for the population size of the mutant are then governed by

$$\frac{dN_y}{dt} = \left[\left(b + (1-\phi) u_x q_{x|y} + (1-\phi) u_y q_{y|y} - C(u_y, m_y) \right) q_{\theta|y} - d \right] N_y, \quad (4)$$

where $q_{k|y}$ is the average local frequency of sites in state k neighboring a mutant individual.

Obviously, the dynamics of the neighborhood depend also on the state of higher order terms including the pairs' neighbors, and so on. A complete description of the lattice dynamics therefore requires an infinite hierarchy of statistics governed by an infinite system of correlation equations, each one describing the spatial structure on a particular scale in relation to the subsequent one. To make a model tractable at the level of pair dynamics, we use a pair-approximation to close the exact system at that scale (Matsuda et al. 1992; Morris 1997, Appendix B).

The spatial invasion fitness $s_x(y)$ can then be defined as the per capita exponential growth rate of the mutant population governed by equation (4) (see Ferrière and Le Galliard 2001; Metz et al. 1992). The initial population dynamics of a rare mutant involve two distinct phases (van Baalen 2000b). In a first, short phase, a single mutant individual is born near its resident progenitor and either dies without living any descendants, or begins to invade locally until the spatial correlation structure stabilizes at a pseudo-equilibrium neighborhood structure denoted by $\tilde{q}_{0|y}$, $\tilde{q}_{x|y}$, $\tilde{q}_{y|y}$. Conditional on non-extinction during this first phase, the mutant population then expands or contracts while keeping its pseudo-equilibrium correlation structure. At the same time, the resident population remains close to its own equilibrium correlation structure. Spatial invasion fitness can therefore be defined as the mutant population growth rate during this phase (van Baalen and Rand 1998), and is given by

$$s_x(y) = \left[\left(b(m) - C(u_y, m_y) \right) \tilde{q}_{0|y} - d \right] + (n-1)\phi u_x \tilde{q}_{0|y} \tilde{q}_{x|y} + (n-1)\phi u_y \tilde{q}_{0|y} \tilde{q}_{y|y} \quad (5)$$

A positive fitness implies that the invasion process enters a third phase during which the mutant phenotype displaces the resident. This expression relates to the notion of “direct” or “neighbor-modulated” fitness obtained by adding the effects on a focal individual's fitness of all phenotypes present in the neighborhood (see Frank 1998). Likewise, the spatial invasion fitness of a focal mutant sums the mutant neighbor-independent fitness (first term) and the effects of a resident (second term) and a mutant neighbor (third term), each weighed by the probabilities of such neighborhoods.

In practice, the spatial invasion fitness is determined by the equilibrium correlation structure of the resident population, as characterized by $\bar{q}_{x|x}$ and $\bar{q}_{x|0}$, and the pseudo-equilibrium correlation structure of the mutant population. The latter can be derived from the dynamics of a dimorphic population, when the mutant phenotype is rare and the resident phenotype is at equilibrium (Appendix D). The former is obtained from a model of the monomorphic resident population (Appendix C). The spatial statistics $\bar{q}_{x|x}$ and $\bar{q}_{x|0}$ relate to the empirical notion of habitat saturation, as originally introduced by (Brown 1978; Emlen 1982). The complementarity of $\bar{q}_{x|x}$ and $\bar{q}_{x|0}$ as descriptors of the population spatial structure pinpoints that, in fact, habitat saturation involves two distinct aspects of the population structure: “local aggregation”, measured by $\bar{q}_{x|x}$, which is the level of crowding felt

locally by any given individual; and “local contention”, measured by $\bar{q}_{x|0}$, which is the level of competition between the neighbors of any vacant site, in which each of them could lay down an offspring.

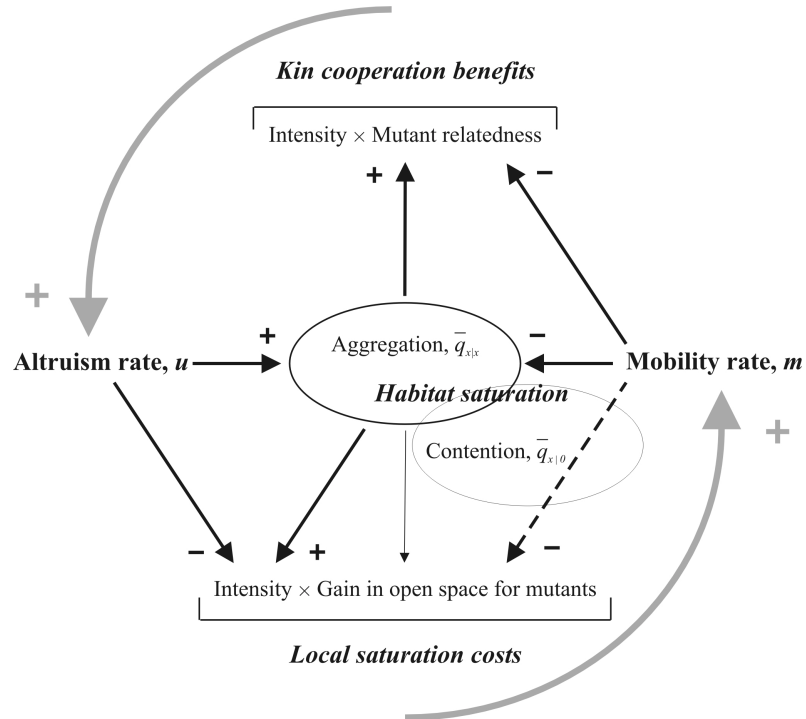


Figure 1. Selective pathways affecting altruism and mobility. The multiple links of both eco-evolutionary feedbacks (altruism→habitat saturation→kin cooperation benefits→altruism, and mobility→habitat saturation→local saturation costs→mobility) and of the selective interactions (altruism→habitat saturation→local saturation costs→mobility, and mobility→habitat saturation→kin cooperation benefits→altruism) can all be traced on this diagram. Curved gray arrows indicate selective pressures. Each pressure is evaluated as a marginal gain or loss in fitness, multiplied by an intensity factor. The pressure exerted by local saturation costs on altruism is negligible and thus not displayed here. Plain arrows refer to positive or negative effects established from the analysis of equations (6) to (8) (see also Appendix D). The strength of the effects is modulated by underlying parameters (cost parameters, habitat connectivity, life-history traits). The thinner arrow indicates a constantly weak effect. The dotted arrow indicates a complex combination of direct and indirect (via local contention) effects of mobility on the marginal gain in open space; the negative sign of this effect was established numerically. No arrow points to the intensity of the kin cooperation benefits, which depends solely on habitat connectivity (fixed parameter).

SELECTION GRADIENT AND SELECTIVE INTERACTION

The selection gradient (bracketed term in the right hand-side of the canonical eq. [1]) determines the direction of the adaptive process. Its first coordinate measures the selective pressures acting on mobility (see Appendix D)

$$\partial_m s_x(y) = \bar{q}_{\theta|x} \left[\left(\frac{d}{\bar{q}_{\theta|x}^2} - (1-\phi)u_x \right) \partial_m \tilde{q}_{\theta|y} - \partial_m C \right], \quad (6)$$

where ∂_m denotes the derivative with respect to m_y evaluated at $m_y = m_x$. The derivative $\partial_m C$ is the marginal cost of mobility which measures the selective pressure for reducing the physiological cost of mobility ($\partial_m C = \nu$, the cost sensitivity). A second selective pressure is represented by $\partial_m \tilde{q}_{\theta|y}$, which is the marginal gain (or loss) of open space in the neighborhood of a mutant individual. This shows that the evolution of mobility is driven primarily by the advantage conferred during invasion to mutants who are surrounded by more open space than residents are. The intensity of this pressure, i.e.

$\left(\frac{d}{\bar{q}_{\theta|x}^2} - (1-\phi)u_x \right)$, is determined by the death rate, habitat connectivity, altruism rate, and local

aggregation. The marginal gain of open space for mutants, $\partial_m \tilde{q}_{\theta|y}$, translates into a positive pressure on the mobility rate, whose strength appears to be a complex combination of the current mobility rate, local aggregation, and local contention (app. D).

The second coordinate of the selection gradient is given by

$$\partial_u s_x(y) = \bar{q}_{\theta|x} \left[(1-\phi)\bar{q}_{y|y} - \partial_u C \right] \quad (7)$$

(Appendix D). This expression describes two selective pressures acting on altruism (Le Galliard et al. 2003). The derivative $\partial_u C$ indicates the pressure for reducing the physiological cost of altruism. The local frequency $\bar{q}_{y|y}$ reflects the benefit of increasing altruism among mutants; the intensity of this selective pressure, i.e. $(1-\phi)$, only depends on habitat connectivity. The statistic $\bar{q}_{y|y}$ measures the probability that the recipient of an action performed by a mutant individual is a mutant itself, and so provides an appropriate measure of relatedness (Day and Taylor 1998; Ferrière and Le Galliard 2001). Equation (7) (from which a marginal Hamilton's rule can be derived, see Le Galliard et al. 2003) identifies the role that kin selection plays in the evolution of altruism. Relatedness can be expressed as a function of the basic environmental and life-history parameters

$$\bar{q}_{y|y} = \frac{d \phi}{d + (1-\phi) m \bar{q}_{\theta|x}} \quad (8)$$

which shows that the marginal gain resulting from interactions between relatives is higher in more aggregated populations (lower $\bar{q}_{\theta|x}$).

These results show altogether that the adaptive dynamics are mediated by eco-evolutionary feedback loops involving both altruism and mobility, a selective interaction between altruism and mobility (fig. 1), and a physiological feedback loop on altruism. Eco-evolutionary feedback loops

involve the effects of one trait on the individuals' environment which in return modifies the selective pressures acting on adaptive variation in that trait. Insofar as the selection component $\partial_m \tilde{q}_{0|y}$ decreases with mobility (see Appendix D), equation (6) demonstrates a negative feedback of mobility on its own adaptive dynamics: the marginal gain in open space for mutants diminishes as mobility increases. This feedback involves both local aggregation (through the coefficient of $\partial_m \tilde{q}_{0|y}$ and the expression of $\partial_m \tilde{q}_{0|y}$ itself) and local contention (upon which $\partial_m \tilde{q}_{0|y}$ depends). In the degenerate though instructive case of a zero mobility cost, local aggregation becomes independent of mobility, whereas local contention increases monotonically with the mobility rate (Appendix C); thus, the corresponding eco-evolutionary feedback on mobility is mediated by local contention—not by local aggregation. From extensive numerical analysis it appears to be general that local contention plays the predominant role over local aggregation in shaping the eco-evolutionary feedback on mobility.

Likewise, given that in general local aggregation ($\bar{q}_{x|x}$) correlates positively with the level of altruism, equations (7) and (8) establish a positive feedback on altruism mediated by the local aggregation-component of habitat saturation and its effect on relatedness: local aggregation, hence relatedness, are usually higher in more altruistic populations, which favors the evolution of even more altruistic phenotypes. The evolution of altruism is also controlled by a physiological feedback when the cost pattern is non-linear. Then the pressure to reduce the physiological cost of altruism depends on the altruism rate: when costs are decelerating (accelerating) the marginal cost of altruism decreases (increases) with the level of altruism. Thus, the effect of this physiological feedback is positive for decelerating costs of altruism and negative for accelerating costs.

The selective interaction of altruism and mobility has five components (fig. 1)—two involving an effect of mobility on the selection gradient of altruism; three involving an effect of altruism on the selection gradient of mobility. As for the effect of mobility, equation (8) shows that mutant relatedness is negatively affected by mobility both directly (dependence on m of the right-hand side of eq. [8]) and indirectly via local aggregation ($\bar{q}_{x|x}$). Thus, increasing mobility tends to weaken the selective pressure acting on altruism. As for the effect of altruism, the intensity of the selective pressure for

opening space, measured by $\left(\frac{d}{\bar{q}_{0|x}^2} - (1-\phi)u_x \right)$, indicates that there is, first, a direct, negative effect

(term $-(1-\phi)u_x$) which arises because it pays off to interact with more neighbors in a strongly altruistic population. Notice that the corresponding cost of opening space due to the loss of help received from neighbors has been highlighted in the empirical literature as a 'benefit of philopatry' (Stacey and Ligon 1991). Second, there is an indirect, positive effect (term $d/\bar{q}_{0|x}^2$) which stems from the fact that there is more of a selective advantage to be gained from opening space by moving when

local aggregation is high. The net effect depends on the level of altruism in the population. Numerical simulations show the selective pressure for mobility is weakened at low altruism, whereas it is enhanced at intermediate rates of altruism. Moreover, in species with accelerating costs, a further rise of altruism results in reduced local aggregation (for the large cost of altruism then severely depletes natality), hence a reversal to a negative net effect on the intensity of selection for opening space. Finally, there is an additional effect of altruism on the selection derivative $\partial_m \tilde{q}_{0|y}$ through local aggregation (see Appendix D), but this effect turns out to be negligible.

ADAPTIVE EVOLUTION OF SINGLE TRAITS

In general, the evolutionary dynamics of each single trait are monotonous and converge to a point attractor (which, under certain circumstances, depends on the population ancestral state). Each attractive point corresponds to a singularity of the adaptive dynamics where the selection derivative vanishes. Any small mutation arising around these singularities is selected against and fails to invade.

Altruism

Qualitatively, the adaptive dynamics of altruism primarily depends upon the pattern of physiological cost of altruism (see Le Galliard et al. (2003) for more details). Under the assumption of decelerating costs, ancestral selfishness can only be displaced by altruism as a result of rare, large mutations. There is a ‘waiting time’ for the adaptive rise of altruism that increases with the mobility rate. Only in the limiting case of a linear cost of altruism may pure selfishness remain unbeatable. This occurs mainly in species characterized by both (i) a ‘strong’ linear cost, for which the cost sensitivity κ is larger than a threshold equal to $\phi(1-\phi)$, which decreases as habitat connectivity increases; and (ii) a mobility rate larger than a threshold

$$m_l = b \frac{\phi(1-\phi) - \kappa}{v(\phi(1-\phi) - \kappa) + \kappa(1-\phi)}. \quad (9)$$

Thus, the most unfavorable conditions for the evolution of altruism involve high cost sensitivity to altruism, high mobility, and high habitat connectivity.

In species with accelerating costs of altruism, the altruism rate evolving is lower in organisms that are more mobile. Under ‘rapidly’ accelerating costs (high κ and/or γ much larger than 1), the relationship between mobility and selected altruism is smooth, and at all mobility rates the selected rate of altruism is low. In contrast, under ‘slowly’ accelerating costs (low κ and γ close to 1) the relationship between mobility and selected altruism shows a sharp discontinuity: high levels of altruism evolve in species with low mobility whereas quasi-selfishness evolves in species with high mobility. When mobility is low, the high level of altruism that evolves can be approximated as

$$u^* = [\phi(1-\phi)/\kappa\gamma]^{1/(\gamma-1)}. \quad (10)$$

which depends only on habitat connectivity and the parameters of the physiological cost of altruism. At intermediate mobility, the evolutionary outcome depends on the ancestral state of the population: if the ancestral altruism is low, quasi-selfishness evolves; if the ancestral altruism is sufficiently high, a high level of altruism approximated by equation (10) evolves.

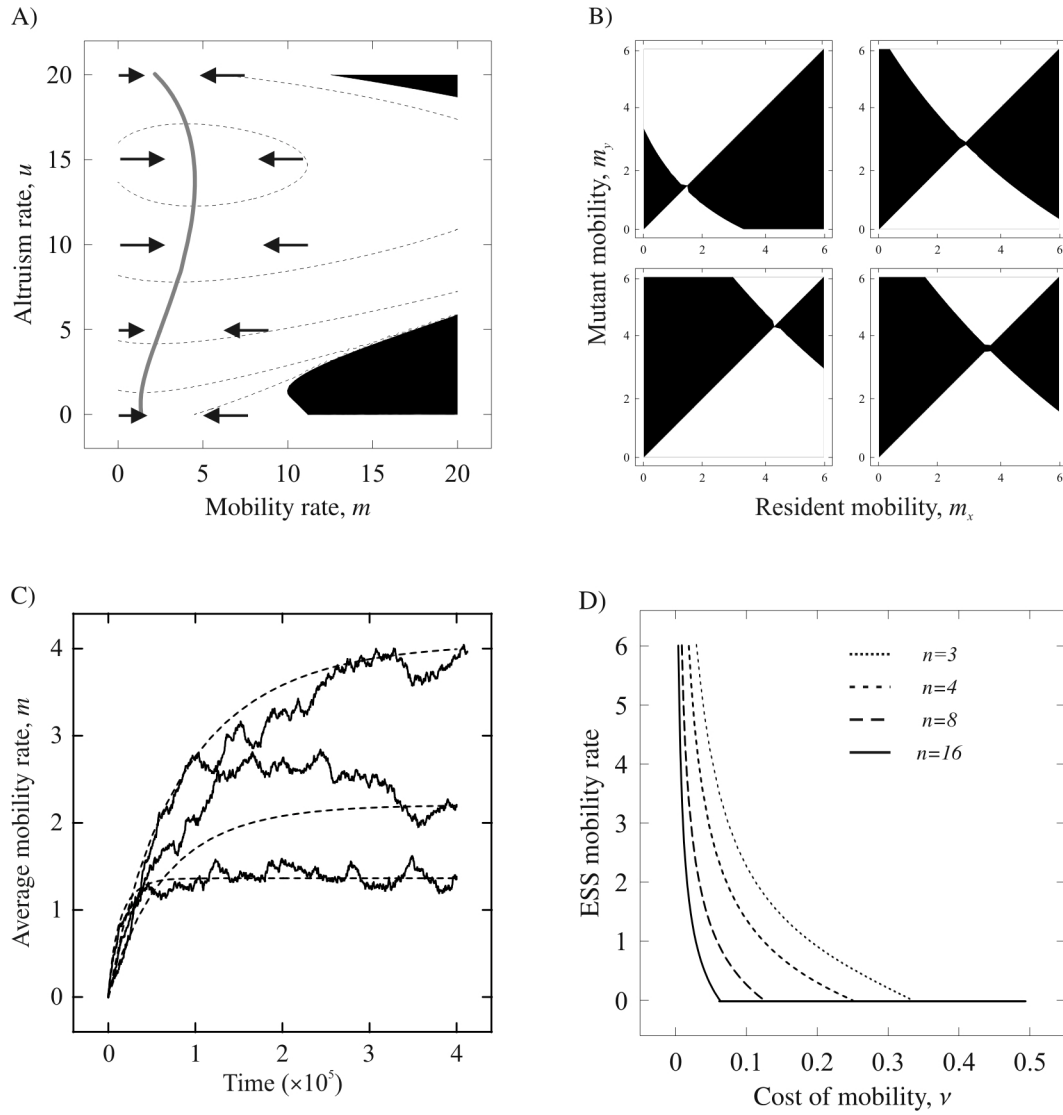


Figure 2. Adaptive dynamics of mobility. A, Singular mobility rates for an accelerating cost of altruism. Gray curve: mobility isocline; arrows indicate that the isocline is attractive. Dashed curves: contour lines of the spatial statistics $\bar{q}_{x|0}$ (local contention). Dark area: population extinction domain. Parameter values: $\gamma = 3$, $\kappa = 0.001$ and $\nu = 0.1$. B, Pairwise invasibility plots display fitness sign as a function of resident and mutant mobility rates. Dark (white) area: positive (negative) fitness. Singularities obtain as intersections between zero-fitness contour lines and the diagonal. A singularity is locally uninvadable if the fitness is negative above and below. A singularity is attractive if fitness is positive above the diagonal on the left and below the diagonal on the right. Parameter values from left to right, and from top to bottom: $u_x = 0$, $u_x = 5$, $u_x = 10$, $u_x = 17$. Other parameter values as in A. C, Average of ten independent stochastic simulations (continuous curves) and deterministic

approximation (dashed curves) at three different levels of altruism: $u_x = 0$ in the two lower curves, $u_x = 20$ in the two intermediate curves and $u_x = 10$ in the two upper curves. Mutation parameters: $k = 0.1$, $\sigma = 0.01$. D, Evolutionarily stable mobility rates with respect to the cost of mobility for different values of habitat connectivity. Other parameter values as in A.

Mobility

Mobility as a single adaptive trait always evolves toward a globally attractive and uninvadable singularity (fig. 2A). Below the evolutionary singularity, the selective pressure for opening space is higher than the pressure to reduce physiological costs, which selects for increased mobility. The intensity of this effect decreases up to the evolutionary singularity where the selection gradient vanishes. At high mobility, the selective pressure for decreasing the physiological costs of mobility favors a decreased mobility. Pairwise invasibility plots (fig. 2B) show that no mutant can invade the evolutionary singular point, which means that the attractive evolutionary singularity is also evolutionarily stable.

In purely selfish species ($u = 0$), the mobility ESS can be solved analytically and is given by

$$m^* = \frac{b(\sqrt{v(1-v)\phi(1-\phi)} - v(1-v))}{v(1-v)((1-\phi)-v)} \quad (11)$$

This expression solely depends on the cost of mobility, habitat connectivity, and the intrinsic birth rate. The ES mobility rate decreases with the cost of mobility v , and reaches $m^* = 0$ when $v > \phi$ (fig. 2D); it also decreases with habitat connectivity ($n = 1/\phi$, fig. 2D), and increases with the birth rate. Furthermore, m^* possesses the remarkable property of maximizing the local contention statistic, $\bar{q}_{0|0}$; thus, in selfish species, evolution of mobility alone maximizes habitat saturation around empty sites. Numerical simulations show that the same pattern applies to species at any level of altruism ($u > 0$): m^* responds to parameter variations in the same qualitative way; in addition, lower mobility is selected in response to higher mortality. Also, for all numerically tested parameter combinations, we find that m^* maximizes local contention.

The ES mobility rate m^* varies with the species' degree of altruism u . The empirical expectation is that more altruistic species are less mobile, but the typical pattern is more complex. First, zero mobility is selected for if the mobility cost is too high ($v > \phi$), irrespective of the degree of altruism. Second, whatever the type of altruism cost (decelerating or accelerating), there may be a slight decrease of m^* as u increases through very small values, but the singular mobility rate m^* increases with u over a wide range of degrees of altruism (see fig. 3A for the case of a decelerating altruism cost, fig. 4 for a linear cost, figs. 2A and 5 for accelerating costs). At very high values of u , m^* can decrease again with larger values of u in species with accelerating costs of altruism.

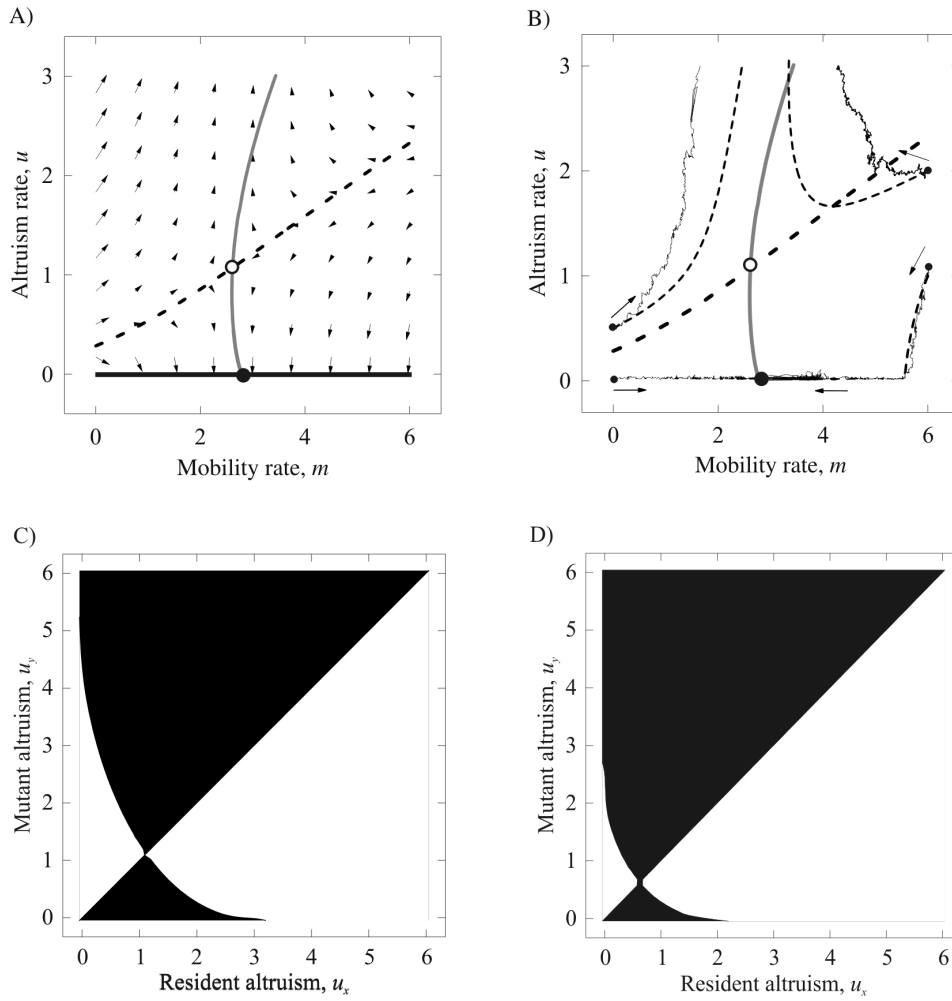


Figure 3. Coevolution of altruism and mobility with decelerating costs of altruism. A, The adaptive dynamics of altruism are bistable. For any mobility rate, with an initial value of altruism below a threshold, the evolutionary dynamics converge toward selfishness, whereas above the threshold, an evolution toward more altruism takes place. Plain gray curve: attractive mobility isocline. Dashed black curve: repelling altruism isocline. Plain black curve: attractive altruism isocline. Arrows: selection gradients. Open circle: repelling singularity. Close circle: attractive singularity. Parameters: $\gamma = 0.5$, $\kappa = 0.2$, $\nu = 0.05$. B, Average of ten stochastic simulations at four different initial conditions (continuous curve) and the deterministic predictions (dashed curves). Mutation parameters $k = 0.01$, $\sigma = 0.01$. C, D, Pairwise invasibility plots of the adaptive dynamics of altruism evaluated at the ESS mobility rate in a selfish population. Selfishness can be invaded by large investments in altruism (dark area), but low costs of mobility increase the threshold for altruism to invade. C. Same parameters as in B. C. Same parameters as in B, except $\nu = 0.1$. Other parameters as in fig. 2.

This pattern can be understood from the selective pressures that operate on m , as given by equation (6) and explained in fig. 1 and Appendix D. Equation (6) shows that local aggregation and the altruism rate have opposite effects on the intensity of the selective pressure to open space. Furthermore, local aggregation itself depends on the altruism rate, which sets an indirect effect of the

latter on this selective pressure. At extremely low values of m , the dependency of local aggregation on u is weak. Therefore, as u increases, its direct, negative effect predominates and m^* tends to decrease. Over a range of larger u values, local aggregation rises rapidly with u , so that the indirect effect of u dominates over its direct effect: more mobility is selected for. As u becomes very large, the case of an accelerating cost of altruism causes a substantial reduction in natality, hence a decrease of local aggregation. Therefore, a larger value of u leads to the evolution of less mobility through both direct and indirect effects on local saturation.

ADAPTIVE CO-EVOLUTION OF ALTRUISM AND MOBILITY

We now consider the joint adaptive dynamics of mobility and altruism. Our study of evolutionary trajectories develops from the model described by the canonical equation (1). In general, the two isoclines calculated from this equation cross at a single attractive and evolutionarily stable singularity (ESS) of the co-adaptive dynamics, denoted by (u^*, m^*) . The main conclusions of our analysis are tested against numerical simulations of an individual-based model that avoid all approximations assumed by the canonical equation (Appendix A).

Origin of altruism

To investigate conditions under which altruism can evolve from a purely selfish state, we use our model under the assumption of a decelerating cost of altruism. Altruism is indeed under the most stringent conditions to appear in species characterized by decelerating costs (Le Galliard et al. 2003). Also, in agreement with the classical empirical view, we assume that the selfish, ancestral state typically involves highly mobile individuals. Starting from selfishness associated with high mobility, the co-adaptive dynamics involves a first phase during which mobility decreases toward the critical value m^* given by equation (11) (see figs. 3A, B). The point $(m^*, 0)$ in the trait space is a halt for the deterministic dynamics predicted by equation (1). However, the stochasticity of the underlying individual process generates a different pattern. In a population where mutations may be large occasionally, mutants characterized by a large degree of altruism will eventually arise by chance, and displace the selfish resident (figs. 3C, D). Therefore, the evolutionary trajectory will sooner or later take off from the point $(m^*, 0)$. It can be seen numerically that the threshold on u increases as m^* increases. According to equation (10), this means that the waiting time for altruism to evolve is determined by the cost of mobility, habitat connectivity, and the intrinsic birth rate (in addition to the characteristics of the mutation process: mutation rate and mutation step variance, see fig. 7B in Le Galliard et al. 2003). The waiting time is shorter as the cost of mobility or habitat connectivity increases, or in species with a smaller birth rate (figs. 3C, D).

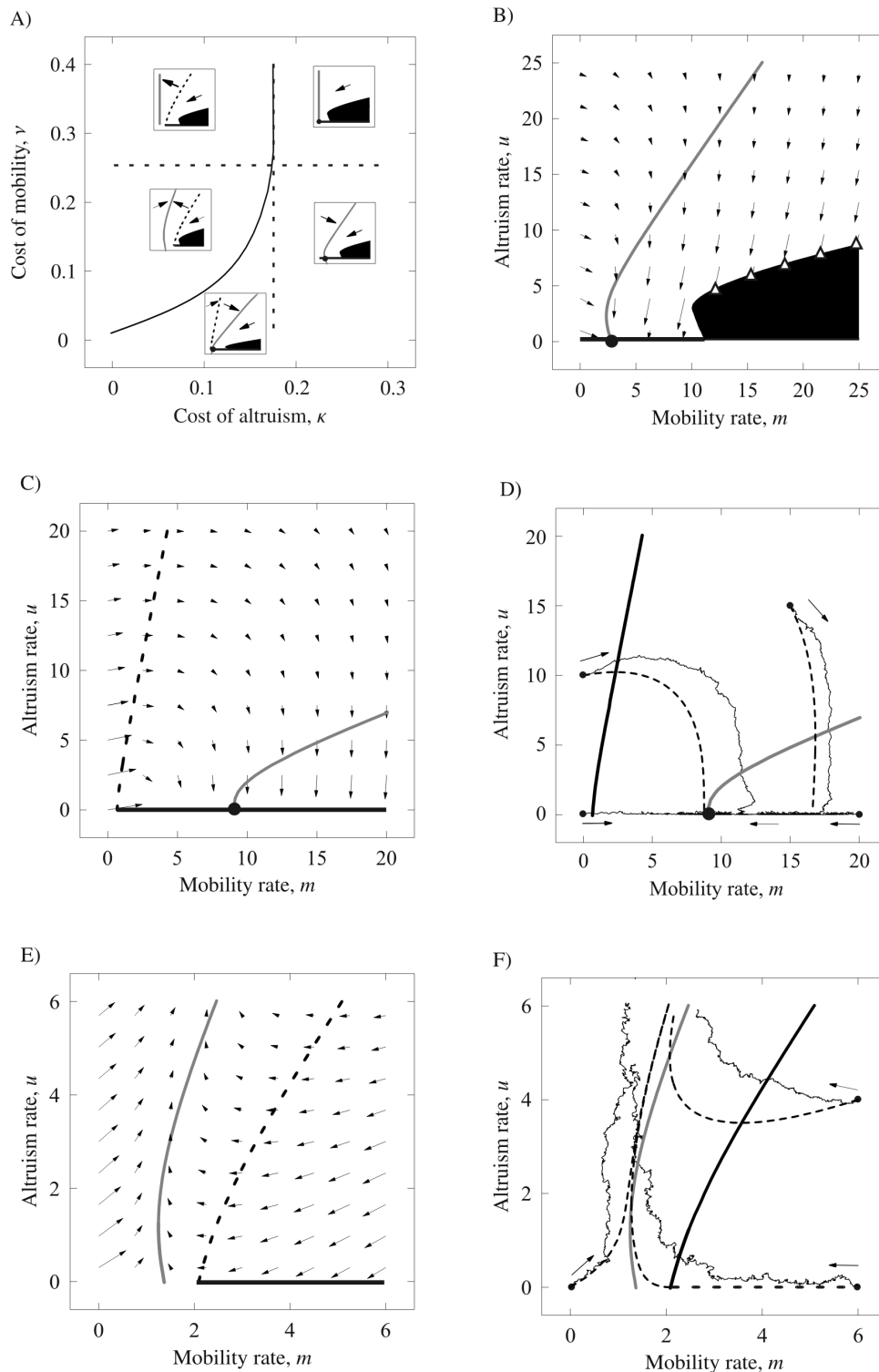


Figure 4. Coevolution of altruism and mobility with a linear cost of altruism. A, Classification of the adaptive dynamics according to the costs parameters κ and v . Insets show the relative positions of the altruism (dashed) and mobility (gray) isoclines, the direction of evolution (arrows) and the population extinction domain (dark). In B-D, close circles indicate attractive ESSs. In D and F, small circles indicate ancestral states, and arrows give the direction of evolution. B, Convergence to selfishness under high cost sensitivity to altruism, $\kappa > \phi(1-\phi)$. Evolutionary suicide (triangles) can be observed when adaptive trajectories collide with the population extinction

boundary. This occurs when ancestral mobility is low and altruism is high, or when ancestral mobility is high and altruism is low. Parameter values: $\kappa = 0.25$, $\nu = 0.05$. C, Convergence to selfishness under low cost sensitivity to altruism, $\kappa < \phi(1 - \phi)$, and low costs of mobility. The evolutionary change in low mobility ancestors involves first higher altruism together with increased mobility, until high mobility sets the stage for the secondary loss of altruism. Parameter values: $\kappa = 0.15$, $\nu = 0.01$. D, Stochastic trajectories. Parameter values as in C. E, Divergence to more altruism under low cost sensitivity to altruism, $\kappa < \phi(1 - \phi)$, and high costs of mobility. Selection against mobility drives the divergence toward more altruism. Once altruism rises, mobility can increase secondarily, unless the physiological cost of mobility is too strong (i.e., $\nu > \phi$). For initial combinations of high mobility and low altruism, evolutionary suicide can occur. Parameter values: $\kappa = 0.1$, $\nu = 0.1$. F, Stochastic trajectories. Average of ten stochastic simulations (continuous curve), and deterministic approximation (dashed curves). Parameter values as in E. Mutation parameters for (D) and (F): $k = 0.01$; $\sigma = 0.05$ (D), $\sigma = 0.01$ (F). Other parameter values as in fig. 2.

Only in the limiting case of a linear pattern of altruism cost may selfishness be permanently uninvadable (fig. 4A). This occurs when the altruism cost parameter κ is large (fig. 4B), or when κ is small and the mobility cost ν is small too (figs. 4C, 4D). In this case, altruism may initially rise through small mutational steps provided that the ancestral state is not too mobile. Yet the trajectory of altruism evolution eventually reverts, heads back to the selfish state and homes in at the mobility ESS m^* , where no small or large mutation can invade (results not shown). In contrast, if κ is small and ν is large enough, selfishness is readily displaced by altruism even through infinitesimal mutations, as a result of selection for lower mobility (figs. 4E, F). Thus, the cost of mobility has a major impact on the origin of altruism, either determining whether the displacement of selfishness is possible (linear costs of altruism), or the timescale over which the evolution of altruism develops (decelerating costs of altruism).

Evolutionary dynamics of social traits

Once the evolutionary rise of altruism from a selfish and highly mobile ancestor is initiated, the assumption of an accelerating cost of altruism becomes more realistic. Then all possible evolutionary dynamics unfold along a continuum bounded by two archetypal templates, each involving two distinctive evolutionary phases. One template corresponds to species with a slowly accelerating cost of altruism (low κ and γ close to 1). Then the first phase is characterized by the evolution of less mobility while altruism shows little change; at the same time, local aggregation is enhanced (figs. 5A, B, C). During the second phase, altruism rises along with some increase in mobility (fig. 5C). How this second phase ends depends upon the cost of mobility. In the case of a high cost of mobility, the evolutionary trajectory simply heads to the ESS (which is a stable node equilibrium). In the case of a moderate cost of mobility, the trajectory tends to spiral around the ESS (which is a stable focus equilibrium in this case, figs. 5A, B). The eco-evolutionary feedback causes the level of local

aggregation to parallel the damping oscillations of the adaptive traits. The ES altruism rate assumes higher values in relation with a larger cost of mobility. Under this pattern, evolutionary suicide can be observed when the evolution toward selfishness at high mobility causes convergence to the extinction boundary (fig. 5B).

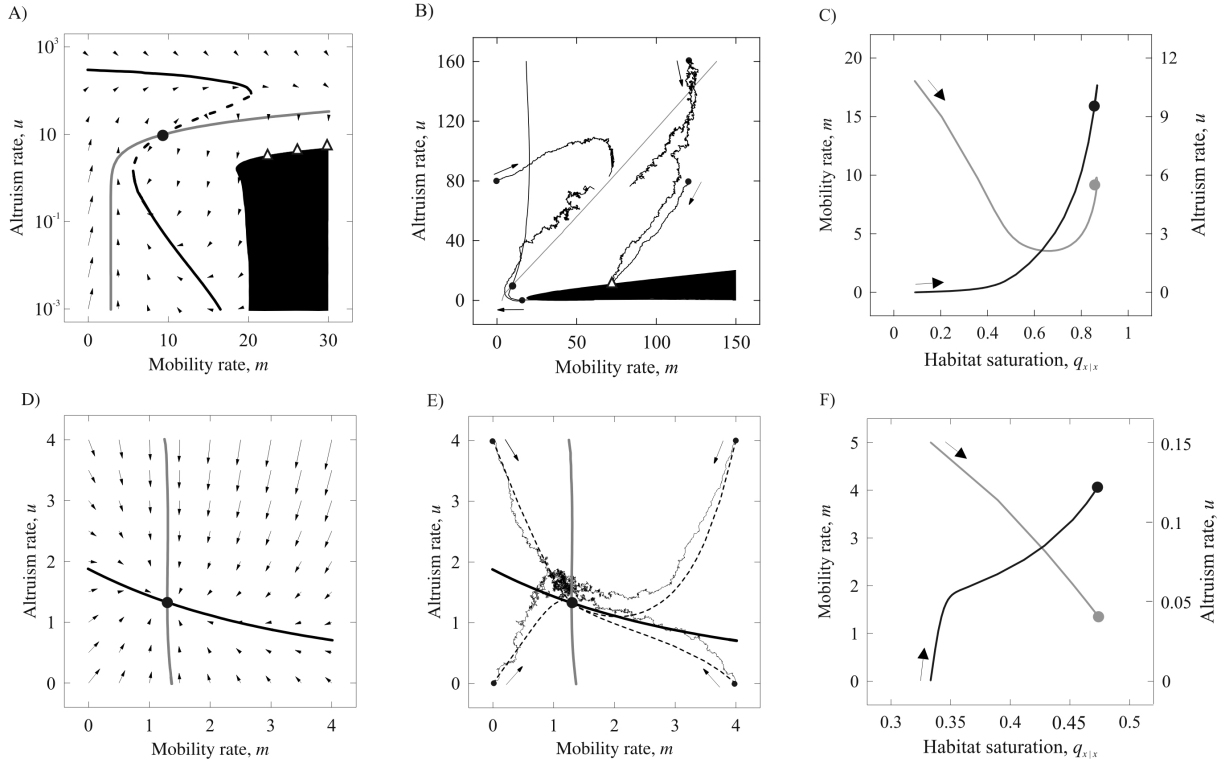


Figure 5. Coevolution of altruism and mobility with an accelerating cost of altruism. In all panels, close circles indicate attractive ESSs, arrows give the direction of evolution. In A and B, dark areas indicate population extinction. A, Convergence to a stable focus under slowly accelerating costs of altruism and intermediate costs of mobility. Parameter values: $\gamma = 1.2$, $\kappa = 0.05$, $\nu = 0.05$. B, Stochastic trajectories. Trajectories differ quantitatively from the deterministic approximation, but remain qualitatively similar. Stochasticity due to the finite population size and the randomness of mutational steps induces contingency: starting from the same mobile, altruistic ancestor, trajectories can either converge to the focus or collide with the extinction boundary (triangle). C, Relationship between mobility, altruism and habitat saturation (local aggregation) in the course of adaptive evolution. Mobility converges non monotonically to the stable focus (gray curve). Altruism remains at low levels as habitat saturation increases, and takes off secondarily (black curve). Parameter values as in A. D, Convergence to a stable node under rapidly accelerating costs of altruism. Parameter values: $\gamma = 2$, $\kappa = 0.05$, $\nu = 0.1$. E, Stochastic trajectories. Parameter values as in D. F, Relationship between mobility, altruism and habitat saturation during adaptive changes. Mobility converges monotonically to the stable node (gray curve). The evolution of altruism involves a first phase of increase while habitat saturation remains low, and increases more secondarily along with habitat saturation (black curve). Parameter values as in D, except $\kappa = 0.5$. Mutation parameters for stochastic trajectories: $k = 0.01$ and $\sigma = 0.01$. Other parameter values as in fig. 2.

The other dynamical template is specific of species with rapidly accelerating costs of altruism (figs. 5E, F). During the first phase of the evolutionary dynamics, the degree of altruism rises while mobility and the level of local aggregation remain essentially constant. The second phase drives the system to the ESS. It is characterized by a marked decrease in mobility, possibly along with a further increase in altruism, while local aggregation is enhanced significantly (fig. 5F). In this scenario, the ES altruism rate is usually low.

Adaptive patterns of altruism and mobility

Variations in the model parameters cause the joint ESS (m^* , u^*) to vary. The result is a correlation curve between u^* and m^* that represents the adaptive pattern of trait covariation in response to some underlying physiological, life-history, or environmental change. Here we analyze the covariation of u^* and m^* in species characterized by accelerating costs of altruism. More specifically, we analyze the correlation patterns obtained in response to life-history variation (i.e. on birth and death rates), and variation in constraints on mobility (i.e. in n and v). These patterns make predictions that could be tested empirically by comparing different populations of the same species (e.g. sharing the same life history, but differing in habitat structure), or different species (e.g. sharing the same type of habitat but differing in life-history traits). We focus on the following issues: When should we expect a negative correlation (or trade-off) to emerge between selected altruism and mobility? Are positive correlations or non-monotonic relationships possible, and which type of underlying changes would be sufficient to produce them?

The intrinsic birth rate b influences the evolution of mobility and altruism via an effect on habitat saturation (Appendix D). As b increases, local aggregation increases, which selects for more mobility and more altruism. Yet the adaptive response of mobility has the secondary effect of opposing the rise of local aggregation, thus selecting for less altruism. The net result can be documented by means of numerical simulations (fig. 6A): u^* decreases while m^* increases among more fecund species. However, the effect is significant only at low values of b , and in species incurring a low cost of altruism (small κ). Thus, from an empirical point of view, we should expect little effect of fertility to be detectable in the relationship between altruism and mobility at evolutionary equilibrium.

The intrinsic death rate d affects directly both local aggregation and relatedness. Increasing d reduces local aggregation, thus selecting for less mobility and less altruism. However, the former effect may be offset by a direct, positive impact of d on the intensity of the selective pressure for mobility (cf. eq. [6]); also, the latter effect may be softened by the non-monotonicity of the relationship between d and relatedness (cf. eq. [8]). Again, numerical simulations are needed to predict the net effect. Figure 6B displays the general pattern: a negative correlation between u^* and m^* , such that less altruism and more mobility occur at evolutionary equilibrium in long-lived species (smaller

d). However, as for the result of a change in fertility, the effect of mortality variation is significant only in species incurring a low cost of altruism.

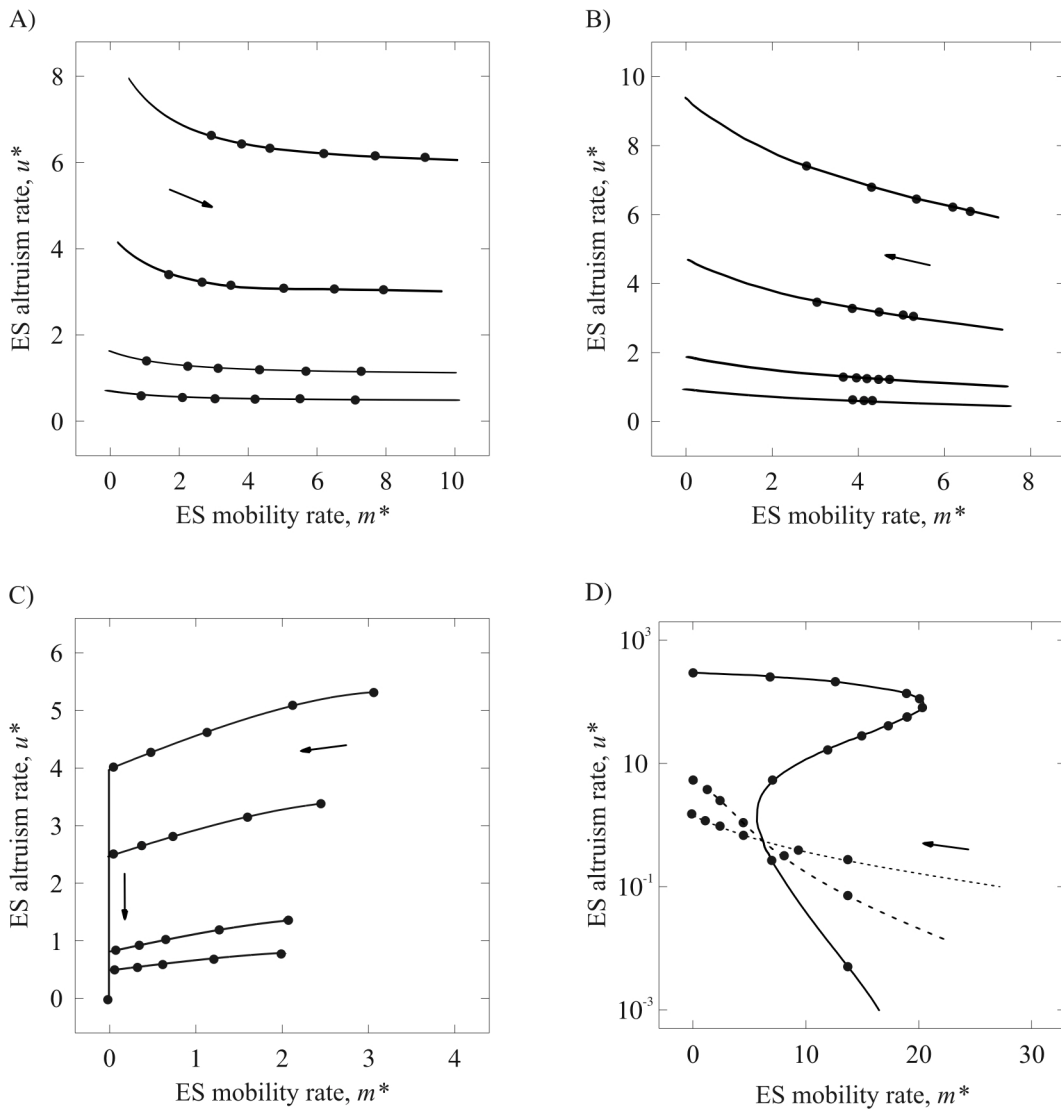


Figure 6. Adaptive correlations between altruism and mobility under accelerating costs of altruism. Arrows indicate the effect of increasing the underlying parameter, and dots correspond to specific values of the parameter. A, Effect of variation in the birth rate, b . The effect is displayed at different values of the cost parameter κ . Parameter values: $\gamma = 2$, $\nu = 0.1$. B, Effect of variation in the death rate, d . The effect is displayed at different values of the cost parameter κ . Parameters: $\gamma = 2$, $\nu = 0.1$, $b = 6$. In A and B, $\kappa = 0.01$, $\kappa = 0.02$, $\kappa = 0.05$, $\kappa = 0.1$ from top to bottom. C, Effect of habitat connectivity, n . The effect is displayed at different values of the cost parameter κ . Parameter values: $\gamma = 2.5$, $\nu = 0.1$; $\kappa = 0.005$, $\kappa = 0.01$, $\kappa = 0.05$, $\kappa = 0.1$ from top to bottom. D, Effect of the cost of mobility, ν . The effect is displayed at three different levels of cost acceleration: $\gamma = 1.2$ (plain curve), $\gamma = 1.5$ (dashed curve), and $\gamma = 2$ (dotted curve). Parameter values: $\kappa = 0.05$. Other parameters as in fig. 2.

Variation in n or v may reflect different environmental constraints on individual mobility. As habitat connectivity n increases, selection for altruism becomes weaker (cf. eq. [7]), as well as selection for mobility. The former effect results from a decrease in habitat saturation when habitat connectivity increases all else being equal, which impacts negatively on the selective pressure to open space among more mobile mutants (cf. eq.[6]). These changes produce a positive correlation between altruism and mobility at evolutionary equilibrium (fig. 6C). In a triangular habitat ($n = 3$), selected altruism and mobility are maximal, whereas with a mean-field interaction ($n \rightarrow \infty$) adaptation always leads to a selfish, sessile behavior.

Increasing the cost of mobility v selects directly for less mobility, which increases mutant relatedness, thereby promoting the evolution of more altruism. In a range of very low values of v , mobility can evolve to high levels, which leads to low relatedness and therefore hampers the evolution of altruism. The resulting pattern is a negative, yet rather flat correlation between selected altruism and mobility (fig. 6D, *nota bene*: the altruism rate is shown on a log-scale). At very high values of v , mobility evolves to low levels, begetting high relatedness and the evolution of high altruism rate. Again the resulting pattern is flat, because the adaptive increase in u in response to increasing v is severely limited by the altruism cost acceleration. If the cost of altruism is slowly accelerating, however, the pattern is reverted over a range of intermediate values of v . Promoting the evolution of more altruism by increasing the cost of mobility then causes a marked increase of local aggregation. In turn, higher local saturation exerts a selective pressure for mobility which exceeds the accrued cost of mobility. Thus, the selective interaction between altruism and mobility favors more altruism along with more mobility (fig. 6D).

DISCUSSION

We have used the notion of spatial invasion fitness to model the adaptive dynamics of altruism and individual mobility, thereby setting up a unifying framework for the evolution of social traits. Our analysis backs up the empirical view that habitat saturation is a critical node of the selective interaction between the two traits (Emlen 1982; Koenig et al. 1992; Lambin et al. 2001). The “habitat saturation hypothesis” states that constraints on independent breeding favors philopatry and helping, and has provided a fruitful concept for approaching the evolution of social traits from the empirical end. Our theory leads to reexamining the basis and scope of this hypothesis, and clarifies the selective pathways whereby habitat saturation influences and becomes influenced by the evolution of social traits. Empirical analyses and recent models have predicted correlative patterns of altruism and mobility in response to different ecological constraints or demographic profiles. This study allows us to recast these various predictions in a single theoretical framework and to uncover alternatives that will hopefully stimulate further empirical research.

The notion of spatial invasion fitness

Defining invasion fitness for spatial ecologies is no trivial matter (Ferrière and Le Galliard 2001). Starting from demographic and behavioral processes operating at the individual level and locally between close neighbors, the invasion exponent of a simple system of correlation equations for the dynamics of a mutant population provides a tractable solution (van Baalen 2000a). The notion of spatial invasion fitness allows one to derive an explicit relationship between distinct components of selection on the one hand, and the characteristics of the individuals and their interactions on the other. Numerical simulations of individual-based models confirm that the spatial invasion fitness can predict qualitatively, and often quantitatively, the dynamics of the stochastic mutation-selection process.

The mathematical derivation of spatial invasion fitness proceeds by averaging over space the transition rates of pairs. This amounts to looking at the local structure of the mutant population as homogeneously replicated across the whole (infinite) lattice. The non-homogeneous distribution of the pairs containing mutants, induced by the finite size of the mutant population and the non-typical clustering pattern that may develop at the earliest stage of invasion, might require to incorporate correction terms (van Baalen 2000a). There is an interesting parallel to be drawn with the theory of evolutionary games in continuous space. In this context, the initial clustering of mutants requires to define fitness not from space averages of individual traits, but as the speed at which the front of a mutant cluster moves forward and propagates mutants through (Ellner et al. 1998; Ferrière and Michod 1996).

The habitat saturation hypothesis

Habitat saturation has long been put forward as a key hypothesis to explain the evolution of social behavior. The “habitat saturation hypothesis” was originally intended to explain the evolution of cooperative breeding in birds (Brown 1978; Emlen 1982; Koenig et al. 1992), and is now underlying theories for the evolution of delayed dispersal (Kokko and Lundberg 2001; Perrin and Lehmann 2001) and reproductive skew models of animal societies (Reeve et al. 1998). The general view is that habitat saturation drives the evolution of philopatry and altruism. By offering an explicit mathematical framework to deal with the interplay of social behavior and population dynamics, our analysis uncovers the whole complexity of the selective pathways whereby habitat saturation is involved in the evolution of social traits.

The habitat saturation hypothesis assumes that sociality evolves in two steps, which requires first the evolution of philopatry, and then the evolution of cooperation (Emlen 1997; Helms Cahan et al. 2002). As sites available for immigration and reproduction are rarely available, individuals competing for such vacancies are expected to incur strong costs of dispersal due to floating and queuing before gaining access to a territory. Thus, habitat saturation is predicted to favor delayed dispersal, conditions under which the cost of local crowding can be ameliorated by cooperating rather

than simply competing (Kokko and Lundberg 2001; Pen and Weissing 2000). What causes habitat saturation in the first place? The scenario of 'ecological constraints' asserts that environmental factors constrain mobility to low levels, hence local crowding. Such environmental factors may involve habitat structure, physical predicaments to movement, or a large physiological cost of moving (Jarvis et al. 1994; Russell 2001). The 'life-history hypothesis' assumes that habitat saturation is more likely to occur in species with low mortality, in which the turnover of breeding sites is assumed to be slow (Arnold and Owens 1998).

Our analysis highlights a rather different evolutionary scenario. First, we show that there are two distinct components to habitat saturation, which play complementary roles in the evolution of social traits. "Local aggregation" ($\bar{q}_{x|0}$) measures habitat saturation *around individuals*, in line with the original definition by (Emlen 1982) of habitat saturation measuring the proportion of neighboring territories available for dispersal and reproduction. "Local contention" ($\bar{q}_{x|0}$) measures habitat saturation *around vacant sites*; it is oppositely related with the degree of clustering ($\bar{q}_{0|0}$), i.e. how isolated groups of neighbors are. Like in the ecological constraints model, a high cost of dispersal and low habitat connectivity are important determinants of the evolution of local aggregation and local contention. However, our model emphasizes that habitat saturation is a consequence of the evolution of low mobility, rather than the primary selective factor for that evolution. In other words, philopatry is a direct adaptive response to environmental constraints and physiological costs, rather than to habitat saturation.

In fact, neither the maximization of local aggregation nor that of local contention appear to be critical features of the co-evolutionary process. In single-trait evolution, however, the mobility rate evolves along with maximizing local contention—a prediction qualitatively similar to the finding that the number of competitors for territories (the limited resource) can be maximized by the evolution of habitat choice strategies (Kokko et al. 2001). Yet this remarkable maximization principle disappears when altruism evolves concomitantly. Furthermore, the evolution of low mobility and strong aggregation does not appear as an obligate evolutionary step toward sociality. Our model unravels the alternative scenario of a population initiated in the selfish-highly mobile ancestral state that first evolves a substantial degree of altruism while aggregation remains low; adaptive evolution secondarily favors less mobility, which may lead to strong aggregation. Such a scenario is expected when the cost of altruism is rapidly accelerating and the cost of mobility is low, in which case the altruism rate eventually selected should be low.

One key feature of our theory is that habitat saturation is not treated as a fixed parameter, but as a pair of dynamical variables that close the eco-evolutionary feedback loops entangling altruism and mobility. Local aggregation and local contention are, respectively, the pivotal factors of the two eco-evolutionary feedback loops cycling through altruism, and mobility. When both traits co-evolve, local

aggregation turns out to be the dominant mediator of the selective interaction between both traits. Local aggregation responds antagonistically to evolutionary change of altruism and mobility, which in return affects the selective pressures acting on both traits. Such essential evolutionary feedbacks and selective interactions have been ignored in most previous models of social evolution (but see Kokko and Lundberg 2001).

Correlative patterns of social traits

Habitat saturation models predict that, at evolutionary equilibrium, (i) altruism and mobility should correlate negatively, and (ii) more altruism, hence less mobility, should be observed in populations characterized by stronger constraints on dispersal or lower mortality. Our theory, however, shows that the evolutionary outcome cannot be predicted solely from the effect of habitat saturation and its hypothesized underlying ecological or demographic determinants. This is because (i) habitat saturation is a dynamic variable entangled in the eco-evolutionary feedbacks involving altruism and mobility; (ii) the adaptive change of either trait also has a direct influence on the selection gradient of the other trait; and (iii) life-history traits (birth and death rates) have effects on the evolutionary dynamics independently of their influence on habitat saturation.

As a consequence, we find that selected altruism correlates positively with the cost of mobility and negatively with habitat connectivity; and we predict a positive correlation between selected altruism and selected mobility in response to changes in habitat connectivity or in the cost of mobility within a range that excludes extremely low and high values. The finding that low habitat connectivity or high cost of mobility selects for more altruism in our model suggests that comparative studies should find consistent relationships between physiological and habitat constraints on dispersal, and levels of cooperation. Some recent intra-specific comparisons in vertebrates (birds, mammals) have reported a negative effect of landscape connectivity on investment in helping (e.g., Russell 2001; Spinks et al. 2000). Also, in the group of African mole rats (Bathyergidae), cooperative breeding has been linked to the scarce and heterogeneous distribution of resources in arid landscapes, which results in high costs of mobility (Jarvis et al. 1994). In agreement with our findings, the comparative analysis of sociality (as measured by reproduction skew) yields a rough correlation between costs of mobility and cooperation, with the eusocial species culminating in correspondence with the most arid environment (Faulkes and Bennett 2001; Jarvis et al. 1994).

Empirical data relating altruism and mobility are scant, especially because quantitative assessments of dispersal abilities in social and asocial species are difficult to obtain. Phylogenetic comparative analyses of social traits in birds are still insufficient to test our prediction that more cooperation, as an adaptive response to ecological constraints, could be associated with higher levels of mobility. However, the observation that the correlation patterns between dispersal and cooperative breeding depends on the taxonomic level at which the analysis is performed (Arnold and Owens 1999) strongly warrants further analyses. The occurrence of a dispersing morph in captive colonies of the

eusocial naked mole rat *Heterocephalus glaber* (O'Riain et al. 1996) could also be the manifestation of an adaptive association between strong altruism and a special ability to disperse. The fact that this dispersing morph participates little in cooperative activities in their new colonies further suggests that constraints on mobility might generate disruptive selective pressures on the social traits, leading to evolutionary branching and a stable genetic polymorphism of selfish-mobile and altruistic-sessile phenotypes. Although the evolutionary branching of social traits was not observed in our study, stable coexistence of different social strategies was first hypothesized by van Baalen and Rand (1998), and has been observed in cellular automaton models involving regular lattices (den Dulk and Brinkers 2000; Koella 2000).

We predict each life-history trait (death rate and intrinsic birth rate) to have, in isolation, little influence on the selected combination of altruism and mobility. On the one hand, we expect an increase in the intrinsic birth rate to drive a decrease in altruism and an increase in mobility, although the predicted pattern is fairly flat and probably difficult to detect in real data. On the other hand, more altruism is expected to evolve among species with the highest mortality rates. Comparative analyses in birds have attempted to relate social behavior with nestling mortality and adult mortality (Hatchwell and Komdeur 2000). It was found that nestling mortality had no detectable influence on the distribution of social characters (Poiani and Pagel 1997), in agreement with our prediction that the intrinsic birth rate (which can be seen as combining reproductive potential and offspring mortality) is likely to have undetectable effects. The analysis of the whole available phylogeny of birds yields a pattern of stronger cooperation along with lower adult mortality (Arnold and Owens 1998). This empirical pattern supports our finding of an effect of the death rate, but opposes the direction of the effect that we predict. The pattern could be recovered in our model, however, under the assumption that lower mortality trades-off across species with lower natality, which is known to occur in birds (Arnold and Owens 1998). This suggests that, in general, covariation of life-history traits are important to understand adaptive patterns of social traits.

Co-evolution versus single-trait evolution

The study of correlative patterns was made possible by considering the joint adaptive evolution of social traits. The fact that adaptive evolution takes place in a two-dimensional trait space has indeed major consequences on the evolutionary trajectory of either trait. One basic structural reason is that evolutionary trajectories on a more-than-one dimensional adaptive landscape can by-pass fitness valleys which would block the population if only one dimension was available to evolutionary change.

The dimensionality of the trait space has a major influence on the evolutionary onset of altruism under the assumption of a weak linear cost of altruism. With only the altruism trait evolving, a selfish and mobile ancestor is always uninvadable (Le Galliard et al. 2003). In contrast, assuming that mobility can co-evolve, selfishness can be readily displaced, even through infinitesimal mutations, provided that the cost of mobility is high enough. When the cost of mobility is low, altruism is

expected to evolve as a single trait in selfish and poorly mobile ancestors, whereas traits co-evolution drives an adaptive rise of mobility, which prevents altruism to gain a permanent foothold in the population. Therefore, evolutionary constraints on mobility (as opposed to mere low mobility) are critical for altruism to evolve and maintain.

The coevolutionary dynamics also have considerable impact on the evolution of mobility. As a single trait, the evolution of mobility is driven by the selective pressure to open space for mutants during invasion, and opposed by physiological costs. The strength of the former is directly and indirectly (through local aggregation) modulated by the degree of altruism. First, more altruism weakens the positive selective pressure to open space for mutants, which emphasizes that the so-called benefits of philopatry operate against the evolution of dispersal (Perrin and Goudet 2001; Stacey and Ligon 1991). Second, and less intuitively, altruism influences the spatial structure of the population, by increasing local aggregation, which selects for more mobility. When both traits evolve, the selective pressure induced by the benefits of philopatry will be opposed by the enhanced aggregation experienced by more altruistic phenotypes, which in turn favors higher mobility rates. Typically, this synergistic selective interaction between altruism and mobility impacts species characterized by slowly accelerating costs of altruism and moderate costs of mobility (see fig. 5A). In such species, mobility selected through the coevolutionary process can be considerably higher than that predicted in a selfish species, and considerably lower than that predicted in a highly altruistic species. Thus, neglecting the propensity for altruism to co-evolve with mobility can lead to dramatically underestimate or overestimate the level of mobility that can be favored by natural selection.

The dimensionality of the trait space also has a marked effect on the evolutionary dynamics of altruism when the physiological cost is slowly accelerating. In this case, intermediate degrees of altruism are evolutionarily unstable when the altruism is the only trait evolving. In the co-evolutionary scenario, the strong evolutionary attractiveness of the mobility rate that maximizes fitness for each of these altruism trait values suffices to turn one mobility-altruism phenotype into an attractive strategy. This ESS still bears the footprint of the altruism one-dimensional instability in the fact that it behaves as a focus to evolutionary trajectories that spiral around it. This geometrical property has consequences when interpreting variation in social behavior across populations or species. Even if populations originate in the same ancestral state and share the same physiological, demographic and ecological features, they may present radically different suites of social traits should they be observed at different epochs of their evolutionary history. The spiraling dynamics around an ESS entails indeed that the same trajectory will display consecutively high and low levels of mobility and altruism in all four possible combinations. This is yet one more complication that could inform comparative analyses confronting the lack of regularities in patterns of social traits and potential correlates (Arnold and Owens 1999).

Concluding remarks

The “habitat saturation hypothesis”, the “ecological constraint model”, the “life history hypothesis” represent multiple attempts at singling out simple and general factors of social evolution. Each approach has contributed to a better understanding of the evolution of sociality. By integrating some of their key ingredients, our model leads to the conclusion that no simple determinism should be expected for the origin of social behavior or the evolution of strong cooperative interaction. This emphasizes that inferences from empirical or theoretical studies based on univariate analyses are likely to be hindered by the very complexity and diversity of factors involved in the evolution of social traits (Crespi and Choe 1997). However, some general principles apply: physiological or ecological constraints on mobility are essential to explain the origin of altruism; all evolutionary trajectories can be related to only two archetypes, contrasting routes to sociality; adaptive patterns of covariation among social traits could be understood in response to multivariate changes.

Eco-evolutionary feedbacks and selective interactions are key to the co-evolutionary dynamics of social traits. Taking them into account allows us to address one of the currently most debated issue in the biology of social behavior: whether the high relatedness predicted by Hamilton’s original kin selection theory (1964), and found between interacting individuals of several social species, is the direct consequence of physiological or ecological constraints on dispersal, or that of more involved mechanisms of active assortment, involving communication, cognition, and habitat choice (Hamilton 1975). We offer the alternative views that in some social systems, both limited mobility and strong altruism can form the *joint* adaptive response to a complex web of multiple, interacting selective mechanisms; and that in other social systems, the dynamical structure of the population can cause evolution to promote high mobility without compromising the likelihood of passive assortments between altruistic individuals.

These conclusions are illustrative of a wealth of evolutionary dynamics structurally rooted in the multi-dimensionality of the adaptive trait space. Most evolutionary modeling of quantitative characters has concentrated on single traits so far. Hopefully this study will foster the appreciation that multidimensional adaptive evolution can proceed in radically different directions, and will pave the way toward the incorporation of important genetic factors (like genetic correlations between traits or trait-dependent genetic variation) into theories of phenotypic evolution. Multidimensional models of evolutionary dynamics should eventually allow one to make more robust and testable predictions, and to assess the scope of adaptive factors across broader ranges of biological phenomena.

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APPENDIX A

We simulate the evolutionary process on a random lattice with periodic boundaries and 900 sites. The simulation starts by distributing individuals of an ancestral phenotype randomly over half of the lattice. Mutations generate variability with a probability k per birth event. The mutant phenotype is obtained by adding a mutation effect drawn randomly from a normal probability distribution, with zero mean and mutational variance σ^2 . When a negative value is produced, the mutant phenotype is reset to zero. We use the minimal process method to simulate the time-continuous stochastic dynamics of the population (Gillespie 1976).

APPENDIX B

Notations of the models are defined in Appendix E. We consider a random, regular network with a large number of homogeneous sites, and a dimorphic population of mutants, called y , and residents, denoted by x . A mutant located at a site z on the lattice is affected by birth, death and movement, respectively

$$\begin{aligned} b_y(z) &= (b + \sum_{j=(x,y)} \phi u_j n_{j|y}(z) - C(u_y, m_y)) \phi n_{o|y}(z), \\ d_y(z) &= d, \\ m_y(z) &= m \phi n_{o|y}(z). \end{aligned} \tag{B1}$$

To derive the mean path of the mutant population size, we average the birth and death rates described in equation (B1) over all sites of the lattice occupied by the mutant, which gives

$$\frac{dN_y}{dt} = ((b - C(u_y, m_y)) \phi n_{o|y} - d) N_y + \sum_{j=(x,y)} \phi^2 u_j \sum_z n_{j|y}(z) n_{o|y}(z), \tag{B2a}$$

where $n_{o|y}$ is the average of $n_{o|y}(z)$ over the lattice. The third expression in (B2a) is a cross-product between random variables describing alternative neighborhoods of a mutant individual. Assuming that sites are distributed according to a multinomial probability distribution law and that the neighbors of pairs of sites can be considered as independent (Morris 1997), this term simplifies in

$$\sum_z n_{j|y}(z) n_{o|y}(z) = N_y n(n-1) q_{j|y} q_{o|y}, \tag{B2b}$$

where $q_{k|y} = n_{k|y}/n$ is the average local frequency of type k sites neighboring a mutant. Then, the mean path of the mutant population size follows

$$\frac{dN_y}{dt} = \left((b + \sum_{j=(x,y)} (1-\phi)u_j q_{j|y} - C(u_y, m_y)) q_{0|y} - d \right) N_y = \lambda_y N_y. \quad (\text{B2c})$$

which involves the configurations of pairs of sites through $q_{k|y}$ terms.

We now derive the rates of three events affecting pairs. Following the notations given by van Baalen and Rand (1998), we call α_{ij} the average rate at which type i enters a pair $0j$ when $j \neq i$, β_i the average rate at which type i enters a pair $0i$, and δ_{ij} the average rate of loss of type i from ij pairs. We detail only the derivation of the third rate. In this case, a pair ij with site i located at z can change to a $0j$ pair by a dispersal event or by a death event with the per capita rate

$$\delta_{ij}(z) = d + m_i \phi n_{0|ij}(z). \quad (\text{B3a})$$

Averaging over the lattice leads to the average rate

$$\bar{\delta}_{ij} = \sum_{ij} \delta_{ij}(z) = (d + m_i \phi n_{0|ij}) N_{ij}, \quad (\text{B3b})$$

and assuming that $n_{k|ij} = (n-1)q_{k|i}$, gives

$$\bar{\delta}_{ij} = (d + m_i (1-\phi) q_{0|i}) N_{ij} = \delta_i N_{ij}, \quad (\text{B3c})$$

The second rate involves either a birth inside the pair, either a birth or a dispersal from a type i neighbor connected to the empty site of the pair, and is given by

$$\begin{aligned} \bar{\beta}_i = \beta_i N_{0i} = & (b + \sum_j u_j (1-\phi) q_{j|i} - C(u_i, m_i)) \phi N_{0i} \\ & (b + \sum_j u_j (1-\phi) q_{j|i} - C(u_i, m_i)) + m_i (1-\phi) q_{i|0} N_{0i}. \end{aligned} \quad (\text{B4})$$

The third rate involves the birth or dispersal of a type i neighbor connected to the empty site of the pair, and is given by

$$\bar{\alpha}_{ij} = \alpha_i N_{ij} = (b + \sum_j u_j (1-\phi) q_{j|i} - C(u_i, m_i)) + m_i (1-\phi) q_{i|0} N_{ij} = \alpha'_i q_{i|0} N_{ij}. \quad (\text{B5})$$

A closed dynamical system describing the pair dynamics is obtained by bookkeeping the three types of events using equations (B3c), (B4) and (B5)

$$\begin{aligned} \frac{dN_{0y}}{dt} &= (\alpha'_y q_{0|0} - \beta_y - \delta_y) N_{0y} + \delta_x N_{xy} + \delta_y N_{yy} \\ \frac{dN_{xy}}{dt} &= (\alpha_x + \alpha'_y q_{0|0}) N_{0y} - (\delta_x + \delta_y) N_{xy} \\ \frac{dN_{yy}}{dt} &= 2\beta_y N_{0y} - 2\delta_y N_{yy} \end{aligned} \quad (\text{B6})$$

APPENDIX C

In the case of a resident population, equilibria can be found using monomorphic versions of (B2c) and (B6). In general, the resident population converges to one stable equilibrium spatial structure $(\bar{q}_{x|x}, \bar{q}_{0|0})$. After (B2c), the non-trivial population equilibrium $\bar{q}_{x|x}$ satisfies a quadratic equation $((b + u_x(1 - \phi)\bar{q}_{x|x} - C(u_x, m_x))(1 - \bar{q}_{x|x}) - d = 0$, and after (B6), $\bar{q}_{0|0} = \alpha'_x / \delta_x$. If b is sufficiently larger than d , the resident population is non-viable when $\Delta < 0$, where Δ denotes the discriminant of the quadratic equation.

APPENDIX D

Let $\tilde{q}_{0|y}$, $\tilde{q}_{x|y}$ and $\tilde{q}_{y|y}$ denote the pseudo-equilibrium correlation structure of the mutant population during invasion. These terms are the steady states of (B6) when x is a resident type at ecological equilibrium and y is a rare mutant type, which gives

$$\begin{aligned} (\bar{\alpha}_x + \tilde{\alpha}'_y \bar{q}_{0|0}) \tilde{q}_{0|y} - (\tilde{\delta}_y + \bar{\delta}_x + \tilde{\lambda}_y) \tilde{q}_{x|y} &= 0 \\ 2\tilde{\beta}_y \tilde{q}_{0|y} - (2\tilde{\delta}_y + \tilde{\lambda}_y) \tilde{q}_{y|y} &= 0 \end{aligned} \quad (D1)$$

Noting that $\tilde{q}_{y|0} = 0$ when the mutant is rare, the non-linear system involves three unknowns ($\tilde{q}_{0|y}$, $\tilde{q}_{x|y}$ and $\tilde{q}_{y|y}$) and two equations, along with the constraint $\tilde{q}_{0|y} = 1 - \tilde{q}_{x|y} - \tilde{q}_{y|y}$. The non-linear system (D1) can be used to evaluate numerically the spatial invasion fitness defined by equation (5) in the main text.

A first-order Taylor expansion of the first coordinate of the spatial invasion fitness reads

$$s_x(x + \varepsilon) = s_x(x) + \varepsilon \left. \frac{\partial s_x(y)}{\partial y} \right|_{y=x} + o(\varepsilon). \quad (D2a)$$

For the degenerate mutant, $y = x$, we can solve analytically the non-linear system (B7). This yields the solutions $\tilde{q}_{0|y} = \bar{q}_{0|x}$, $\tilde{q}_{y|y} = \bar{q}_{y|y}$ after equation (8) in the text, and $s_x(y) = s_x(x) = 0$. For a slightly deviant mutant phenotype $u_y = u_x + \varepsilon$, then $\tilde{q}_{0|y} = \bar{q}_{0|x} + a\varepsilon$ and $\tilde{q}_{y|y} = \bar{q}_{y|y} + b\varepsilon$ where a measures the marginal variation of empty space in a mutant's neighborhood relative to a resident and b the marginal gain or loss of relatives. The first coordinate of the spatial invasion fitness then reads

$$s_x(x + \varepsilon) = \varepsilon \bar{q}_{0|x} \left((1 - \phi) \bar{q}_{y|y} - a \left((1 - \phi) u_x - \frac{d}{\bar{q}_{0|x}^2} \right) - \frac{C(u_y, m_x) - C(u_x, m_x)}{\varepsilon} \right). \quad (D2b)$$

We solved the system (B7) with the help of the computer package Mathematica (Wolfram 1991) to obtain symbolic expressions for a . Our numerical simulations showed that a terms are negligible, which leads to the equation (6) in the main text (see also Le Galliard et al. 2003).

We can also consider a slightly perturbed mobility phenotype, i.e., $m_y = m_x + \varepsilon$, $\tilde{q}_{\theta|y} = \bar{q}_{\theta|x} + a\varepsilon$ and $\tilde{q}_{y|y} = \bar{q}_{y|y} + b\varepsilon$. A first-order Taylor expansion of the second coordinate of the spatial invasion fitness then reads

$$s_x(x + \varepsilon) = \varepsilon \bar{q}_{\theta|x} \left(\left(\frac{d}{\bar{q}_{\theta|x}^2} - (1 - \phi)u_x \right) a - \frac{C(u_x, m_y) - C(u_x, m_x)}{\varepsilon} \right). \quad (D3)$$

Symbolic evaluation of the expression a in (D3) yielded a complicated formula indicating that a was affected directly by mobility, altruism rate, death rate, cost of mobility, and habitat connectivity, and also indirectly by the effects of all model parameters on the resident spatial statistics $\bar{q}_{x|x}$ and $\bar{q}_{\theta|\theta}$.

Therefore, we conducted numerical sensitivity analyses of the selection components over a large range of model input values to understand the details of the selective interactions. The general pattern found was that the a term was primarily sensitive to changes in mobility rates (with a negative feedback of m on this selection component), while the multiplicative bracketed term was primarily sensitive to changes in altruism rate, life history traits, and habitat structure through both direct and indirect effects mediated by habitat saturation $\bar{q}_{x|x}$ (see text and fig. 1 for detailed explanations of the direction of these effects).

APPENDIX E

Table E1. Parameter definitions.

Parameter	Definition
N	Total size of the network
n	Neighborhood size (habitat connectivity)
$\phi = 1/n$	Probability to draw a connection at random within a given neighborhood
b	Intrinsic per capita birth rate
d	Intrinsic per capita death rate
m	Intrinsic per capita mobility rate (<i>adaptive trait</i>)
u	Intrinsic per capita rate of investment in altruism, or altruism rate (<i>adaptive trait</i>)
$C(u, m)$	Cost of altruism and mobility impacting the birth rate
κ	Cost sensitivity to the altruism rate
γ	Cost acceleration to the altruism rate
ν	Cost sensitivity to the mobility rate
$n_{k i}(z)$	Number of sites k neighboring of a site i at location z (<i>random variable</i>)
$n_{k ij}(z)$	Number of sites k neighboring a site i located at z within a pair ij (<i>random variable</i>)
N_i	Number of sites in state i
N_{ij}	Number of pairs in state ij
$q_{i j}$	Local frequency of sites i neighboring a j site
$q_{i jk}$	Local frequency of state i sites neighboring a site j within a pair in state jk

Note: The subscripts i, j , and k indicate the state of a site of the lattice. The parameters under selection (altruism and mobility) have subscript x if they refer to a resident population and y if they refer to a mutant population.

CHAPITRE 4 – RELATIONS MERE A ENFANTS ET DISPERSION NATALE



“Overall, the available evidence in favour of kin competition influencing dispersal is little more than anecdotal, and moreover is restricted to vertebrates. As more data on the genetic structure of populations become available, a clearer picture may emerge. Despite the paucity of empirical evidence for kin competition, individuals in most species must experience some level of competition with their immediate relatives. However, the contribution of kin and global competition is undetermined in most cases.” X. Lambin, J. Aars & S. Piertney dans *Dispersal*. 2001. p. 119.

LES INTERACTIONS MERE A ENFANTS AFFECTENT LA DISPERSION NATALE CHEZ UN LEZARD

Jean-François Le Galliard, Régis Ferrière & Jean Clobert

RESUME

Les interactions entre apparentés génèrent des pressions de sélection fortes sur la dispersion. Récemment, une étude corrélative sur le lézard vivipare (*Lacerta vivipara*) a suggéré que la dispersion natale pouvait répondre de façon plastique aux interactions entre une mère et ses enfants. Ici, nous décrivons une expérience factorielle supportant cette observation. Deux traitements croisés ont été appliqués à des populations expérimentales du lézard vivipare : (i) présence versus absence de la mère, induisant une différence d'apparement dans le voisinage social des enfants, et (ii) densité haute ou faible, résultant dans deux niveaux d'abondance en congénères et modulant l'effet de la présence de la mère au niveau de l'apparement moyen de la population. La dispersion d'une même cohorte d'individus a été observée aux stades juvénile et sub-adulte. Nous avons trouvé une réponse de la dispersion natale au retrait de la mère dépendante du sexe pendant les deux stades. Pendant le stade juvénile, les filles ont dispersé plus en présence de leur mère, les fils n'étant pas affectés. Pendant le stade sub-adulte, les réponses des mâles et des femelles à la présence de la mère ont été opposées, les filles tendant à disperser plus en présence de la mère alors que les fils dispersaient moins. En plus, nous avons trouvé une relation négative entre la dispersion et la densité de la population au stade juvénile. Aucune interaction entre la densité et la présence de la mère n'a été détectée, suggérant que les réponses comportementales à l'apparement et à la densité sont déconnectées, et que l'apparement est évalué à une petite échelle sociale. Nous discutons le rôle de la compétition et de l'évitement de la consanguinité pour expliquer nos résultats.

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Mots-clés : dispersion natale, apparement, densité, lézard vivipare

MOTHER-OFFSPRING INTERACTIONS AFFECT NATAL DISPERSAL IN A LIZARD

Jean-François Le Galliard, Régis Ferrière & Jean Clobert

PAPER AND PUBLIC ABSTRACT

Interactions between relatives operate strong selective pressures on dispersal. Recently, a correlative study in the common lizard (*Lacerta vivipara*) suggested that natal dispersal might respond plastically to mother-offspring interactions. Here, we describe a factorial experiment supporting this observation. Two crossed treatments were applied to experimental patches of the common lizard: (i) presence versus absence of the mother, inducing a difference of kinship in offspring neighbourhoods; and (ii) high versus low patch density, resulting in two levels of conspecifics abundance and modulating the effect of mother presence on the average kinship within a patch. Dispersal of the same cohort of offspring was observed at the juvenile and yearling stages. We found a sex-dependent response of offspring dispersal to the removal of the mother at the two stages. During the juvenile stage, higher dispersal was found in females in the presence of the mother, with males unaffected. During the yearling stage, the responses of both sexes to the presence of the mother opposed each other. In addition, we found a negative relationship between dispersal and patch density at the juvenile stage. No interaction between density and the presence of the mother was detected, which suggests that behavioural responses to kinship and density are disconnected and that kinship is assessed at a small social scale. We discuss the role of competition and inbreeding avoidance to explain the observed pattern.

Social interactions often involve genealogically related individuals. In most terrestrial vertebrates, the mother is present in the neighbourhood of offspring, which generates conflict and common interest between mother and offspring over the use of local resources. Here, we use an experiment to show that female offspring of a lizard disperse to avoid interactions with their mother. Male offspring were affected in the opposite way, suggesting that they behave to avoid inbreeding with their sisters. This experiment shows that social interactions within families can affect dispersal.

Reference : Le Galliard, J.-F., Ferrière, R. and Clobert, J. 2003. « Mother-offspring interactions affect natal dispersal in a lizard ». *Proceedings of the Royal Society London B*. 270: 1163-1169.

Key-words : natal dispersal, kinship, density, common lizard

INTRODUCTION

The habitat of many species tends to be fragmented (Hanski 1999). In response to habitat fragmentation, populations may develop local adaptations to local conditions, or evolve dispersal adaptations (Thomas *et al.* 1998, Ronce *et al.* 2001). Because offspring dispersal has major consequences on the demography and genetic structure of populations, understanding the selective forces driving the evolution of dispersal strategies has become an important issue at the interface of evolutionary theory, behavioural ecology and population demography.

Hamilton and May (1977) established that interactions between relatives drive the evolution of offspring dispersal in stable and homogeneous habitats. They demonstrated that dispersal can be modelled as a parental manipulation or an offspring strategy evolving under kin selection. Dispersal reduces competition between relatives, which generates some indirect genetic benefits trading against the direct costs of movement following on an Hamilton's rule (Hamilton & May 1977). Despite several developments of the original scenario to more complex spatial and demographic structures (Clobert *et al.* 2001, chapters 5, 9, 11 and 24), almost all these elaborations consider dispersal as a fixed strategy unconditional on local kinship (but see Crespi & Taylor 1990, Ronce *et al.* 1998). However, some empirical observations suggest that natal dispersal may actually depend on local relatedness. In some mammals, offspring dispersal correlates with the intensity of sib-sib competition in meadow voles (Bollinger *et al.* 1993), and dispersal of the heaviest female in a litter is a response to stronger sister-sister interactions in red-backed voles (Kawata 1987). In the common lizard, offspring dispersal decreases with lower maternal condition or during mother senescence, hence with a diminishing expected risk of competitive interactions with the mother (Massot & Clobert 1995, Léna *et al.* 1998, Ronce *et al.* 1998).

A further issue is the spatial scale at which the behavioural sensitivity to kinship is expressed, which may expand from the scale of a familial unit (Hamilton & May 1977, Ronce *et al.* 1998) to the scale of a whole patch (Crespi & Taylor 1990, Perrin & Mazalov 2000). If dispersal is a response to the expected relatedness of a patch of habitat, then the potential impact of a kin member may be diluted by the presence of non-relatives. A complete assessment of the effect of a specific relative should therefore require to control the abundance of unrelated individuals. We performed such an experiment by constructing replicated populations of the common lizard (*Lacerta vivipara*). We studied the effect of the presence of the mother on offspring dispersal during two successive life-history stages (juvenile and yearling). Local kinship was manipulated by swapping mothers between different populations, while other populations acted as controls (mothers released with their offspring). Local density was manipulated independently by doubling the number of unrelated individuals released into half of the populations. This treatment produced two contrasting levels of patch density and also two levels of patch relatedness when the mother was present, high relatedness at low density

and low relatedness at high density. The two treatments were crossed so that we could investigate (i) whether juvenile dispersal responded to the presence of the mother, (ii) whether juvenile dispersal depended upon local crowding, and (iii) whether the effect of maternal presence was mediated by the level of local crowding.

METHODS

Model organism

The common lizard, *Lacerta vivipara* (Jacquin, 1787), is a viviparous species inhabiting humid habitats across Eurasia. Populations can be structured into three distinct life-history stages: juveniles (year born), yearlings (one-year old) and mature adults. Individuals share overlapping home ranges, as evidenced by the absence of any obvious spatial segregation in natural populations (Clobert *et al.* 1994). Juveniles originate from annual clutches of offspring laid synchronously during June or July. Hatching begins quickly after parturition, juveniles are autonomous at birth and offspring dispersal starts within 10 days of age (Clobert *et al.* 1994). Most dispersal occurs during the two first life-history stages, both in natural and experimental populations (Clobert *et al.* 1994, Boudjemadi *et al.* 1999). Moreover, laboratory trials have demonstrated that offspring discriminate maternal olfactory cues at birth (Léna *et al.* 2000).

Running of the experiment

The experiment was conducted on a sample of individually marked lizards collected from their natural habitats in June 1999 and released at our experimental site in July. Offspring dispersal away from the experimental populations was monitored daily until the end of December 2000. This procedure allowed us to estimate dispersal at the juvenile stage during 1999 and at the yearling stage during 2000.

(i) *Collection.* During June 1999, lizards were sampled in a natural habitat on the Mont Lozère (France, Lozère, 44°27'N, 3°44'E) before translocation at the Field Station of Foljuif (Seine-et-Marne, 48°17'N, 2°41'E). Altogether we collected 144 gravid females, 96 adult males and 240 yearlings to establish background populations. Lizards were individually marked, measured for length and weight, and maintained in plastic terraria at the Field Station with food and water provisioned regularly until the laying of gravid females (mid-July). Offspring were individually marked by toe clipping and measured for length and weight. Gender was determined by counting ventral scales (Lecomte *et al.* 1992). We assumed that yearlings and adults were initially unrelated to each other.

(ii) *Experimental system.* Sixteen experimental enclosures were constructed, each with a squared patch (10 × 10 m) and a one-way, 20 m long corridor (Fig. 1). Dispersal was defined as the movement out from an initial patch along a one-way corridor. This structure corresponds to both the

size of natural home range and the minimum dispersal distance measured in natural populations (Boudjemadi *et al.* 1999). Enclosures were closed to avian predators by nets and to intrusive mammals by daily trapping. However, we were unable to preclude intrusions of greater white-toothed shrews (*Crocidura russula*) in five of our enclosures in 1999 (Fig. 1). In 2000, efficient traps (Ugglan, Grahnbab™, Sweden) were used inside and on the outskirts of the enclosures, so that predation was prevented in all enclosures.

(iii) *Experimental design.* In July 1999, we initiated our experimental system with a bifactorial design. We manipulated the initial density and crossed this factor with the mother presence-absence (kinship) using enclosure as a replicate (Fig. 1). We contrasted eight low-density patches (14 yearlings and adult males, 6 females, 36.5 offspring \pm 2.4 s.e.) with eight high-density patches (28 yearlings and adults, 12 females, 71.2 offspring \pm 3.9 s.e.). We maintained a similar population age- and sex-structure in all patches. Starting densities were chosen to frame the estimated carrying capacity of our experimental habitat (Lecomte pers. com.). We applied the kinship treatment by replacing the mother of each litter with an unrelated, unfamiliar adult female in half of the experimental populations. This swapping was conducted just prior to introduction to avoid familiarisation. In the remaining half of the populations, offspring were introduced with their mother. The kinship effect was crossed with the density manipulation such that four population replicates were initiated for each combination of the two factors (Fig. 1).

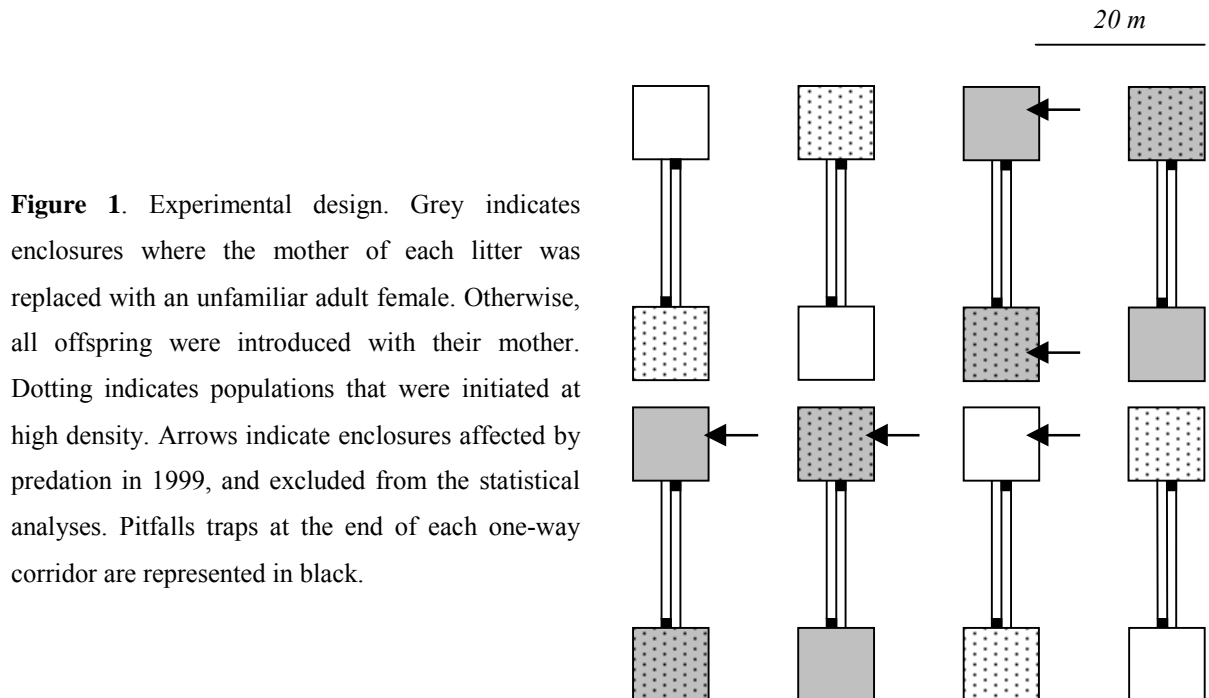


Figure 1. Experimental design. Grey indicates enclosures where the mother of each litter was replaced with an unfamiliar adult female. Otherwise, all offspring were introduced with their mother. Dotting indicates populations that were initiated at high density. Arrows indicate enclosures affected by predation in 1999, and excluded from the statistical analyses. Pitfalls traps at the end of each one-way corridor are represented in black.

(iv) *Introduction and monitoring.* Individuals were randomly allocated to the experimental populations. Yearlings and adult males were released during the same day in July 1999, and siblings

were released with their mother or a surrogate female following birth. The randomisation procedure used to introduce the lizards was effective at producing an initially homogeneous set (homogeneity tests for population size and individual characteristics among treatments, all $p > 0.4$). Philopatric individuals were monitored by hand recaptures during sessions in August and September 1999, and in April, August and September 2000, with multiple attempts per session (usually three independent days). This robust design allowed very efficient capture (estimated capture probability ranging from 0.80 to 0.98 per session). Dispersers were caught systematically in a trap located at the corridor extremities (checked daily), identified and immediately released in a new enclosure adjacent to the trap (Fig. 1). This methodology generated a simple metapopulation of two patches mutually coupled by migration.

Data analysis

Dispersers were defined as individuals caught at least once during a year within a corridor pitfall trap. Philopatric individuals were considered as the remaining set of individuals, excluding the non captured individuals, which were either dead or philopatric (Boudjemadi *et al.* 1999). Two separate analysis were conducted at the two life-history stages using the same cohort of offspring. Indeed, the sample of individuals used to model dispersal was not the same due to mortality from the juvenile to the yearling stage.

Data were analysed using generalised linear mixed models (GLMM) in SASv8.02 (Littell *et al.* 1996). The timing of dispersal was modelled with the MIXED procedure, which amounts to specify a gaussian error distribution and an identity link function in the GLMM framework. The average per family was used as a response variable. Dispersal status was modelled with the GLIMMIX macro, using a binomial error term, a logit link function and individual dispersal status (philopatry or dispersal) as a response variable (Littell *et al.* 1996). The GLMM approach described the clustering of individual observations, owing to the fact that populations were nested within treatments (Fig. 1), and accounted for the presence of both fixed treatment effects and random replicate effects (Littell *et al.* 1996). Estimations and test statistics were calculated with a restricted maximum likelihood approach. Statistical inferences for the fixed part of the model were obtained from type III F statistics and two-tailed tests. The assumptions of those models were investigated by the analysis of residuals. In the case of binomial dispersal data, no significant overdispersion was detected (Chi-square tests, $p > 0.05$).

Body condition was calculated as the residual from a linear regression of body mass against body size. Body condition and body size were not independent of offspring gender (body condition: $F_{1,700} = 141.9$, $p < 0.001$; body size: $F_{1,700} = 16.1$, $p < 0.001$). Males were on average more corpulent at birth than females, while females were larger than males. Therefore, we accounted for both covariates in the analysis of offspring dispersal. The fixed part of the models included the two experimental factors, individual covariates (length, body condition, gender) and interactions. The random part of the model included the effects of populations nested within the treatments. Model selection was conducted

by backward simplification of the fixed effects. Populations affected by predation were excluded from all analyses, although this did not modify the nature and significance of kinship effects.

Table 1. Selected generalised linear mixed models describing offspring dispersal at the juvenile stage (476 observations) and at the yearling stage (*b*, 214 observations) depending on offspring body condition, gender, kinship treatment and density manipulation. The model also included the random effect of patch identity nested within combinations of kinship and density treatments.

Juvenile dispersal predictors	F statistic <small>ndf, ddf</small>	P value
Body condition at birth	5.32 <small>1, 462</small>	0.02
Gender	5.79 <small>1, 462</small>	0.03
Kinship	2.10 <small>1, 7</small>	0.19
Gender × Kinship	3.66 <small>1, 462</small>	0.06
Density	6.09 <small>1, 7</small>	0.04
Density × Kinship	0.08 <small>1, 7</small>	0.78
Yearling dispersal predictors	F statistic <small>ndf, ddf</small>	P value
Body condition in spring	0.27 <small>1, 199</small>	0.60
Gender	2.68 <small>1, 199</small>	0.10
Kinship	0.05 <small>1, 7</small>	0.83
Gender × Kinship	5.80 <small>1, 199</small>	0.02
Body condition × Kinship	9.19 <small>1, 199</small>	0.003
Density	0.93 <small>1, 7</small>	0.37
Density × Kinship	0.01 <small>1, 7</small>	0.93

RESULTS

Effects of treatments on dispersal chronology

There was no evidence that dispersal chronology was affected by our manipulation during the two first stages of offspring lifetime. Juveniles dispersal was bimodal with a first, early dispersal period (age 2 to 25 days, $n = 23$) and a second more important dispersal period at an older age (30 to 60 days, $n = 55$). This bimodality was not affected by experimental treatments (logistic regression, density: $\chi^2_1 = 0.001$, $p = 0.97$; kinship: $\chi^2_1 = 0.04$, $p = 0.85$, $n = 78$). Similarly, age at dispersal did not differ between treatments (density: $F_{1,7} = 0.13$, $p = 0.73$; kinship: $F_{1,7} = 0.68$, $p = 0.44$, $n = 78$). Most yearlings movements occurred before June-July. The chronology of these movements was not influenced by the experimental treatments (density: $F_{1,7} = 0.01$, $p = 0.92$; kinship: $F_{1,7} = 2.57$, $p = 0.15$, $n = 42$).

Effects of treatments on dispersal status

In 1999, juvenile dispersal was affected by body condition, gender, a marginal interaction between gender and kinship, and density (Table 1). First, dispersal was associated with higher corpulence at birth than philopatry (dispersal: 0.005 ± 0.002 , $n = 65$; philopatry: -0.008 ± 0.009 , $n = 411$), and males disperse more on average than females (odds male : odds female = 1.22). Second, females dispersed more in the presence of their mother than in the presence of a surrogate adult female (female sample, kinship: $F_{1,7} = 6.53$, $p = 0.04$, $n = 236$), whereas male offspring displayed no significant response to the presence of the mother (male sample, kinship: $F_{1,7} = 0.01$, $p = 0.94$, $n = 240$). Together, these two different responses generated the marginal interaction between gender and kinship detected in the selected model (Fig. 2a). Third, the effect of density on patch dispersal was significant. Contrary to expectations, a lower dispersal was observed in the high-density treatment (Fig. 2b). There was no indication that density interacted with kinship (Table 1) nor with the sex-dependent response (gender \times kinship \times density: $F_{1,460} = 1.17$, $p = 0.28$).

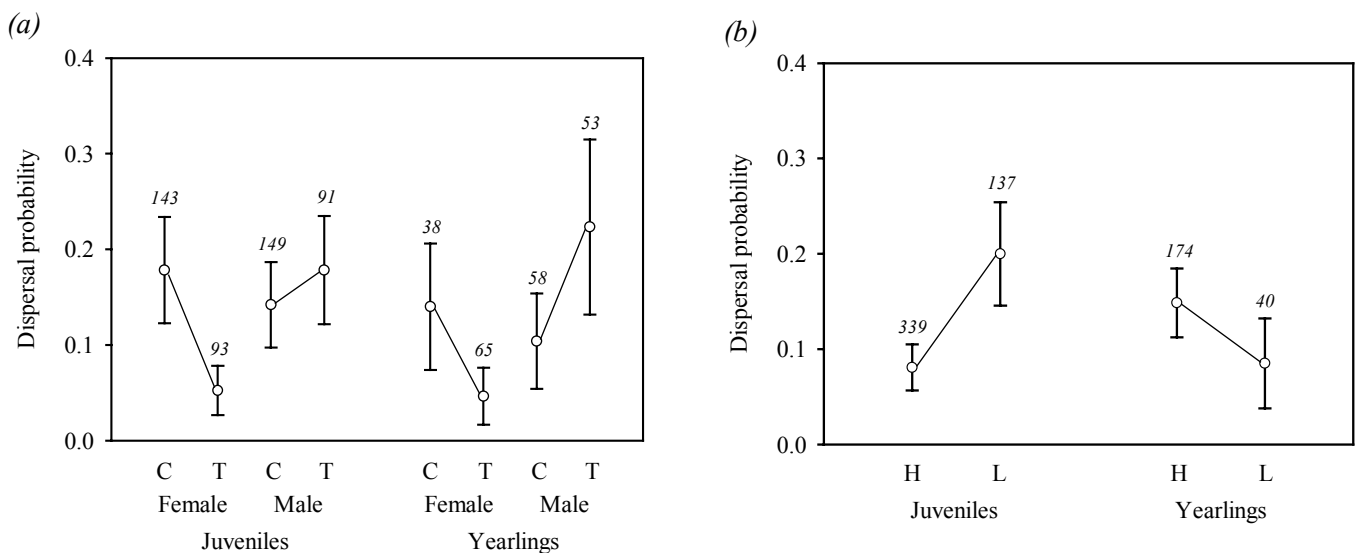


Figure 2. a. Kinship treatment, offspring gender and dispersal. During the juvenile stage (1999) and the yearling stage (2000), the presence of the mother had a significant effect on the sex-biased dispersal. C: Control, offspring introduced with their mother. T: Mother removal treatment, offspring introduced with a surrogate mother. b. Patch density and offspring dispersal. Dispersal decreased at high density during the juvenile stage, but was unaffected during the yearling stage. H: High-density patches. L: Low-density patches. Values are back-transformed from the GLMM presented in Table 1 (least-square means \pm s.e.). Numbers indicate sample sizes.

In the following, the study of yearling dispersal showed persistent effects of the kinship treatment modulated by gender and by spring body condition, whereas the effect of density disappeared (Table 1). The interaction between kinship and gender originated from the fact that females displayed a response to the presence of the mother opposite to that of male offspring (Fig. 2a),

albeit both responses were not significant (males, $F_{1,7} = 0.88$, $p = 0.38$, $n = 111$; females, $F_{1,7} = 1.09$, $p = 0.33$, $n = 103$). Males tended to disperse more in the absence of the mother, while females tended to disperse more in the presence of the mother. Also, irrespective of gender, the body condition of dispersers was higher than the residents' in the presence of the mother, whereas the reverse was observed when an unrelated female replaced the true mother (Table 2). Finally, the effect of density was not significant (Fig. 2b), and did not interact with kinship (Table 1) nor with the sex-dependent response (gender \times kinship \times density: $F_{1,197} = 1.72$, $p = 0.19$).

Table 2. Body condition according to the dispersal status and the presence of the mother at the yearling stage (offspring dispersing at the juvenile stage were excluded from the analysis). The first line indicates average value across gender, and data are also illustrated separately for females (F) and males (M) in the next lines. Dispersers were more corpulent than philopatric individuals when the mother was present ($F_{1,7} = 4.94$, $p = 0.03$), but less corpulent when the mother was replaced by a surrogate female ($F_{1,7} = 4.63$, $p = 0.03$). Bracketed numbers indicate sample sizes. C: Control, offspring introduced with the mother. T: Mother removal treatment, offspring introduced with a surrogate mother.

	C	T
Philopatry	- 0.002 \pm 0.018 ($n = 82$)	- 0.009 \pm 0.012 ($n = 99$)
	F: - 0.036 \pm 0.018	F: - 0.056 \pm 0.015
	M: 0.020 \pm 0.017	M: 0.059 \pm 0.017
Dispersal	0.125 \pm 0.062 ($n = 14$)	- 0.033 \pm 0.042 ($n = 19$)
	F: 0.053 \pm 0.09	F: - 0.174 \pm 0.08
	M: 0.177 \pm 0.08	M: 0.032 \pm 0.04

DISCUSSION

Our experiment demonstrates that maternal presence has a significant effect on sex-biased dispersal from natal patch. During the juvenile stage, higher dispersal was found in female offspring in the presence of the mother, while males were unaffected. This result lends experimental explanation to some correlations observed between the intensity of mother-offspring interactions and natal dispersal under natural conditions in the same species. For example, Ronce *et al.* (1998) observed that old females had lower annual survival than young females, which should decrease the likelihood of future mother-offspring interactions for offspring born from older females. This maternal ageing was associated with a stronger female offspring philopatry, while male dispersal was not affected (Ronce *et al.* 1998). Other maternal effects, possibly reflecting potential mother-offspring interactions, have been shown to influence offspring dispersal in the same species, including food availability (Massot & Clobert 1995), parasitism (Sorci *et al.* 1994) and hormonal stress (de Fraipont *et al.* 2000, Meylan *et al.* 2002). Such correlations could result from proximal constraints of producing different types of offspring, independently from the ultimate cause involving mother-offspring interactions that we manipulated here. Nevertheless, our experimental suppression of all mother-offspring interactions

yields exactly the behavioural response observed in Ronce *et al.*'s (1998) correlative study. These concordant results go to prove that female offspring disperse to avoid competitive interactions with the mother in this species. Whether the behaviour documented here results from offspring control on dispersal, or from parental manipulation of offspring behaviour (Hamilton & May 1977, Ronce *et al.* 1998) is difficult to assess. Against the latter hypothesis, we know at least that adults female do not seem to demonstrate any particular behaviour forcing offspring to leave their natal environment (Clobert *et al.* 1994, Léna *et al.* 1998).

The fact that male behaviour was unaffected at the juvenile stage and opposed the female response at the yearling stage requires alternative explanations. Despite offspring have been shown experimentally to suffer from competition with adults (Massot *et al.* 1992), competitive interactions may differ between sexes. For example, females tend to compete for resources, while males tend to compete for mates (Pilorge 1987, Massot *et al.* 1992). Thus, young males might suffer less from competition with the mother than young females. Additionally, males may avoid potential mating with their sisters rather than their mother, and therefore adopt a dispersal strategy opposite to that of their sisters (Massot & Clobert 2000). Indeed, the likelihood that one brother and one sister of an average clutch (3 males and 3 females) both survive to sexual maturity is high (0.11-0.30, with survival data from Massot *et al.* 1992), and exceeds the risk of inbreeding with mother (0.07-0.20, with survival data from Ronce *et al.* 1998). This scenario (female dispersal to avoid competition with mother, and male philopatry to avoid inbreeding with sisters) would match a model of sex-biased dispersal evolving under the joint influences of kin competition and inbreeding avoidance by Perrin and Mazalov (2000).

Dispersers' phenotypes and behaviour are not random. This is particularly evident in some species with dispersing morphotypes, but less extreme differences are also found in many other species (Swingland 1983). Our experiment showed that when dispersal occurred in response to presence of the mother, dispersers were more corpulent than philopatric individuals, which confirms previous observations (Clobert *et al.* 1994, Léna *et al.* 1998). On the contrary, when offspring were released with a surrogate mother, yearling dispersers were leaner than yearling residents. This result supports the view that individuals can differ morphologically depending on their dispersal strategy, but indicates that the actual dispersal decision is made by the offspring in response to proximal cues of potential kin competition.

In species exhibiting intense intraspecific competition, natal dispersal is expected to be positively density-dependent (e.g., Aars *et al.* 2000). In contrast, we found that offspring dispersal was inversely related to local crowding during the juvenile stage. Such a response may indicate constraints of habitat saturation acting on dispersal (see review in Lambin *et al.*, 2001). This would imply that the cost of movement and settlement are higher at high density in natural populations and limit emigration

(e.g., Jones *et al.* 1988). A density manipulation in the field has indeed shown that social fences can prevent immigration (Massot *et al.* 1992). Also, it is possible that some individuals choose their habitat based on the presence of conspecifics (conspecific attraction, Stamps 1991). This hypothesis would apply if the fitness of individuals increases with density (e.g., Allee effect) or if settlement costs are reduced in the presence of conspecifics (Greene & Stamps 2001). Finally, our transfer to an unfamiliar environment might have increased the benefits of the public information offered by neighbouring conspecifics as opposed to the individual private information (Valone 1989, Danchin *et al.* 2001). For example, offspring may cue on conspecifics to learn the location of suitable habitats (Stamps 1991). As private and public information built up in the population, one would expect the response to density to vary over time, as was observed here (see also, Clobert *et al.* *in press*). Whether negative density-dependence in our experiment reflects information sharing, social attraction, or habitat saturation remains to be established.

Local crowding did not influence the response of female and male offspring to the presence of the mother. Therefore, offspring did not react to relatedness at the level of the whole patch but at a smaller scale, such as that of a family unit. This behaviour suggests that assuming a few relatives per patch (Hamilton & May 1977, Ronce *et al.* 1998) is not an unrealistic modelling hypothesis to describe natal dispersal in our species. Alternatively, other lizard species might assess relatedness at different social scales and using different proximate cues. For example, recent evidences gathered in the side-blotched lizard (*Uta stansburiana*) indicate that dispersal promotes the local aggregation of genetically similar individuals irrespective of genealogy (Sinervo *et al.* 2001, Sinervo pers. com.). Thus, identity by state rather than by descent may also influence dispersal behaviour. More generally, the additivity between the effects of crowding and kinship suggests that the evolution of dispersal responses to both factors might have taken place along two independent pathways. This calls for a more detailed investigation of the distinct physiological and behavioural mechanisms involved in both responses (Dufty *et al.* 2002).

CONCLUSION

Evolutionary theory has long shown that kin interactions can be important in the evolution of dispersal. Following the parallel made by Hamilton and May (1977) between dispersal and altruism, theoretical studies of the evolution of kin recognition in cooperative species (Agrawal 2001) can be used to predict that kinship-dependent dispersal is likely to evolve. Our experimental results provide evidence for a more complicated scenario of a sex-dependent relationship between mother presence and natal dispersal. The direction of the relationship (here positive in females, negative in males) is likely to depend upon the relative influences of kin competition, inbreeding and kin cooperation (Perrin & Mazalov 2000, Lambin *et al.* 2001). Indeed, whereas the first two effects seem to prevail in

our species, studies with some mammals and birds indicate that different responses may actually exist when costs of inbreeding or benefits of kin cooperation dominate (Cockburn *et al.* 1985, Wolff 1992, Lambin *et al.* 2001).

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ADDENDA

This part presents some unpublished results on the emigration behaviour of yearlings and adults (and not only juveniles), on the immigration behaviour (and not only emigration), on delayed density dependence on dispersal, and on the correlation between offspring affinity toward maternal olfactory cues and natal dispersal in 1999.

Dispersal of yearling and adult cohorts

There is no evidence that dispersal chronology of yearlings and adults is affected by our manipulations during the two years of the study. For example, yearling movements are regularly spread over the summer and insensitive to manipulations in 1999 (density: $F_{1,6} = 0.49$, $P = 0.51$; kinship: $F_{1,6} = 0.07$, $P = 0.81$; gender: $F_{1,14} = 4.06$, $P = 0.06$, $n = 24$). At the same time, the chronology of adult movements is not influenced by treatments (density: $F_{1,8} = 1.05$, $P = 0.34$; kinship: $F_{1,8} = 1.87$, $P = 0.21$, $n = 33$).

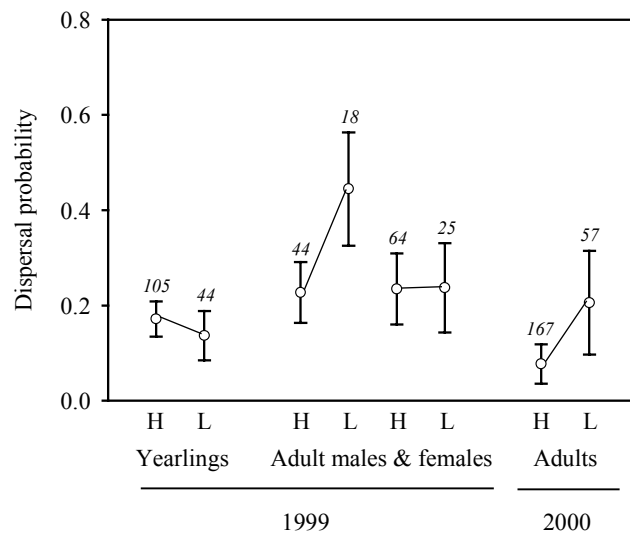


Figure A1. Population density and dispersal probability in 1999 for yearlings, adult males, and adult females, and in 2000 for adults. H: High-density patches. L: Low-density patches. Values are back-transformed from the GLMM discussed in the text (least-square means \pm s.e.). Numbers indicate sample sizes.

Mother-offspring interactions have no detectable effect on dispersal probability of yearlings and adults in 1999 and in 2000 (e.g., effect of offspring removal on adult female dispersal probability in 1999: $F_{1,9} = 0.08$, $P = 0.79$, $n = 89$; Offspring absence: 0.19 ± 0.09 , Offspring presence: 0.16 ± 0.06). Therefore, we only report the effects of population density on dispersal probability during the two years of the study. In 1999, we analysed yearlings and adults separately. Yearling dispersal is not influenced by conspecifics density ($F_{1,9} = 0.28$, $P = 0.61$, $n = 149$, Fig. A1). Adult male dispersal in 1999 is not affected by population density ($F_{1,9} = 2.73$, $P = 0.13$, $n = 62$, Fig. A1), but the trend is for increased philopatry at high density. Adult females dispersal in 1999 is also density-independent ($F_{1,9} = 0.97$, $P = 0.35$, $n = 89$, Fig. A1). Pooling together adult males and females yields increased power, but the results remained unchanged (Density: $F_{1,9} = 2.78$, $P = 0.13$, odds Low density : odds High density = 2.25; Gender: $F_{1,139} = 0.28$, $P = 0.61$, odds Male : odds Female = 2.05, $n = 151$, Fig. A1). We then compared patterns of density-dependent dispersal among age and gender classes in 1999. This analysis shows that the difference between juveniles, yearlings and adults suggested by separate analyses was close to significance (Table A1).

In 2000, we analysed together yearlings and adult cohorts to investigate patterns of density-dependent dispersal on mature individuals, accounting for age and gender effects. There is no effect of density on dispersal probability (Density: $F_{1,9} = 1.68$, $P = 0.23$, odds Low density : odds High density = 3.11; Age: $F_{1,211} = 0.03$, $P = 0.86$, odds Two years old : odds Three years old = 1.07; Gender: $F_{1,211} = 14.91$, $P = 0.0002$, odds Male : odds Female = 4.77, $n = 224$). The tendency is for a higher dispersal probability at low population density (Fig. A1).

Table A1. Selected generalised linear mixed models describing dispersal probability in 1999 depending on age and gender classes, and density manipulation ($n = 776$). The model also included the random effect of patch nested within density treatments.

Lizard dispersal predictors	F statistic <small>ndf, ddf</small>	P value
Density	1.54 <small>1, 9</small>	0.21
Age class	3.37 <small>1, 758</small>	0.03
Gender	2.88 <small>1, 758</small>	0.09
Age class \times Gender	2.82 <small>2, 758</small>	0.06
Age class \times Density	2.48 <small>2, 758</small>	0.08

Immigration

The maximal number of individual moves between patches in 1999 is equal to 3, and 27 individuals did not settle in their patch of arrival. The occurrence of settlement is not affected by age (G-test, $G_2 = 0.52$, $P = 0.77$) which allowed us to analyse pooled data. The probability of settlement is not affected by density in the arrival patch ($\chi^2_{1df} = 0.02$, $P = 0.90$, $n = 164$). The trend is for a higher probability of settlement in high density patches (87%) than in low density patches (70%). Among transient individuals leaving their arrival patch, the time spent in the arrival patch is not affected by patch density ($F_{1,10} = 0.77$, $P = 0.40$, $n = 27$). Although less powerful, separate analyses within each age class give similar results (treatment level analysis, Student's and contingency tests, all $P > 0.3$). Multiple moves are more pronounced in 2000, with a maximum of 5 moves during the year by the same adult male. The probability of settlement after a dispersal event is not influenced by density (density: $\chi^2_{1df} = 1.0$, $P = 0.32$, $n = 102$, pooled sample). The time elapsed between the initiation of two movements is similar in arrival patches at high versus low density for all age classes (treatment level analysis, Student's tests, all $P > 0.9$). Therefore, we found no evidence that settlement was influenced by the density of the arrival patch.

Delayed density dependence

Individuals captured at the end of experiment were classified (i) according to the patch densities encountered during the two years of the study (cohorts introduced in 1999), leading to four classes of life histories depending on whether patch density was low or high during the first or the second year of the experiment, or (ii) according to the patch densities encountered during the last year of the study (cohort born locally in 2000). These individuals were then introduced into unfamiliar populations in 2001, which enabled us to test the effects of past history on dispersal following release in this new environment (see chapter 5 for a description of the standard population structure). The effect of maternal history on natal dispersal can also be tested because offspring born from adult females captured at the end of the experiment were randomly introduced in standard enclosures. Significant effects of the life history type would indicate delayed density dependence.

When dispersal behaviour is compared among life history types, we find no differences in adults (GLMM on dispersal probability including patch of release as a random effect, Life history type: $F_{3,92} = 1.49$, $P = 0.22$; Age class: $F_{2,92} = 1.38$, $P = 0.26$; Gender: $F_{1,92} = 3.41$, $P = 0.07$, $n = 107$, Table A2) and yearlings (Life history type: $F_{1,32} = 2.41$, $P = 0.13$; Gender: $F_{1,32} = 4.12$, $P = 0.05$, $n = 43$, Table A2). The effect of maternal history on offspring dispersal is also not significant (Life history type: $F_{3,162} = 1.25$, $P = 0.29$; Gender: $F_{1,162} = 2.22$, $P = 0.14$, $n = 175$, Table A2).

Table A2. Delayed density dependence on dispersal probability in adults and yearlings captured at the end of the experiment and in offspring born from adult females captured at the end of the experiment. Dispersal probability was measured following release in new, unfamiliar enclosures. Results are the back-transformed least-square means (\pm s.e.) from the GLMM described in the text. Life history is given as first year of study – second year of study.

Age class	Life history type	Dispersal probability
Adults	Low density – Low density	0.27 ± 0.11 ($n = 21$)
	Low density – High density	0.10 ± 0.07 ($n = 23$)
	High density – Low density	0.10 ± 0.08 ($n = 10$)
	High density – High density	0.07 ± 0.04 ($n = 53$)
Yearlings	Low density	0.05 ± 0.04 ($n = 18$)
	High density	0.17 ± 0.09 ($n = 25$)
Offspring	Low density – Low density	0.124 ± 0.06 ($n = 54$)
	Low density – High density	0.064 ± 0.05 ($n = 19$)
	High density – Low density	0.105 ± 0.06 ($n = 22$)
	High density – High density	0.215 ± 0.08 ($n = 80$)

Maternal olfactory cue and natal dispersal

Affinity toward maternal odour was assessed in 1999 to determine whether olfactory maternal cue is a proximal factor involved in dispersal behaviour depending on mother presence (Léna and de Fraipont 1998). Less than eight hours after laying, mothers were isolated for 36 hours in dry individual terraria ($17 \times 11 \times 12$ cm high) covered with blotting paper. About 1 ½ h before the start of each experiment, each of a control blot and the maternal odour blot was randomly assigned under one of two cardboard shelters, symmetrically disposed in a clean, empty terrarium ($25 \times 15 \times 15$ cm high). After introducing around 5 a.m. one juvenile per terrarium with a maternal odour, all terraria were heated during two hours using a 25W incandescent bulb to trigger movements. Juvenile behaviour (outside a shelter, inside a control shelter, or inside a shelter with maternal odour) was recorded at 12 a.m. and 8 p.m.

Results from this laboratory experiment allows us to analyse the effects of behaviour and kinship on dispersal status. The choice of a shelter and the affinity toward a maternal odour

conditional on shelter choice were analysed independently (Table A3). In the morning, there are more individuals outside the shelters ($G_1 = 37.94$, $P < 0.001$), but overall there is no significant preference toward a maternal cue (midnight: $G_1 = 0.16$, $P = 0.31$; early morning: $G_1 = 0.11$, $P = 0.26$). There is no association between affinity toward the maternal cue, kinship and dispersal status (e.g., at midnight, kinship: $\chi^2_{1df} = 0.15$, $P = 0.70$; odour choice: $\chi^2_{1df} = 0.62$, $P = 0.43$; odour choice \times kinship: $\chi^2_{1df} = 1.44$, $P = 0.23$, $n = 460$). In contrast, the relationship between dispersal and shelter use is somewhat modulated by kinship (e.g., on early morning observations, kinship: $\chi^2_{1df} = 0.45$, $P = 0.50$; shelter use: $\chi^2_{1df} = 1.60$, $P = 0.20$; shelter use \times kinship: $\chi^2_{1df} = 3.88$, $P = 0.05$, $n = 537$). Individuals refusing a shelter tend to disperse more than individuals using a shelter in the presence of the mother, whereas the reversed is observed in the absence of the mother (Table A3). Analysing the number of observations under a shelter during two consecutive observations (Léna et al. 2000) instead of shelter use yields a similar pattern (kinship: $\chi^2_{1df} = 3.14$, $P = 0.07$; number of visits outside a shelter: $\chi^2_{1df} = 1.57$, $P = 0.21$; number of visits \times kinship: $\chi^2_{1df} = 4.74$, $P = 0.03$, $n = 537$).

Table A3. Summary statistics of the experiment characterising shelter choice, affinity toward maternal cue and dispersal behaviour in 1999 (midnight and early morning observations). Predicted dispersal probability from two GLMM (see text for details) with behaviour and kinship as explanatory variables (logit scale, \pm s.e.), using all recaptured individuals from the early morning observation. Similar results were obtained with midnight observations. C, Control. T, Mother removal treatment.

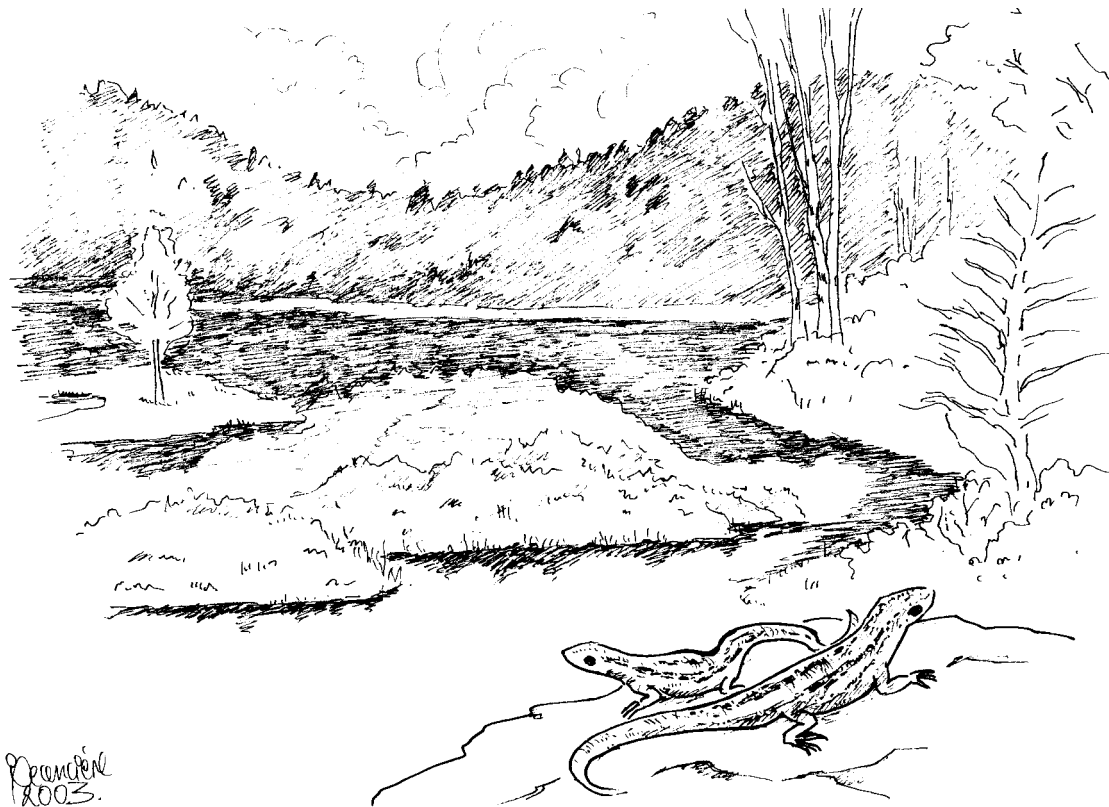
	Midnight ($n=537$)	Early morning ($n=537$)	Dispersal probability	
			C	T
Outside the shelter	77	160	-1.63 ± 0.4 ($n = 89$)	-2.57 ± 0.54 ($n = 71$)
Inside a shelter	460	377	-1.85 ± 0.34 ($n = 209$)	-1.58 ± 0.34 ($n = 168$)
Control shelter	236	193	-1.90 ± 0.37 ($n = 106$)	-1.38 ± 0.36 ($n = 87$)
Odour shelter	224	184	-1.77 ± 0.36 ($n = 103$)	-1.71 ± 0.38 ($n = 81$)

Addenda literature

Léna, J.-P. & de Fraipont, M. 1998 Kin recognition in the common lizard. *Behav. Ecol. Sociobiol.* **42**, 341-347.

Léna, J.-P., de Fraipont, M. & Clobert, J. 2000 Affinity towards maternal odour and offspring dispersal in the common lizard. *Ecol. Lett.* **3**, 300-308.

CHAPITRE 5 – IMMIGRATION DANS LES METAPOPOPULATIONS



“According to the classical metapopulation concept, which Levins established, all local populations have a substantial probability of extinction, and hence the long-term persistence of the species can occur at the regional or metapopulation level.

Alternatively, migration among local populations might affect their dynamics, as in the case of voles and their predators. [...] The metapopulation concept appeals to ecologists because the world is patchy, has always been so, and is sadly becoming, for many species, ever more patchy.” I. Hanski dans *Metapopulation ecology*. 1999. p. 2-3.

IMMIGRATION DANS LES METAPOPOPULATIONS: CONSEQUENCES COMPORTEMENTALES ET DEMOGRAPHIQUES CHEZ LE LEZARD VIVIPARE

Jean-François Le Galliard, Régis Ferrière & Jean Clobert

RESUME

Ce chapitre présente une manipulation de métapopulations du lézard vivipare (*Lacerta vivipara*) pour évaluer les conséquences comportementales et démographiques de l'immigration dans des habitats vides (colonisation) ou des habitats occupés (augmentation). Le traitement expérimental implique soit deux habitats occupés connectés pour créer les conditions de l'augmentation, soit un habitat occupé connecté à un habitat vide pour créer les conditions de la colonisation. Les conséquences de la manipulation ont été évaluées sur les comportements de dispersion et de fixation, et sur les paramètres démographiques des résidents et des immigrants de trois classes d'âge (juvéniles, sub-adultes, et adultes).

Deux composantes de la valeur sélective des juvéniles – croissance et reproduction – ont été augmentées lors de la colonisation. Une plus forte croissance pendant la colonisation a permis aux immigrantes de se reproduire plus tôt que dans un habitat occupé. Aucun effet sur la croissance et la reproduction des sub-adultes et des adultes n'a été détecté. La probabilité de fixation n'a pas été influencée par la présence de congénères dans l'habitat d'arrivée, en accord avec l'hypothèse d'une fixation aléatoire. La relation entre la condition corporelle des sub-adultes et leur statut de dispersion dépendait de la présence de congénères dans l'habitat connecté au sein de la même métapopulation, signifiant que différents individus ont dispersé dans différentes structures de métapopulation.

Cette expérience met en évidence les effets de l'immigration sur l'individu et la population chez le lézard vivipare. Au niveau de l'individu, nos résultats suggèrent que la colonisation génère une pression de sélection positive sur l'évolution de la dispersion des juvéniles, mais pas pour les sub-adultes et les adultes. Ceci pourrait expliquer que la dispersion soit essentiellement natale chez cette espèce. Au niveau de la population, aucun effet de Allee n'a été détecté dans les habitats colonisés. Au contraire, une compétition réduite a conduit à un recrutement reproductif plus élevé et, conjointement à un flux d'immigration, a permis une croissance plus forte de la population. Ceci pourrait contribuer à la capacité de l'espèce à développer et maintenir une distribution géographique large.

Référence : Le Galliard, J.-F., Ferrière, R. and Clobert, J. « Immigration within metapopulations: behavioral and demographic consequences in the common lizard ». Soumis à *Ecology*, avec du matériel supplémentaire inclus.

IMMIGRATION WITHIN METAPOPOPULATIONS: BEHAVIORAL AND DEMOGRAPHIC CONSEQUENCES IN THE COMMON LIZARD

Jean-François Le Galliard, Régis Ferrière & Jean Clobert

ABSTRACT

This paper presents a manipulation of two-patch metapopulations of the common lizard (*Lacerta vivipara*) to assess the behavioral and demographic consequences of immigration into initially empty patches (colonization) versus immigration into occupied patches (augmentation). The experimental treatment involves two types of metapopulations: two initially occupied patches connected to create the condition for augmentation, and an occupied patch connected to an initially empty patch to create the condition for colonization. Consequences of manipulation on dispersal behavior, settlement behavior, and demographic parameters in residents and immigrants of three age classes (juveniles, yearlings, and adults) were measured.

Two fitness components – growth and reproduction – were positively influenced in juveniles by colonization, whereas no difference between immigrants to occupied patches and residents was observed. Faster growth during colonization allowed female immigrants to reproduce earlier than females immigrating into occupied patches. No effect on growth and reproduction was detected in yearlings or adults. Settlement probability was not influenced by conspecifics presence, in agreement with the hypothesis of random settlement and against the hypotheses of social attraction or social fence. The relationship between yearlings body condition and dispersal status was affected by conspecifics presence in the connected patch of the same metapopulation, meaning that different yearlings disperse depending upon metapopulation structure.

This experiment highlights the effects of immigration at the individual and population levels in the common lizard. At the individual level, our results suggest that colonization generates a positive selective pressure on the evolution of dispersal in juveniles, but not in yearlings or adults. This might provide an ultimate explanation for why dispersal occurs primarily at the offspring stage in this species. At the population level, no Allee effect was detected in colonized patches; rather, reduced competition resulting in increased reproductive recruitment and immigration led to higher population growth in colonized patches. This may contribute to the species' capacity to develop and maintain a wide geographic distribution.

Reference : [Le Galliard, J.-F., Ferrière, R. and Clobert, J. « Immigration within metapopulations: behavioral and demographic consequences in the common lizard ». Submitted to *Ecology*, with supplementary material included.](#)

INTRODUCTION

Dispersal is under the influence of multiple selective pressures, arising from social interactions (Perrin and Goudet 2001), and heterogeneity in space and time (Gadgil 1971). In homogeneous populations (no temporal or spatial variability), several lines of theoretical work and empirical research on vertebrates have shown that dispersal patterns are affected by the costs and benefits of emigration, resulting from interactions between relatives (kin competition, risks of inbreeding) and from intraspecific competition (see review in Lambin et al. 2001). However, fragmented populations are likely to be heterogeneous to some degree, in which case dispersal strategies can also be affected by the costs and benefits associated with the immigration phase of dispersal (Ims and Yoccoz 1997). Even in uniform landscapes, spatial and temporal variation in population size must arise among and within patches due to demographic and environmental stochasticity. The classical notion of a metapopulation offers a simple approximation of this process by contrasting two patch states: empty (following on extinction and prior to recolonization) versus occupied (Levins 1969). In this context, immigration results either in the *augmentation* of the recipient population when the arrival patch is already occupied by conspecifics, or in *colonization* if the arrival patch is initially empty of congeners (Ebenhard 1991, Ims and Yoccoz 1997). Understanding the proximate and ultimate factors of dispersal therefore requires that the immigration behaviour is evaluated and compared between these two types of patches. This study is aimed at gaining experimental insights into the demographic costs and benefits, as well as the behavioral consequences, of augmentation versus colonization.

Understanding the demographic costs and benefits of colonization is important because dispersal from occupied to empty patches of habitat is a key factor of metapopulation persistence and of the invasion of new habitats (Levins 1969, Ebenhard 1991). Augmentation can be beneficial if conspecifics decrease the costs of settlement in unfamiliar habitats (review in Greene and Stamps 2001, Fig. 1C). For example, in lizards, the location and behavior of resident individuals can be used by immigrants to select suitable basking and feeding sites (Stamps 1987, 1988). Positive density dependence due to reproductive interactions (Allee effects) also reduce the demographic success of adult colonizers, hence the potential for invading new habitats and metapopulation persistence (e.g., Veit and Lewis 1996, Stephens and Sutherland 1999). However, immigration into already occupied patches can increase the costs of intra-specific competition directly with individuals already present in the patch, and later with other immigrants (review in Lambin et al. 2001, Fig. 1B). For example, enclosed prairie voles (*Microtus ochrogaster*) emigrating in empty patches survive and reproduce better than residents in occupied patches (Johnson and Gaines 1985, 1987). Immigrants might also suffer from asymmetric competition with settled individuals due to a prior-resident advantage arising from familiarity with the habitat or social dominance (Anderson 1989, Massot et al. 1994). To our knowledge, however, no experiment has attempted to tease apart these different effects by comparing the fitness of immigrants in situation of colonization versus augmentation.

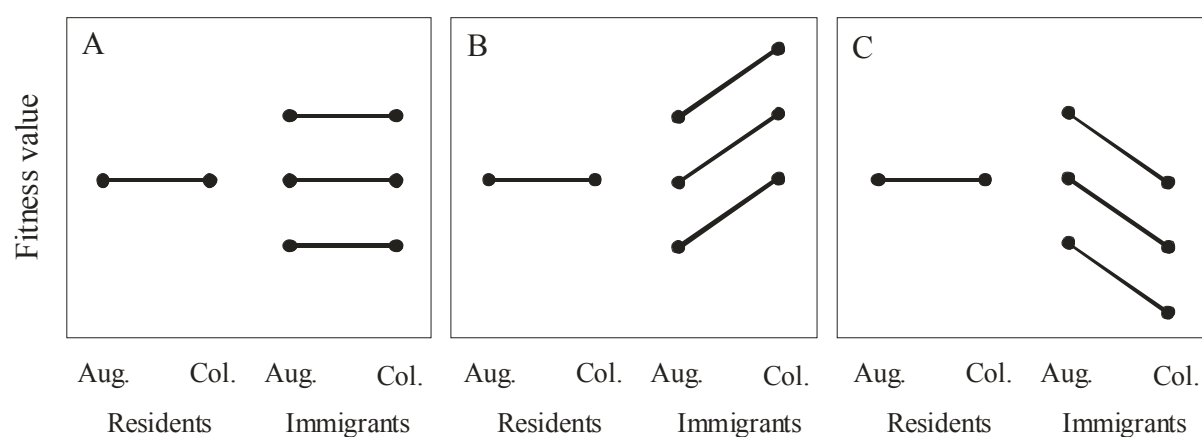


Figure 1. Three scenarios predicting the dependence of fitness on immigration status (resident versus immigrant) and immigration context (Aug.: augmentation, Col.: colonization). A. Neutral colonization scenario. Difference between residents and immigrants can be revealed by a significant effect of immigration status (top: immigrants fitness higher than residents, middle: no difference, bottom: residents fitness higher than immigrants). B. Beneficial colonization scenario. C. Costly colonization scenario.

The settlement behavior of dispersers may also differ during augmentation and colonization (Doligez et al. 2003). Such differences could affect metapopulation dynamics because settlement behavior influences colonization rate and rescue effects (Smith and Peacock 1990). Individuals may adopt three distinct patch choice strategies depending on their sensitivity to conspecifics. First, settlement could be independent of habitat occupancy, such as most metapopulation models assume (random settlement, Levins 1969). Second, settlement could involve a preference for already occupied sites, as a response to the presence of conspecifics (social attraction, Stamps 1991), or to the public information provided by the performance of conspecifics (Valone 1989). Immigrants would then cue on patch reproductive performance, assessed by the density of juveniles present in a patch (Danchin et al. 2001). A contrasting, third settlement strategy could involve aggressive interactions or competition with residents (Hestbeck 1982), resulting in repulsion for already occupied sites (social fence). Social attraction has been investigated at the individual level, and it has been found that individuals can cue on conspecifics presence for territory choice (Stamps 2001). Population level studies have only recently been initiated, and patch selection based on public information has been suggested in several birds (Frederiksen and Bregnballe 2001, Boulinier et al. 2002, Doligez et al. 2002). However, only two population-level experiments have addressed the effect of conspecifics presence on settlement in vertebrates (Danielson and Gaines 1987, Gundersen et al. 2002), and both concluded to the occurrence of social repulsion (but see Meadows and Campbell (1972) for patch level social attraction in marine invertebrates). Yet, these studies were based on the translocation of individuals into established populations, meaning that they investigated emigration following artificial transfer rather than

immigration following voluntary dispersal (*sensu* Ims and Yoccoz 1997). Such an approach may be problematic to assess the effect of conspecifics presence on settlement behavior of dispersers in natural populations. Indeed, dispersers are not a random subset of the population (e.g., Swingland 1983, Massot et al. 1994), and dispersers are often engaged in social interactions with conspecifics that differ from residents (e.g., Honekamp 1986, Léna et al. 2000). Therefore, population-level experiments comparing dispersers are needed to understand the dependence of settlement choice on conspecifics presence.

Here, we report the results of an experiment designed to analyze the effect of conspecifics presence on immigration success and dispersal behavior in juveniles, yearlings, and adults of the common lizard (*Lacerta vivipara* Jacquin). We established two types of experimental units: in O—O units, two connected occupied patches created the condition for augmentation; in O—E units, an occupied patch connected to an empty patch created the condition for colonization. We monitored emigration, as measured by the probability of leaving the patch of introduction, and immigration, as the probability to settle in the arrival patch. We measured several life history traits (growth, survival and female reproduction), and analyzed their dependence upon immigration status (resident or immigrant) and treatment. As shown in Figure 1, the relationship between fitness, immigration status and treatments can be of one of three kinds: “neutral colonization”, “beneficial colonization”, or “costly colonization” scenario. The analysis of life history components allows us to identify the scenario that provides the best interpretation of our data.

METHODS

Model system

The experimental system consisted of 7 metapopulation units located in a meadow at the Ecological Research Center of Foljuif (Seine et Marne, 48°17'N, 2°41'E). Each unit consists of two patches of enclosed habitat (10 m × 10 m) connected by 20 m long one-way corridors (Fig. 2). The length of the corridors corresponds to the upper-limit of a standard home range, and is used to define dispersal status in natural populations (Clobert et al. 1994). Patch size is matched to the size of the overlapping home ranges of this species, and each patch can sustain a local population (Lecomte and Clobert 1996). Enclosures are delimited by plastic walls to prevent lizards from escaping and to preclude the intrusion of terrestrial predators. Corridors allow movements of lizards from one patch to another, and are delimited by plastic walls (1 m width, 60 cm high) covered with mesh. Pitfall traps at the end of each corridor are used to capture dispersers. More details on the experimental system can be found in Lecomte and Clobert (1996) and in Boudjemadi et al. (1999).

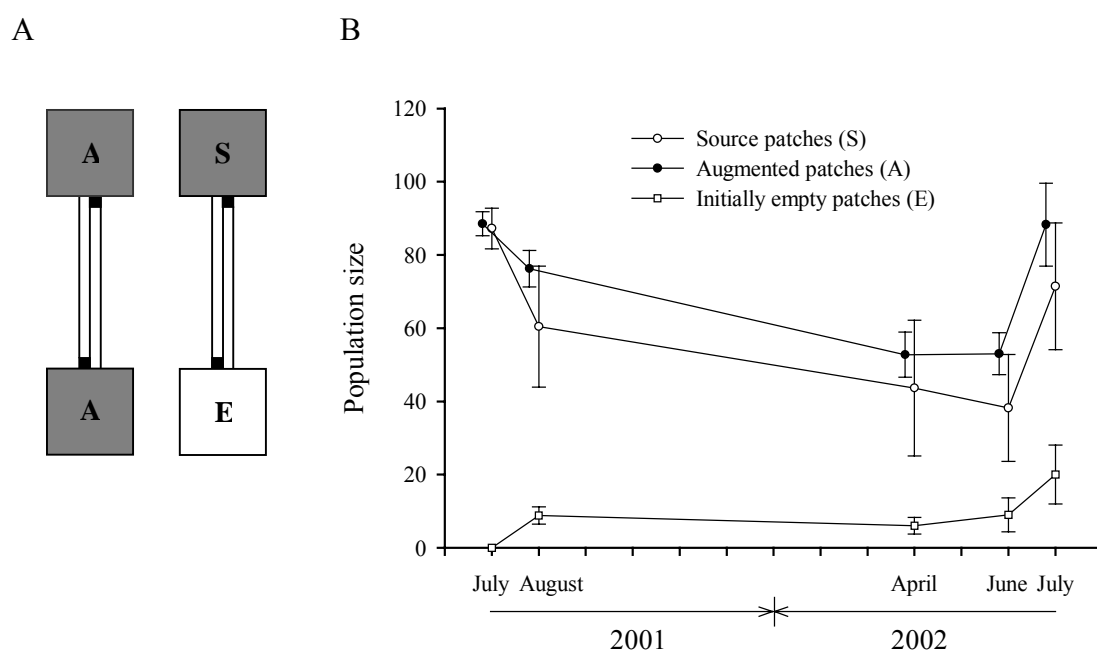


Figure 2. Experimental design and population dynamics. A. Experimental units contained either two occupied patches (A), or one occupied, source patch (S) and one empty patch (E). Pitfall traps used to monitor dispersal are the black squares at the end of each corridor. B. Population dynamics in the three types of patches (mean patch size \pm SD).

Lizards can disperse from one patch to the other within the same unit, and we distinguish three classes of individuals: *residents*, *immigrants* (individuals that established in their arrival patch), and *transients* (individuals that move at least twice between patches). This characterization of movement status based on the interpatch distance fixed in the study seems appropriate. Indeed, the timing and intensity of movements events, and the morphological attributes of dispersers reported in previous studies have been found to agree with natural dispersal patterns (Lecomte and Clobert 1996, Boudjemadi et al. 1999, Le Galliard et al. 2003). Furthermore, average dispersal distances are typically smaller than the scale of landscape heterogeneity and long dispersal distances have not been reported in natural populations (Clobert et al. 1994), suggesting that habitat colonization proceeds through short-distance movements.

Experimental design

The experiment was conducted from June 2001 to June 2002. Two types of units were established at the start of the experiment: (1) two connected occupied patches to create the condition for augmentation (denoted by O—O, 2 replicates), or (2) one occupied patch connected to one empty patch to create the condition for colonization (O—E, 5 replicates). This design generated three different types of patches (Fig. 2): augmented patches, occupied from the start of the experiment and connected

to similar, occupied patches (denoted by A, 4 replicates); source patches, occupied at the start of the experiment and connected to an initially empty patch (S, 5 replicates); and initially empty patches (E, 5 replicates). We treated these patches as independent observations in patch-level analyses, although pairs of patches are connected in the same unit.

Lizards were initially captured in June 2001. One sample came from populations maintained at the Ecological Research Center of Foljuif since 1999 (60 m a.s.l., sample called Fo, $n = 175$). A second sample came from one natural population in the Cévennes, Southern France (1400-1600 m a.s.l., sample called Cv, $n = 164$). All lizards were kept in individual terraria until females gave birth to autonomous offspring. The length (to the nearest mm) and body mass (to the nearest mg) of neonates were recorded, and their sex was determined by counting ventral scales (Lecomte et al. 1992). Each individual was given a unique code by toe-clipping. We initiated the experimental populations during June and July 2001 by releasing individuals into patches with which they had no prior familiarity. Sixteen yearlings were released in each population, involving 3 Fo males, 5-8 (5.8 ± 0.8 SD) Cv males, 2 Fo females and 3-6 (5.2 ± 0.8 SD) Cv females. There was no difference in the yearling sex-ratio between treatments ($\chi^2 = 0.35$, $P = 0.55$). Five adult males from each sample were also released in each population. Finally, ten post-gravid females along with their offspring and one non-reproductive female were released per patch (7-8 Fo and 3-4 Cv females per patch). Body size, body condition, introduction date, sex-ratio, and litter size did not differ between treatments at the start of the experiment (ANOVAs of treatment effect, all $P > 0.3$).

Census and sampling effort

Dispersal was monitored daily from July to November 2001 and from March to June 2002 by inspecting pitfall traps located at the end of each corridor. Dispersers were measured for body size and body mass, and released in the other patch of the same unit during the same day. Patches were monitored by hand recaptures in August 2001 (three recapture days), September 2001 (one recapture day), and April 2002 (two recapture days). All individuals were captured in June 2002. Individuals never caught in a dispersal trap were considered as residents provided they were captured at least once. We recorded body size and body mass at each capture. At the end of the experiment, all lizards were isolated in individual terraria, and the brood characteristics of gravid females were recorded. The data set contained 790 individuals released at the start of the experiment, 645 individuals and 2102 captures in 2001, and 446 individuals and 1131 captures in 2002.

Statistical comparisons of individual behaviour and life history traits between treatments assume adequate sampling, such that capture probabilities during the censuses have to be high and unbiased. To check these assumptions, we estimated capture probability from capture-recapture data (not seen, captured as resident, or captured as an immigrant) in August 2001, September 2001, and April 2002, assuming capture of all lizards in June 2002. We modeled capture probability as a function of

treatment, season and unit within treatment using multi-strata models (Nichols et al. 1992). Results indicated significant seasonal changes in capture probability in all age classes (all $P < 0.01$), but no significant difference between treatments (all $P > 0.36$). Capture probabilities were high in August ($> 90\%$) compared to September ($> 60\%$) and April ($> 75\%$). Therefore, comparisons between treatments were conducted on data from the censuses of August 2001 and June 2002.

Statistical methods

We estimated population size per age and sex classes in August 2001 and April 2002 using capture-recapture models (Otis et al. 1978). Patch demography was then compared between treatments with repeated measurements analyses using August 2001 as an offset term. Patch was included as a random effect. Temporal variation was modeled as a within-patch effect using a variance-covariance structure minimizing the Akaike Index Criterion of the model (Littell et al. 1996). We used logistic analyses for age and sex structure, and log-linear models for population size.

For movements and life history traits, individuals were used as observations in hierarchical models incorporating random replicate effects nested within treatments. When we compared residents and immigrants between augmentation and colonization, unit was used as a replicate and transients were excluded from the analyses. When we compared residents between augmented and source patches, or immigrants between augmented and empty patches, patch was used as a replicate. Dispersal and settlement probabilities were modeled with mixed-effect logistic regressions (Littell et al. 1996). Individual covariates (body size, body condition, sex, geographic origin) and their interactions with treatment were included in these analyses because they have been shown to influence dispersal (Massot et al. 2002). For dispersers, we also analyzed the time between introduction and emigration, and, for transients, the time spent in the immigration patch.

We compared individual growth, survival, and reproduction between treatments. First, we calculated daily growth rates as body size differences between two measurements divided by the time separating them. Variation in body condition was also measured, but females were excluded from these analyses because of the confounding effects of reproductive burden. Body condition was computed within each session as the residual of the linear regression of body mass against body size. Second, we measured survival probability by assuming that individuals not captured in 2001 and in June 2002 were dead. Third, we assessed female reproduction in June 2002 by palpation of vitellogenic eggs. Clutch size was measured as the total number of eggs laid, and relative clutch mass was calculated as the mass loss during parturition divided by the post-parturition body mass. We measured the number of vitellogenic eggs, aborted eggs, and viable eggs per clutch to calculate the proportion of fertilized eggs within total clutch, and the proportion of viable eggs within fertilized eggs. The sex-ratio, body size, and body condition of neonates were also measured. Continuous life history traits were analyzed with mixed-effects linear models (Littell et al. 1996). Because these models assume homoscedasticity and normality of residuals, we checked the residuals with Shapiro-

Wilk tests of normality and with Bartlett's tests for homogeneity of variance. Assumptions were met in all models presented here. Binary life history traits (e.g., survival probability) were modeled with mixed-effects logistic regressions. In all cases, the full model included treatment effects, individual covariates (body size, body condition, sex, geographic origin) and interactions, and selection was done through backward elimination of the non-significant terms. Results are given as mean \pm SE unless otherwise stated.

Table 1. Influences of treatment (augmentation or colonization) or patch type (augmented, source, or initially empty) on dispersal and settlement probabilities.

Movement type	Predictor effect	Test statistic	P value
Summer dispersal	Age	$F_{2,633} = 1.49$	$P = 0.23$
	Sex	$F_{1,633} = 7.47$	$P = 0.006$
	Treatment	$F_{1,7} = 0.47$	$P = 0.51$
Spring dispersal	Age	$F_{2,457} = 3.14$	$P = 0.04$
	Sex	$F_{1,457} = 8.63$	$P = 0.003$
	Patch type	$F_{2,11} = 1.44$	$P = 0.28$
Summer settlement	Age	$F_{2,103} = 0.81$	$P = 0.45$
	Sex	$F_{1,103} = 2.01$	$P = 0.16$
	Treatment	$F_{1,7} = 0.32$	$P = 0.59$

In addition to the fixed terms, the generalized linear mixed models also included a random replicate effect (unit for treatment or patch for patch type). Significant terms are highlighted in bold.

RESULTS

Population dynamics

All initially empty patches became colonized within one month (Fig. 2), and no colonized patch went extinct during the experiment. Starting one month after introduction, the average population size of colonized patches was 7.3 ± 3.5 SD individuals, a value lower than in initially occupied patches ($F_{2,11} = 31.4$, $P < 0.001$, contrast between initially empty and occupied patches: $P < 0.001$). There was no detectable difference between population sizes of source and augmented patches (S: 47.4 ± 18.2 SD individuals, A: 60.7 ± 12.6 SD individuals, contrast: $P = 0.23$). Also, from one month after introduction onward, sex structure and age structure remained similar in initially empty, source and augmented patches (patch specific proportion of males: $F_{2,11} = 0.93$, $P = 0.42$; patch specific proportion of juveniles: $F_{2,11} = 1.37$, $P = 0.29$).

Population growth rate before reproductive recruitment in July 2002 was calculated as the log-transformed ratio of population size in June 2002 to population size in August 2001. Populations declined in augmented patches (per capita growth rate: $r = -0.37 \pm 0.08$) and in source patches ($r = -0.49 \pm 0.06$), while colonized populations increased at the same time ($r = 0.26 \pm 0.26$; effect of patch type: $F_{2,11} = 5.34$, $P = 0.02$; Fig. 2). The reproductive recruitment rate was measured as the number of juveniles produced per female in the patch. The reproductive recruitment rate was higher in colonized patches (3.02 ± 0.58), than in source patches (2.04 ± 0.39) and augmented patches (1.43 ± 0.22 ; contrast between initially empty and occupied patches: $P = 0.04$). Therefore, the population growth rate from August 2001 to the end of offspring recruitment was again higher in colonized patches ($F_{2,11} = 6.95$, $P = 0.01$). At the metapopulation level, units growth rates calculated from the time of introduction to the end of offspring recruitment did not differ between treatments (O—O units: $r = -0.006 \pm 0.39$, O—E units: $r = 0.01 \pm 0.10$; treatment effect: $F_{1,5} = 0.02$, $P = 0.89$).

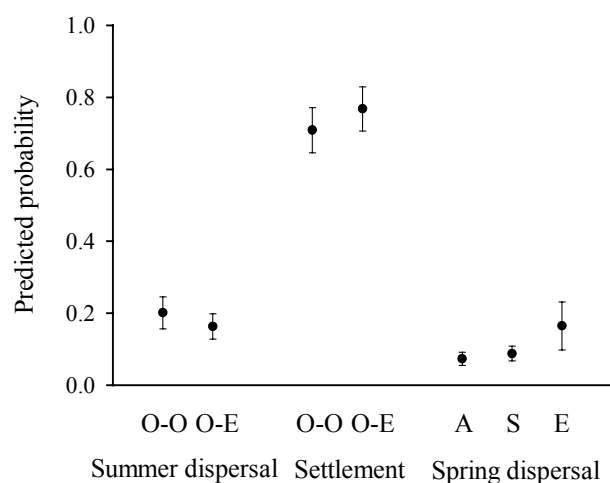


Figure 3. Effect of manipulation on dispersal and settlement probability during 2001 (O—O: augmentation, O—E: colonization), and effect of patch type on dispersal during spring 2002 (A: augmented patches, S: source patches, and E: initially empty patches). Values are back-transformed predicted means \pm SE derived from the models described in Table 1.

Dispersal probability

Of the 790 lizards introduced, 645 individuals were captured at least once and 116 individuals (52 juveniles, 27 yearlings, and 37 adults) moved at least once before hibernation. Overall, males were 1.8 times more likely to leave the introduction patch than females. However, dispersal probability was not different between source patches and augmented patches (Table 1, Fig. 3). Of the 474 individuals surviving after hibernation, 45 individuals (12 juveniles, 13 yearlings, and 20 adults) moved at least once before the end of the experiment. Because these individuals were captured in all patches, it was possible to compare dispersal probability between source, augmented, and colonized patches (Table 1, Fig. 3). Yearlings and adults dispersed earlier than juveniles (juveniles: 4 May \pm 5.1 days, yearlings: 9 April \pm 5.5, adults: 7 April \pm 4.3; $F_{2,97} = 9.95$, $P < 0.001$; contrast between juveniles and yearlings-adults = 26.2 days \pm 6.17, $P = 0.002$). Also, yearlings and adults dispersed more than juveniles during spring (odds yearlings and adults : odds juveniles = 2.31, $P = 0.02$), and dispersal was male-biased

(odds male : odds female = 2.86). However, movement probability was not affected by patch type (Table 1, Fig. 3).

We also analyzed the effects of individual covariates on dispersal probability with multiple logistic regressions. In 2001, there was no effect of juvenile body size, sex, maternal origin, clutch size, or maternal body size on dispersal probability (all $P > 0.08$), but there was a correlation between dispersal status and juvenile body condition at birth ($F_{1,303} = 8.74$, $P = 0.003$). Juvenile dispersers were more corpulent at birth than residents irrespective to the treatment (Residents: -0.0016 ± 0.001 , $n = 280$; Dispersers: 0.009 ± 0.003 , $n = 52$). In yearlings, dispersal was affected by an interaction between body condition at introduction and experimental treatment ($F_{1,120} = 4.96$, $P = 0.03$). Yearling dispersers tended to be more corpulent at introduction than yearling residents in O—O units (odds ratio per condition unit = 2.19, $P = 0.19$), while they tended to be leaner at introduction in O—E units (odds ratio = -3.77, $P = 0.07$, Table 2). Adult dispersal probability was correlated with body size, sex and geographic origin irrespective to experimental treatment in the multiple regression. Adult dispersers had larger body size than residents (odds ratio per mm = 1.22, $F_{1,170} = 7.72$, $P = 0.006$), adult males dispersed more than females (odds males : odds females = 10.7, $F_{1,170} = 11.95$, $P < 0.001$), and adults from the local area dispersed more than individuals translocated from the mountain area (odds Fo : odds Cv = 3.25, $F_{1,170} = 6.53$, $P = 0.01$).

Settlement probability

Settlement observations during 2001 involved 87 immigrants that settled in their patch of arrival, and 29 transients that returned to their patch of introduction. Across all age and sex classes, settlement probability was not different between augmented and initially empty patches (Table 1). Nevertheless, settlement probability in initially empty patches might have been influenced by the timing of dispersal in the course of the colonization process as predicted by a social attraction hypothesis (Stamps 1991). Against this hypothesis, late dispersers were not more likely to settle in an initially empty patch than early dispersers (logistic regression of settlement probability on the rank of arrival in an empty patch, $F_{1,44} = 0.25$, $P = 0.62$).

Table 2. Initial body condition for resident, immigrant and transient yearlings in the two treatments.

Type	Augmentation	Colonization
Residents	-0.04 ± 0.03 ($n = 46$)	0.04 ± 0.02 ($n = 58$)
Dispersers	0.04 ± 0.05 ($n = 13$)	-0.06 ± 0.05 ($n = 14$)
Immigrants	0.14 ± 0.06 ($n = 8$)	-0.09 ± 0.05 ($n = 10$)
Transients	-0.12 ± 0.05 ($n = 5$)	0.03 ± 0.11 ($n = 4$)

Data are means \pm SE, and sample size is indicated in brackets

Due to the low number of transients (15 juveniles, 9 yearlings, and 5 adults spread over 12 different patches), we analyzed the effect of morphology on settlement probability ignoring patch identity. For juveniles, there was no difference between body size, body condition, and origin of immigrants and transients (all $P > 0.33$). For yearlings, transients were heavier at introduction than immigrants in colonized patches, whereas the opposite was observed in augmented patches (Settlement status \times Patch type effect: $\chi^2_1 = 9.12$, $P = 0.002$; Table 2). Transient adults were leaner than immigrants at introduction irrespective to the type of patch (Settlement status effect $\chi^2_1 = 4.00$, $P = 0.04$; Transients: -0.43 ± 0.11 , $n = 7$, Immigrants: 0.10 ± 0.12 , $n = 30$).

Table 3. Effects of conspecific presence on the timing of dispersal and transience.

Time spent in	Predictor effect	Test statistic	P
Introduction patch	Age	F_{2,102} = 12.01	P < 0.001
	Sex	F_{1,102} = 5.90	P = 0.02
	Age \times Sex	F_{2,102} = 3.19	P = 0.045
	Treatment	F _{1,7} = 0.56	P = 0.48
Arrival patch	Age	F _{2,19} = 0.94	P = 0.41
	Sex	F _{1,19} = 1.53	P = 0.23
	Treatment	F_{1,5} = 7.35	P = 0.042

The time spent in a patch is calculated as the number of days between arrival in and departure from a patch. Significant terms are highlighted in bold.

Timing of dispersal and settlement

Time spent within a patch before dispersal was found to be similar between augmented and source patches (Table 3). Adult and yearling males dispersed earlier than adult and yearling females (contrast between females and males = 17.8 days \pm 5.65, $P = 0.002$), but juvenile males and juvenile females had similar timing of dispersal (contrast between females and males = -3.9 days \pm 6.48, $P = 0.55$). In the case of transients, the time spent within the patch of arrival before moving back was not affected by age or sex, but depended on the presence of conspecifics (Table 3). Transients stayed longer in initially empty patches than in augmented patches (31.1 \pm 5.9 days versus 10.8 \pm 4.8 days).

Growth

Changes in body size were studied in both sexes, but body condition was investigated only in males due to the confounding effects of reproduction (see *Reproduction* section). The body condition of male juveniles was not affected by treatment or immigration status (all $P > 0.11$). The body size growth was sex-dependent in all age classes (Table 4), and females had higher growth rates than

males. In a linear mixed-effect model of juvenile body growth, the interaction between treatment and immigration status was significant (Table 4). As predicted by the beneficial colonization scenario (see Fig. 1B), the annual growth rate was higher for immigrants in O–E units than for immigrants in O–O units and for residents (independent contrasts, all adjusted $P < 0.05$, Fig. 4), and immigrants in O–O units were not different from residents ($P > 0.13$). The growth rates of juvenile immigrants before dispersal were not different between source and augmented patches ($F_{1,6} = 1.02$, $P = 0.35$, $n = 52$), whereas growth following settlement until the end of 2001 was higher in colonized patches than in augmented patches ($F_{1,5} = 31.45$, $P = 0.002$, $n = 19$) and over the study year ($F_{1,4} = 7.81$, $P = 0.05$, $n = 24$). A comparison among siblings within families with at least one resident and one immigrant led to the same result (Immigration status \times Treatment effect: $F_{1,49} = 5.08$, $P = 0.03$).

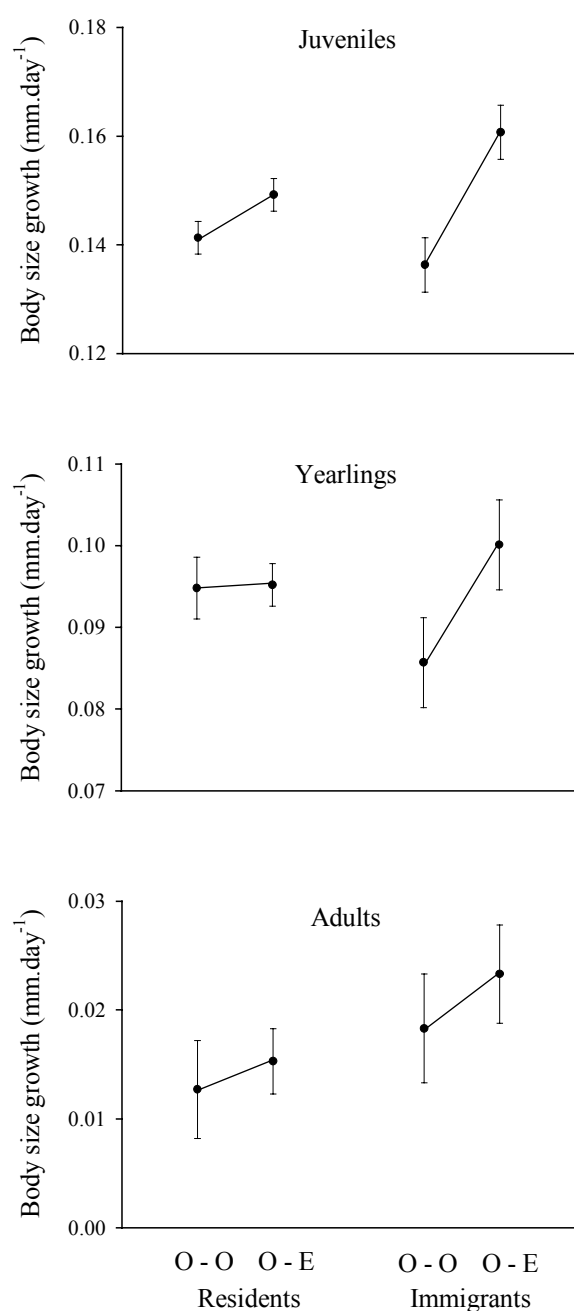


Figure 4. Annual body size growth depending on immigration status (residents or immigrants) and manipulation within juveniles, yearlings and adults (O–O: augmented units, O–E: colonization units). Data are predicted means \pm SE after the models described in Table 4.

Table 4. Demographic consequences of colonization versus colonization on annual growth in body size.

Age cohort	Predictor effect	Test statistic	P
Juveniles	Sex	F_{1,118} = 10.2	P = 0.002
	Immigration status	F _{1,118} = 0.85	P = 0.36
	Treatment	F_{1,5} = 7.47	P = 0.04
	Immigration status × Treatment	F_{1,118} = 7.08	P = 0.009
Yearlings	Sex	F_{1,73} = 46.75	P < 0.001
	Immigration status	F _{1,73} = 0.31	P = 0.58
	Treatment	F _{1,5} = 2.06	P = 0.21
	Immigration status × Treatment	F _{1,73} = 3.54	P = 0.06
Adults	Sex	F_{1,113} = 86.6	P < 0.0001
	Immigration status	F_{1,113} = 6.92	P = 0.01
	Treatment	F _{1,5} = 0.45	P = 0.53
	Immigration status × Treatment	F _{1,113} = 0.20	P = 0.66

Statistical models included a random unit effect, and a random family effect in the case of juveniles. Significant terms are highlighted in bold.

Among yearlings, immigration status and experimental treatment tended to affect annual growth rates in body size (Table 4), and the trend was concordant with the beneficial colonization hypothesis (see Figs. 4 and 1B). Among adults, immigrants grew more than residents over the study year independently of treatment (Table 4, Fig. 4). Annual variation in body condition of yearling males was not affected by the treatment ($P > 0.20$). The annual variation in body condition of adult males was influenced by an interaction between immigration status and treatment ($F_{1,47} = 8.39$, $P = 0.006$, 57 observations). As predicted by the benefits of colonization hypothesis (see Fig. 1B), body condition of male immigrants increased in O—E units relative to O—O units (contrast between colonization and augmentation units = 0.56 ± 0.18 , $P = 0.016$, Fig. 5). Treatment had no effect on body condition variation for adult male residents ($P = 0.95$).

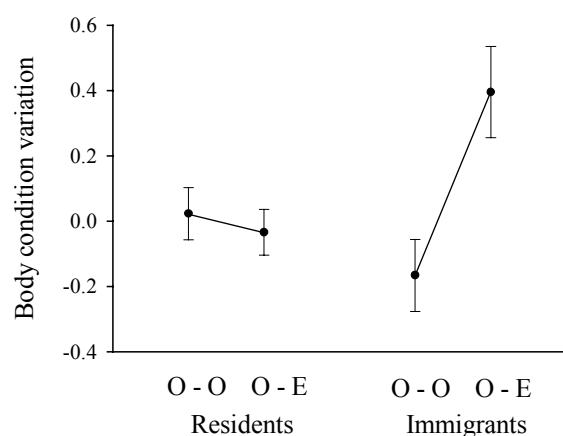


Figure 5. Annual variation in the body condition of adult males depending on immigration status (residents or immigrants) and experimental treatment (O—O: augmentation, O—E: colonization). Data are predicted means \pm SE after the model described in the text.

Survival

Individuals that were captured during 2001 but not in June 2002 were assumed to be dead at the end of the experiment. The post-summer survival of juveniles, yearlings or adults was not influenced by experimental treatment and immigration status (Table 5). Annual survival was affected by age, and juveniles had lower annual survival than yearlings and adults (odds juveniles : odds yearlings and adults = 0.49, $P < 0.001$).

Table 5. Demographic consequences of colonization versus non-colonization on post-summer survival.

Predictor effect	Test statistic	P
Age	F_{2,595} = 15.43	P < 0.001
Sex	F _{1,595} = 0.001	P = 0.98
Immigration status	F _{1,595} = 0.76	P = 0.38
Treatment	F _{1,5} = 0.10	P = 0.76
Immigration status × Treatment	F _{1,595} = 0.06	P = 0.81

Significant terms are highlighted in bold.

Reproduction

In a logistic regression model of the proportion of females maturing before the age of one year, the interaction between treatment and immigration status was significant ($\chi^2_1 = 5.84$, $P = 0.02$). As predicted by beneficial colonization scenario (Fig. 1B), the proportion of mature females before the age of one year was independent of treatment in residents (Fisher's exact test, $P = 0.50$, $n = 94$), whereas this proportion was higher in colonized patches than in augmented patches in immigrants (Fisher's exact test, $P = 0.01$, $n = 11$; Table 6). Because age at first reproduction can depend on post-natal growth, we tested whether reproduction of immigrants was correlated with rates of body growth. In agreement with this hypothesis, the post-natal growth in body size was positively correlated with the probability of reaching maturity before the age of one year ($\chi^2_1 = 34.52$, $P < 0.001$). When the post-natal growth rate was accounted for, the interaction between treatment and immigration status had no effect on the probability to reach maturity ($\chi^2_1 = 1.28$, $P = 0.26$).

Among yearling and adult females, some females were not gravid at the end of the experiment. The probability that a female older than one-year was gravid increased with female body size ($F_{1,97} = 12.63$, $P < 0.001$), but was not affected by the treatment ($F_{1,5} = 1.03$, $P = 0.36$), the immigration status ($F_{1,97} = 0.87$, $P = 0.35$) or the interaction between treatment and immigration status ($F_{1,97} = 1.72$, $P = 0.19$, Table 6). Clutch size, laying date and reproductive effort were all influenced by female body size ($P < 0.001$), but not by the treatment or the immigration status ($P > 0.24$). The 92 gravid females

produced a total of 480 eggs among which 40 were not fertilized and 63 were fertilized but not viable. Fertilization success, developmental success, clutch sex-ratio, offspring body size and offspring condition at birth were not influenced by experimental treatment or immigration status of the mother (all $P > 0.23$).

Table 6. Probability for females to reproduce in the two treatments.

Age cohort	Type	Augmentation	Colonization
Less than one-year old	Resident	0.08 [0.03, 0.19] ($n = 51$)	0.14 [0.06, 0.28] ($n = 43$)
	Immigrant	0.0 ($n = 5$)	0.83 [0.37, 0.97] ($n = 6$)
More than one-year old	Resident	0.80 [0.65, 0.90] ($n = 41$)	0.74 [0.60, 0.85] ($n = 51$)
	Immigrant	0.50 [0.16, 0.84] ($n = 6$)	0.89 [0.48, 0.98] ($n = 9$)

Results are the predicted means and 95% CI after the models described in the main text. Sample size is in parentheses.

DISCUSSION

In contrast with most previous experiments, our manipulation of experimental two-patch metapopulations involved the spatial structure of the population rather than the structure of the habitat (Hansson 1991, Clobert et al. 2001). By comparing individuals moving into occupied patches and those moving into initially empty patches, our study outlines the behavioral and demographic consequences of colonization versus augmentation in the common lizard.

Costs and benefits of immigration

Two fitness components (rates of body growth and female reproduction) were enhanced for offspring immigrating into initially empty patches compared to offspring immigrating into occupied patches, whereas the latter did not differ from resident offspring. No difference between colonization and augmentation was detected in yearling and adult immigrants. These results agree with the “beneficial colonization” scenario for juveniles, and with the “neutral colonization” scenario for yearlings and adults (Fig. 1).

These effects of colonization can be explained by intraspecific competition. It has been shown in the common lizard that population density influences competition for food, space or social partners (Massot et al. 1992, Lecomte et al. 1994), especially through natal growth (Massot et al. 1992). Therefore, competitive interactions and social stress were probably reduced in colonized patches, resulting in enhanced body growth. Furthermore, prey availability was affected by initial patch occupancy: at the end of the experiment, the abundance of spiders (one of the main preys of the common lizard, see Avery 1962) was double along 10 m length transects in initially empty patches (22.2 ± 1.7 spiders per transect) compared to initially occupied patches (11.2 ± 1.2 ; $F_{1,10} = 22.2$, $P <$

0.001). This suggests that the short-term benefits of colonization are tightly associated with a greater food availability. The fact that the growth of yearlings and adults was not influenced in the same way as juveniles growth may reflect the lower growth plasticity of older lizards. Also, older individuals occupy a dominant position in the population, and may be less sensitive to competition than juveniles (Lecomte et al. 1994).

The increase in body growth within colonized patches caused most female juveniles immigrating into initially occupied patches to reach a critical body size before the age of one year, enabling them to reproduce earlier than females immigrating into occupied patches. This experimental shift in the age of reproduction parallels the spatial variation described in this species. Along an altitudinal gradient, constraints on thermal opportunities delay reproduction from the age of one year in lowland populations up to the age of three years in most upland populations (Bauwens et al. 1986). Our results suggest further that age at first reproduction is plastic within lowland habitats depending on the intensity of competition experienced during post-natal growth.

Nevertheless, the short-term benefits of colonization evidenced here could be offset by delayed fitness costs. First, some intraspecific comparisons suggest that post-natal growth and reproductive efforts can decrease future survival in lizards (e.g., Olsson and Shine 2002). Second, compared to more than one-year old females, less than one-year old females laid their clutches significantly later (contrast between less and more than one-year old females = 12.5 ± 2.5 days, $P < 0.001$), produced smaller (contrast = -0.94 ± 0.33 mm, $P < 0.001$), and leaner offspring (contrast = -0.019 ± 0.006 , $P = 0.001$). The delay between young and old females relates to the fact that smaller females keep growing during the spring before they are receptive to mates, whereas larger females engage in mating right after hibernation (Bauwens and Verheyen 1985). The correlation between maternal age and offspring phenotype may originate from allometric constraints due to the lower sizes of abdominal cavity and pelvic girdles in younger females (Sinervo 1999). Delayed laying, and lower offspring condition and size are likely to be associated with poor offspring survival in the common lizard (Sorci and Clobert 1999). To assess the importance of these compensatory effects, we computed lifetime reproductive success of two life-history strategies: reproduction before the age of one year, and reproduction after the age of one year (Fig. 6). We neglected the fact that benefits of colonization can affect females later in life. We assumed that earlier reproduction trades off with reduced reproductive recruitment, due to lower fecundity and lower offspring survival, and with some unknown reduction in survival to adulthood. The model gave us an upper bound on survival costs of earlier reproduction such that benefits of colonization hold through entire life:

$$S_1 - S'_1 \leq \frac{B_1}{B_2} \times (1 - S_2) \cong 0.20,$$

where terms and estimations are explained in Figure 6. To our knowledge, such a decrement of female yearling survival has never been recorded in any demographic study of the common lizard (Massot et al. 1992, Sorci et al. 1996, Ronce et al. 1998).

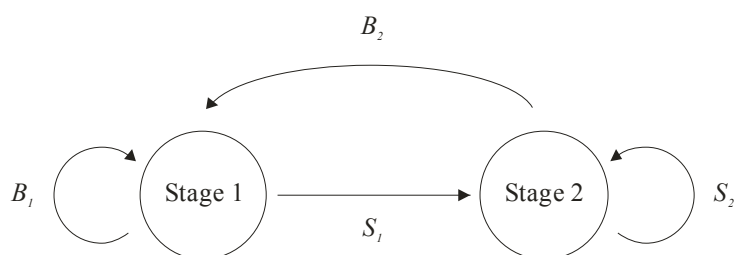


Figure 6. Two-stage life cycle of female common lizards with less than one-year old (stage 1) and more than one-year old individuals (stage 2). Parameters are reproductive recruitment rates (B) and survival (S). Reproductive recruitment involves stage-specific fecundity (F) and offspring survival (s), and is given by $B_i = F_i \times s_i$. Lifetime reproductive success (R_0) is given by $R_0 = B_1 + S_1 B_2 / (1 - S_2)$. Parameters for females maturing after one year are: $F_1 = 0$, $F_2 = 5.2$, $S_2 = 0.70$, and $S_1 = 0.60$. Parameters for females maturing before one year are: $F_1 = 4.1$, $F_2 = 5.2$, $S_2 = 0.70$, and S'_1 . Offspring survival s can be estimated from offspring phenotype and independent data on phenotypic selection gradients, which yields $s_1 = 0.36$ and $s_2 = 0.44$ (Le Galliard et al. *unpublished manuscript*³).

The significant short-term increase in offspring immigrant fitness associated with colonization has implications for our understanding of the dispersal patterns in the common lizard. Theory suggests that a negative relationship between fitness and patch occupancy, jointly with a variability in patch density favor the evolution of dispersal (Gadgil 1971, Olivieri et al. 1995). The second condition is likely to be fulfilled in our species since there is significant variation of population density at the spatial scale over which most dispersal occurs (Massot *personal communications*). This experiment provides evidence that the first condition applies to dispersing offspring, which suggests that opportunities of colonization could generate a significant selective pressure for the evolution of natal dispersal in this species. The non significant effect of colonization on adult and yearling immigrants further indicates that selective pressures associated with colonization decrease with age. This result might explain why dispersal occurs primarily at the offspring stage in this species (Clobert et al. 1994).

Settlement behavior

Settlement probability was not influenced by conspecifics presence in the patch of immigration. Transient individuals stayed longer in colonized patches than in augmented patches. Conspecifics presence affected the body condition of yearling immigrants, which were leaner in colonized than in augmented patches, but not the morphology of juvenile and adult immigrants. Nevertheless, low sample sizes in transients call for caution when interpreting these comparisons. Thus, although some qualitative differences between settlement in augmented and colonized patches were detected, our

³ See Appendix 5 of the thesis

results are more consistent with the hypothesis of random settlement flow (Levins 1969) than with the hypotheses of conspecific attraction (Stamps 1991) or social fence (Hestbeck 1982).

Social fence phenomena have been illustrated by studies of dispersal movements in saturated populations of small mammals and cooperatively breeding birds (Lambin et al. 2001). In these species, it has been suggested that habitat saturation increases the frequency of aggressive social interactions, raises the risks of predation during movement, and decreases the opportunities of independent breeding (e.g., Jones et al. 1988, Komdeur 1992, Gundersen et al. 2002). The absence of any sign of social fence in our study is somewhat puzzling, since it has been found in the common lizard that competition increases with habitat saturation (Massot et al. 1992), that habitat occupancy affects the success of immigration (this study), and that habitat density decreases transience (Massot et al. 1992).

Conspecific attraction has received support from studies of habitat selection at different spatial scales, ranging from territory to patch or colony choice (Stamps 1991, Danchin et al. 2001). Recent models have shown that cueing on conspecifics can bring some benefits (Greene and Stamps 2001, Doligez et al. 2003). For example, comparing random settlement with settlement strategies based on conspecifics presence or success, Doligez et al. (2003) found that a random strategy is generally defeated, unless habitat quality is really unpredictable. However, these models do not account for the spatial and temporal constraints acting on settlement neither for the fitness costs of habitat rejection. In our species, mobility is restricted and exploration requires to move over distances that are not less than effective dispersal distances. Thus, it is possible that the random settlement strategy observed here could reflect constraints on habitat choice (Stamps 2001).

Metapopulation effects

We created two types of metapopulations by releasing individuals either in one patch or in both patches within a unit, implying two levels of metapopulation density (low in colonization O—E units, high in augmentation O—O units), and two types of interpatch flow (unidirectional in colonization units, bi-directional in augmentation units). Demographic and behavioral processes acting at the metapopulation level could produce differences in the population dynamics, and the dispersal behavior or life history traits of residents between colonization and augmentation units. Indeed, effects of metapopulation structure dispersal in juvenile common lizards were found in a study by Boudjemadi et al. (1999) in response to a manipulation of interpatch connectivity. In our study, we found no effect of treatment on units demography, and life history of residents. Also, emigration probabilities from the patches of introduction were not influenced by metapopulation manipulation. However, the analysis of dispersers morphology indicated that metapopulation structure affected the body condition of yearling dispersers. This response could have been mediated by the arrival of unfamiliar immigrants inducing different social interactions in augmented patches compared to source patches.

Colonization and patch demography

Colonized patches had a higher per capita growth rate from early colonization to the end of the study than other types of patches. This was essentially due to immigration from source patches more than compensating for local mortality. Thus, the success of the settlement phase of colonization was facilitated by an immigration flow acting like the general rescue effect (Brown and Kodric-Brown 1977).

In colonized patches, rescue effects were not cancelled out by reduced reproductive recruitment resulting from Allee effects. On the contrary, reproductive recruitment was higher in colonized patches than in previously occupied patches. It may be that founder populations exceeded any critical threshold density for Allee effects to occur, or that the size of our enclosures was too small to induce such effects. However, Allee effects could also have been cancelled by alternative mate search strategies, population structure, or qualitative aspects of dispersal. First, low population density in colonized patches may be compensated for by higher male mobility during the mating season, increasing the operational sex-ratio and decreasing the risk of Allee effects (e.g., South and Kenward 2001). Second, dispersal can affect the sex ratio of colonized patches, because males dispersed more than females while settlement was independent of sex. Perhaps the low power of the corresponding tests explains why this did not lead to significant sex structure differences at the population level. However, colonized patches tended to host more males than other patches (male proportion, E: 0.61 ± 0.05 , S: 0.53 ± 0.02 , A: 0.53 ± 0.02), and were often subject to male immigration during the mating period (2.4 males per patch). These differences have the potential to mitigate a negative impact of low population density on mating dynamics. Third, any other qualitative difference between dispersers and residents, such as the body condition differences detected in our study, is likely to influence small populations resulting from colonization events, and make them different from small populations resulting from the decrease of formerly large populations.

Overall, reduced competition resulting in increased reproductive recruitment and continuous immigration flow from source patches led to higher population growth in colonized patches than in other patches. Such dynamics may explain the capacity of the common lizard to maintain a large geographic distribution. The species is indeed one of the most widespread lizard on Earth, with populations distributed from northern Spain up to the Arctic circle, from western Europe to the Sakhaline Island, and from sea level up to 3,000 m elevation (Heulin and Guillaume 1989). Also, accelerated colonization could have contributed to the Quaternary invasions of the whole Eurasia by populations of viviparous common lizards spreading from its main southeastern refuges during the ice ages (Surget-Groba et al. 2001).

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CHAPITRE 6 – SEXE RATIO DE LA POPULATION ET DISPERSION



“In many species, one sex is philopatric, settling near its birthplace. The other sex tends to disperse earlier and further from the birthplace. In mammals, males are usually the dispersive sex, while in birds females are more likely to disperse. The sex that disperses appears to represent an interplay between selection for inbreeding avoidance and a tendency of the sex that gains more from resource defence to remain philopatric.” A. Cockburn, S. Legge, & M. C. Double in *Sex ratios: concept and research methods*. 2002.

EFFETS DU SEXE RATIO ADULTE DE LA POPULATION SUR LA DISPERSION DU LEZARD VIVIPARE

Jean-François Le Galliard

Projet en collaboration avec Patrick Fitze, Jean Clobert & Régis Ferrière

RESUME DE L'ETUDE

Chez les espèces polygynes, Greenwood (1980, 1983) a prédit que les mâles dispersent pour éviter la compétition locale pour les partenaires, alors que les femelles sont en compétition pour les ressources et bénéficient de la philopatrie. Dans cette étude, nous testons si la compétition intrasexuelle pour les ressources et les partenaires affecte la dispersion chez un lézard à reproduction polygynandrique. Nous avons manipulé la sexe ratio adulte de la population chez le lézard vivipare (*Lacerta vivipara*) pour créer des populations biaisées vers les mâles, créant les conditions d'une forte compétition intrasexuelle chez les mâles et d'une faible compétition intrasexuelle chez les femelles, et des populations biaisées vers les femelles. Nous avons mesuré la dispersion dans trois classes d'âge (juvéniles, sub-adultes, et adultes) pendant la récupération de l'effort reproducteur (été), et pendant l'investissement dans les appariements et la gestation (printemps). Notre étude donne des résultats confirmant partiellement le scénario envisagé par Greenwood. Premièrement, le biais sexuel de la dispersion natale n'est pas affecté par la sexe ratio adulte de la population. Par contre, la manipulation a induit la dispersion de jeunes lézards de différentes conditions corporelles à la naissance pendant l'été. Deuxièmement, la perturbation de la sexe ratio adulte a affecté la dispersion de reproduction des femelles pendant l'été, mais pas les mouvements de reproduction des mâles. La concordance entre l'augmentation de la dispersion des femelles adultes dans les populations biaisés en faveur du même sexe et la période de restauration des ressources après la gestation suggère que les femelles dispersent pour éviter la compétition pour les ressources plutôt que la compétition pour les partenaires.

Référence : Ces données n'ont pas été publiées, soumises à publication ou révisées par mes collaborateurs.

Mots-clés : sexe ratio, compétition pour les partenaires, compétition pour les ressources, lézard vivipare

EFFECTS OF POPULATION ADULT SEX-RATIO ON DISPERSAL IN THE COMMON LIZARD

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Project in collaboration with Patrick Fitze, Jean Clobert & Régis Ferrière

STUDY ABSTRACT

In polygynous species, Greenwood (1980, 1983) predicted that males disperse to avoid mate competition, while females compete for resources. In this study, we test whether intrasexual competition for resources and mates affects dispersal patterns in a polygynandrous lizard. We manipulated adult sex-ratio in populations of the common lizard (*Lacerta vivipara*) to create male-biased population structures with strong intrasexual competition among males and low intrasexual competition among females, and female-biased population structures. We monitored dispersal across three age classes (juveniles, yearlings, and adults) during reproductive recovery (summer) and during mating and gestation (spring). Our study supports partially Greenwood's scenario. First, sex-biased natal dispersal was not affected by adult sex-ratio. Rather, the manipulation induced different offspring to disperse during summer, as shown by the influence of treatment on the relationship between offspring body condition and natal dispersal probability. Second, sex ratio manipulation affected breeding dispersal in females during summer, but not male breeding movements. The concordance between the increase of adult females dispersal in populations biased toward the same sex and the recovery period following parturition suggests that females dispersed to avoid competition for resources rather than competition for mates.

[Reference](#) : These data have not been published, submitted or reviewed by my collaborators.

Key-words : sex ratio, mate competition, resource competition, common lizard

SHORT INTRODUCTION

Sex-biased dispersal occurs in many species during natal and breeding movements (*sensu* Greenwood, 1980). This pattern is generally efficient to reduce inbreeding, because if one sex disperses, then incestuous matings between residents are less likely (Johnson and Gaines, 1990). Although inbreeding avoidance is important to explain the evolution sex-biased dispersal (e.g., Pusey, 1987; Wolff, 1992; Wolff and Plissner, 1998), several empirical and theoretical studies have suggested that sex-biased dispersal stems from the interaction between inbreeding avoidance and other causes (Dobson and Jones, 1985; Greenwood, 1980, 1983; Perrin and Goudet, 2001; Perrin and Mazalov, 2000). Indeed, the relationship between sex-biased dispersal and inbreeding depression depends systematically upon the mating system. In species with poor male investment in parental care, strong female investment in reproduction, and polygyny, such as many mammals, males usually disperse more than females. In species with symmetric investment in parental care between males and females and monogamy, such as many birds, females usually disperse more than males (Dobson, 1982; Greenwood, 1980; Moore and Ali, 1984; Wolff, 1994).

Familiarity with the local territory and competitive asymmetry between the sexes have been put forward to explain this covariation (Greenwood, 1980; Perrin and Goudet, 2001). Territory defence by males and resource defense by females result in benefits of familiarity with the local territory in males for birds and in females for mammals, respectively, hence in the philopatric sex (Greenwood, 1980). Furthermore, in polygynous species, males compete among themselves to acquire mates (local mate competition, Hamilton, 1967), while females compete among themselves to acquire resources (local resource competition, Clarke, 1978). If local resources are not limited, this asymmetry has the potential to induce male dispersal and female philopatry (Perrin and Goudet, 2001; Perrin and Mazalov, 2000). Although the covariation between sex-biased dispersal and mating systems among high-order taxa and among species substantiates the roles of familiarity and competitive asymmetry (see review in Perrin and Goudet, 2001), relatively few studies have documented the effects of intrasexual competition on sex-biased dispersal within a single species (e.g., Lambin, 1994).

In this study, we investigate the effects of intrasexual competition on natal and breeding dispersal in the common lizard (*Lacerta vivipara*), a polygynandrous species without prolonged bonding. This mating system can promote symmetrical roles between the sexes (Andersson, 1994; Kvarnemo and Ahnesjö, 1996). However, in the common lizard, natal dispersal is slightly male-biased, breeding dispersal is male-biased, males disperse during matings, and females disperse during the summer period when they acquire local resources to recover their reproductive efforts (Clobert et al., 1994; Massot, 1992). This suggests that males disperse to avoid local mate competition, while females disperse to avoid resource competition, as in the polygynous system envisioned by Greenwood (1980, 1983). Moreover, local mate competition among males can be expected because (i)

males contribute only a few sperm cells to reproduction, do not guard females and do not provide parental cares (Clobert et al., 1994); (ii) males are involved in endurance and contest competition before and during matings (Lecomte, 1993; Lecomte et al., 1994); and (iii) adult males growth and survival are insensitive to the overall population density, suggesting weak resource competition among breeding males (Massot et al., 1992; Pilorge, 1987). Local resource competition among females is likely to occur because (i) females invest more time and energy in reproduction than males, due to the burden of gestation (Avery, 1975; Bauwens and Thoen, 1981; Sorci et al., 1996); (ii) females do not compete aggressively for males during the breeding season (Lecomte, 1993); and (iii) competition reduces females reproductive success (Massot et al., 1992; Pilorge, 1987). Therefore, a high proportion of adults from one sex in the population should promote natal and breeding dispersal of the same sex individuals, as a way to escape intrasexual competition.

To test the effects of intrasexual competition on dispersal, we manipulated adult sex-ratio in several experimental populations of the common lizard to create male-biased population structures, setting the conditions for strong intrasexual competition among males and low intrasexual competition among females (hence, high intersexual competition in females), or female-biased population structures. We separated our study in two periods corresponding with mating and investment in reproduction (spring), and with recovery from reproduction (summer). We hypothesised (i) that each sex should disperse to avoid intrasexual competition, (ii) that female dispersal should be associated with resource competition avoidance during the recovery period, and (iii) that male dispersal should be associated with mate competition avoidance during the mating period.

EXPERIMENTAL SYSTEM

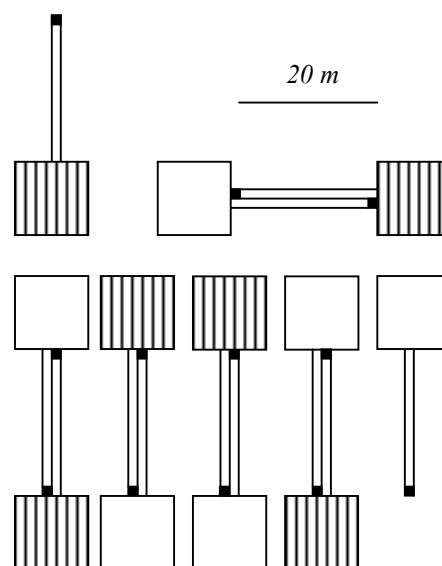
The experimental set up consists of enclosed populations located in a natural meadow at the Ecological Research Station of Foljuif (Seine et Marne, 60 m a.s.l.). In this study, twelve experimental patches of natural habitat (10 × 10 m) were used, each patch being extended by one 20 m length corridor ending with a pitfall trap (see Fig. 1). The patch mimics a natural home range and can sustain a small local population of common lizards for several years, because the spacing system is not territorial in this species (Le Galliard et al., 2003b). Corridors allow movements of lizards out of one patch. The length of the corridor is also used to define dispersal movements in natural populations, and has been found to be efficient to characterise dispersal in several past studies (Boudjemadi et al., 1999; Le Galliard et al., 2003b; Lecomte and Clobert, 1996). More details on the experimental system can be found in Boudjemadi (1999) and in Lecomte and Clobert (1996).

MODEL SPECIES

The common lizard *Lacerta vivipara* (Jacquin 1787) is a small (50-70 mm adult snout-vent size, 15-25 mm offspring size), and viviparous species inhabiting humid habitats (e.g., peatbogs,

heathlands, meadows) across Eurasia. In natural populations, three age classes can be distinguished: juveniles (year born individuals), yearlings (one year old), and adults (equal to or more than two years old, Pilorge and Castanet, 1981). Age at first reproduction is a plastic trait that depends on thermal opportunities and competition for food (Bauwens et al., 1986; Massot et al., 1992). In our experimental system, maturity can be reached before the age of one year, and all individuals are mature at two years old (Boudjemadi et al., 1999).

Figure 1. Experimental design and the allocation of experimental treatments from 2002 to 2003. Dashing refers to populations with a female-biased adult sex-ratio, and blank refers to populations with a male-biased adult sex-ratio. Black dots indicate pitfall traps.



The activity season spreads from February to November (Boudjemadi, 1999). Adult and yearling individuals hibernate first (October), while juveniles delay hibernation up to the start of November. Activity begins from mid-February to early March, where most active individuals are adult males. The early emergence of adult males is linked with the establishment of a social hierarchy and with the ending of the spermatogenic cycle (Bauwens et al., 1989; Lecomte, 1993; Olsson and Madsen, 1998). Adult females and yearlings emerge from hibernation between the end of March and the beginning of April. Matings can be observed during the month of April, and multiple matings usually occur in experimental populations. The average multipaternity level in a female clutch is around 2 fathers per clutch, a pattern concordant with observations derived from several natural populations of the same species (Laloi et al. submitted). Parturitions take place on average two months following matings, therefore from the end of June to the end of July. Females lay a clutch of 5 shell-less eggs on average (range 1-12), and offspring hatch during the same day. Offspring are autonomous at birth and the mother does not provide direct parental care. Dispersal movements usually start in a few days following birth (de Fraipont et al., 2000).

EXPERIMENTAL DESIGN

Spatial design

The experiment was conducted from July 2002 to June 2003 using twelve populations. In one half of the system, we initiated the populations with a female-biased adult sex-ratio, whereas we initiated the populations with a male-biased adult sex-ratio in the other half (Fig. 1). The spatial distribution of treatments among populations within the experimental system was chosen to optimise interspersions, especially along the edges of the system and with respect to an experiment done one year ago with the same enclosures (see chapter 5, Hurlbert, 1984).

Release protocol

Populations were initiated with juveniles, yearlings, and adults from natural populations of the Cévennes mountain range (South France, 1500 m a.s.l., see Clobert et al., 1994). Two different samples of yearlings and adults were used depending on when these individuals have been translocated at our site in the past (Le Galliard et al., 2003a, 2003b). Some lizards belonged to a cohort introduced in 2001 and acclimated during one year in 14 different populations (type A individuals, $n = 60$ yearlings, $n = 96$ adults). The others belonged to a cohort introduced in 1999, and acclimated during more than one year in 16 populations (type B individuals, $n = 84$ yearlings, $n = 120$ adults). This classification was accounted for during the experiment because translocation effects have been detected in the past (Boudjemadi, 1999). Furthermore, two different samples of juveniles were used. A first sample was obtained from gravid females maintained at the experimental site (type A and B mothers, $n = 324$). A second sample was obtained from gravid females of natural populations from the Cévennes (type C mothers, $n = 197$). All individuals were allocated to populations to which they had no prior familiarity, and juveniles were introduced in different populations than their mother to avoid the confounding effects of the presence or absence of the mother (Le Galliard et al., 2003b).

Table 1. Age and sex structure at the start of the experiment. Number of juveniles is given as mean \pm SD.

Age class	Male-biased treatment ($N = 6$)		Female-biased treatment ($N = 6$)	
	Males	Females	Males	Females
Juveniles	21.3 \pm 0.5	21.8 \pm 0.7	21 \pm 0.6	22.3 \pm 1.1
Yearlings	6	6	6	6
Adults	14	4	4	14

Yearlings and adults were captured from the 18 to the 25 May, and all individuals were kept in the laboratory under similar conditions. Yearlings were isolated in individual terraria ($17 \times 11 \times 12$ cm) distributed on five shelves. Adults were isolated in larger plastic boxes ($25 \times 15 \times 15$ cm) and

distributed randomly on four shelves. Food was provided once per four days, and included crickets (*Acheta domestica*) and mealworms larvae (*Pyralis sp.*) complemented with calcium (calcium Bone Aid™, T-Rex) and vitamin (Tonivit, TVM Laboratory). Basking opportunities were provided from 9h to 12h and from 14h to 17h local time. A heating ensured a thermal gradient encompassing the thermal breadth of the common lizard (van Damme et al., 1986). At parturition, offspring were isolated from their mother and kept during two days before introduction. Offspring sex was determined by the counting of ventral scales (Lecomte et al., 1992). Individuals were measured by the same person for snout-vent length (nearest mm, here called body size), tail length (nearest mm) and body mass (nearest mg). Body condition was calculated as the residual of a linear regression of body mass against body size.

The timing of introduction was dependent upon age. Twelve yearlings were introduced in each population on the 7 June, including 2 type-A males, 4 type-B males, 3 type-A females, and 3 type-B females (Table 1). A total of 42 to 44 juveniles was also introduced in each enclosure from the 15 June to the 27 July, including a half of each sex and nearly one third of type-C individuals. There was no difference between treatment in the sex or origin structure of this sample at the start of the experiment ($p > 0.90$). Eighteen adults were introduced in each population on the 11 July. In male-biased populations, we introduced 14 adult males and 4 adult females. In female-biased populations, we introduced 14 adult females and 4 adult males (Table 1). The female-biased sex-structure equals the equilibrium sex ratio of natural populations in the Cévennes mountain range, where females average 60-70 % of the adult population (Massot et al., 1992). Population structure of adults was matched between treatments for age (two years old versus more than two years old individuals, chi-square tests, $p > 0.65$) and for origin (type-A versus type-B individuals, $p > 0.49$). At the start of the experiment, body size, tail size, and body condition were similar between treatments across all age classes (ANOVA on treatment effects, all $p > 0.25$).

Individual census

Corridors were closed up to the 16 July to avoid exploratory movements of yearlings and adults following introduction (Boudjemadi, 1999). Dispersal was then monitored daily up to November 2002, and from March to June 2003 by inspecting pitfall traps at the end of each corridor. Each disperser was introduced in a new, unfamiliar enclosure randomly chosen within the same treatment during the same day. In addition, we captured lizards in August 2002 (three capture days), September 2002 (one capture day), and June 2003, where all individuals were captured. We analysed movements separately before and after hibernation. During each study period, individuals captured in pitfall traps were called *dispersers*, while individuals caught in habitat patches during demographic censuses but never caught in pitfall traps were called *residents*. Among dispersers, lizards which settled in their

patch of arrival were called *immigrants*, while lizards which did not settle in their patch of arrival but disperse to another patch were called *transients*.

DATA ANALYSIS

We asked whether adult population sex-ratio affects dispersal movements during the two periods by modelling (i) dispersal probability (residency versus dispersal), (ii) settlement probability (immigration versus transience), and (iii) the timing of movements. In the latter case, we defined two types of events: the residency time of dispersers, calculated as the number of days from introduction in a patch to dispersal, and the transience time, calculated as the number of days from arrival in a patch to dispersal. Data were analysed with generalised linear mixed models (GLMM) in SAS, using patch as a random effect (Littell et al., 1996). Dispersal and settlement probabilities were modelled with the GLIMMIX macro, using a binomial error term and a logit link function (McCullagh and Nelder, 1989). When we modelled dispersal probability, we accounted for the effects of treatment, sex, as well as body length, body condition, origin and age, and all pairwise interactions. Indeed, these covariates have been found to influence natal and breeding dispersal in past studies on the common lizard (Le Galliard et al., 2003b; Léna et al., 1998; Massot and Clobert, 2000; Massot et al., 2002; Meylan et al., 2002). The chronology of dispersal was modelled with the MIXED procedure, which specifies a gaussian error distribution and an identity link function. Estimations and test statistics were obtained from restricted maximum likelihood. Statistical inferences for the fixed part of the model are given as type III F statistics for two-tailed tests. Model selection was conducted by backward simplification. Models assumptions were fulfilled in all analyses presented here.

RESULTS

Movements during the recovery period

A total of 681 individuals was captured at least once following release in our enclosed populations and 77 individuals dispersed from these patches (54 juveniles, 6 yearlings, and 17 adults). Overall, dispersal probability was dependent upon age class, and also marginally upon sex (GLMM including patch as a random effect, Age class effect: $F_{2,666} = 7.71$, $p < 0.001$; Sex effect: $F_{1,666} = 3.61$, $p = 0.06$, $n = 681$). Females were 1.59 [0.98, 2.57] more likely to disperse than males across all age classes, a pattern somewhat surprising given the slightly male-biased dispersal in natural populations (Massot, 1992; Massot and Clobert, 1998). Juveniles were more likely to disperse than yearlings and adults across all sex classes (Tukey's contrasts, $p < 0.02$, odds juveniles : odds yearlings and adults = 3.0), while yearlings disperse as frequently as adults ($p = 0.42$).

The dependence of dispersal probability upon treatment and individual covariates was analysed separately for juveniles and adults, because yearling movements were too rare. In juveniles, the adult

sex-ratio of the population did not influence sex-biased dispersal (GLMM with patch as a random effect, Sex-ratio effect: $F_{1,10} = 0.23$, $p = 0.64$; Sex effect: $F_{1,323} = 1.20$, $p = 0.27$; Sex-ratio \times Sex effect: $F_{1,323} = 0.09$, $p = 0.77$, $n = 340$). Offspring males were as likely as females to disperse from male-biased than from female-biased populations (Fig. 2). The model had a significant interaction between offspring body condition at birth and population sex-ratio (Offspring condition effect: $F_{1,323} = 0.45$, $p = 0.50$; Sex-ratio \times Offspring condition effect: $F_{1,323} = 4.22$, $p = 0.04$). In female-biased populations, residents were heavier at birth than dispersers (Residents: 0.0007 ± 0.001 , Dispersers: -0.004 ± 0.003 , $p = 0.04$). In male-biased populations, dispersers tended to be heavier than residents (Residents: -0.001 ± 0.002 , Dispersers: 0.007 ± 0.003 , $p = 0.45$). An additive effect of offspring origin was found, with offspring introduced directly from the mountain area (type C mothers) dispersing less than offspring born from females of the experimental site (Offspring origin effect: $F_{1,323} = 8.30$, $p = 0.004$, odds type C : odds type A-B = 0.34). In adults, the sex-dependent breeding dispersal was affected by the sex-ratio manipulation (logistic regression, Sex-ratio effect: $\chi^2 = 0.62$, $p = 0.43$; Sex effect: $\chi^2 = 2.25$, $p = 0.13$; Sex-ratio \times Sex effect: $\chi^2 = 4.16$, $p = 0.04$, $n = 207$), whatever the age, origin and body size of lizards (all $p > 0.79$). In adult females, dispersal probability was higher in female-biased than in male-biased populations ($\chi^2 = 5.63$, $p = 0.02$, $n = 103$, Fig. 2). Adult males were not affected by the manipulation ($\chi^2 = 0.12$, $p = 0.73$, $n = 104$).

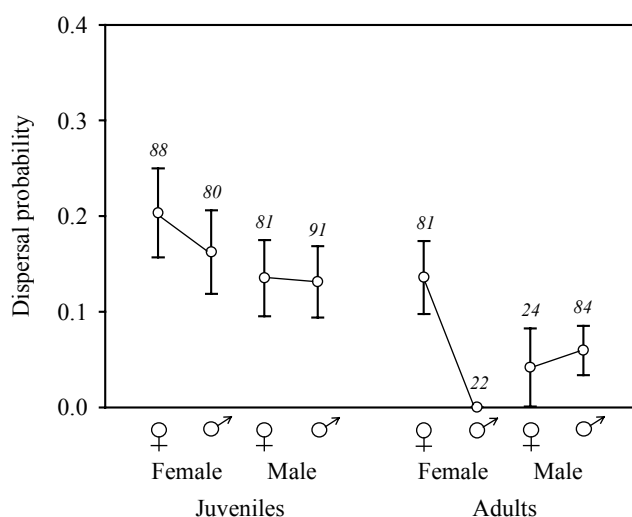


Figure 2. Effect of sex and adult sex-ratio manipulation on dispersal probability in juveniles and adults before wintering. ♀: female-biased populations, ♂: male-biased populations. Values are back-transformed from the GLMMs discussed in the text (least-square means \pm s.e.). Numbers indicate sample sizes.

From the 77 dispersers, only 20 individuals did not establish before wintering in their patch of arrival (15 juveniles, 3 yearlings, and 3 adults). The overall settlement probability was not affected by age ($\chi^2 = 2.69$, $p = 0.26$), and there was only enough observations to conduct analyses in juveniles. In this age class, males and females had similar settlement probabilities across treatments ($p > 0.05$), and adult sex-ratio had a marginal effect on settlement probability ($\chi^2 = 3.33$, $p = 0.07$). The trend was for

a lower settlement probability in female-biased than in male-biased populations (Female-biased: 0.52, $n = 29$; Male-biased: 0.84, $n = 25$).

To study dispersal chronology, we used the day when corridors were opened as a reference for individuals introduced prior to corridors opening, and introduction as a reference for offspring introduced after corridors opening. The time spent in the introduction patch was not influenced by the sex-ratio manipulation (ANOVA on individual observations with patch as a random effect, Age effect: $F_{2,62} = 10.24$, $p < 0.001$; Sex effect: $F_{1,62} = 1.52$, $p = 0.22$; Sex-ratio effect: $F_{1,10} = 0.62$, $p = 0.45$, $n = 77$). Juveniles and adults dispersed at the same time following introduction (Juveniles: 43.1 days \pm 3.2, Adults: 33.9 days \pm 5.5, $p = 0.29$), while yearlings dispersed earlier than juveniles and adults (contrast = 36.5 days \pm 9.2, $p < 0.001$). The transience time within an arrival patch was not affected by the manipulation (Wilcoxon's rank test, $p = 0.86$).

Movements during the mating period

A total of 385 individuals was captured at the end of the experiment and 27 individuals dispersed after hibernation (12 juveniles, 6 yearlings, and 9 adults). Overall, dispersal probability was not affected by age or sex (GLMM including patch as a random effect, Age class effect: $F_{2,370} = 0.22$, $p = 0.81$; Sex effect: $F_{1,370} = 1.59$, $p = 0.21$, $n = 385$). The dependence of dispersal probability on treatments was analysed for juveniles on one side and for adults and yearlings on the other side.

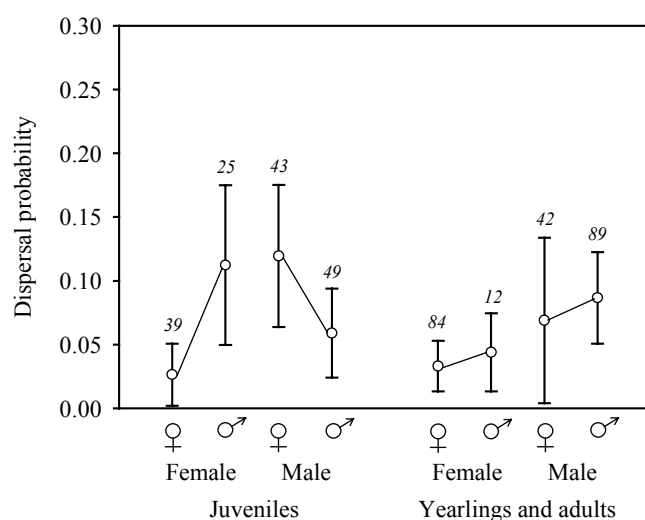


Figure 3. Effect of sex and adult sex-ratio manipulation on dispersal probability in juveniles and in adults and yearlings after wintering. ♀: female-biased populations, ♂: male-biased populations. Values are back-transformed from the GLMMs discussed in the text (least-square means \pm s.e.). Numbers indicate sample sizes.

In juveniles, the adult sex-ratio of the population tended to influence sex-biased dispersal (GLMM with patch as a random effect, Sex-ratio effect: $F_{1,10} = 0.25$, $p = 0.63$; Sex effect: $F_{1,142} = 0.47$, $p = 0.27$; Sex-ratio \times Sex effect: $F_{1,142} = 3.39$, $p = 0.07$, $n = 156$). Contrary to our expectations, male juveniles tended to disperse more from female-biased populations, while female juveniles tended to disperse more from male-biased populations (Fig. 3). The sex-dependent breeding dispersal of yearlings and adults was not affected by the sex-ratio manipulation (GLMM with patch as random

effect, Sex-ratio effect: $F_{1,10} = 0.88$, $p = 0.37$; Sex effect: $F_{1,215} = 0.17$, $p = 0.68$; Sex-ratio \times Sex effect: $F_{1,215} = 0.00$, $p = 0.97$, $n = 229$, Fig. 3).

The timing of these dispersal events during spring varied with age and population sex-ratio (ANOVA on individual observations with patch as a random effect, Age effect: $F_{1,15} = 22.39$, $p < 0.001$; Sex-ratio effect: $F_{1,10} = 5.19$, $p = 0.05$, $n = 27$). Yearlings and adults dispersed earlier than juveniles (contrast = 23 ± 5.1 days), and all age classes tended to disperse earlier from female-biased than from male-biased populations (contrast = 11.3 ± 5.13 days).

SHORT CONCLUSION

Our study supports partially Greenwood's scenario for the evolution of sex-biased dispersal. First, sex-biased natal dispersal was found to be independent of intrasexual competition avoidance before and after wintering. Rather, we observed that sex-ratio manipulation induced different offspring to disperse, as shown by the fact that treatment affected the relationship between offspring body condition and natal dispersal probability, and that males (resp. females) tended to disperse more from female-biased (resp. male-biased) populations during the mating period. Second, sex ratio manipulation affected breeding dispersal in females, but not in males. The concordance between the response of adult females to the sex ratio manipulation and the recovery period following parturition further suggests that females dispersed to avoid local competition for resources rather than local competition for mates. This suggestion deserves complementary experiments where both factors could be disentangled.

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DISCUSSION GENERALE



HETEROGENEITE SPATIALE

HETEROGENEITE LOCALE ET REGIONALE

L'hétérogénéité spatiale résulte de la distribution discrète des individus et des habitats de l'espèce. A l'échelle locale, la limitation des capacités de mouvement, de reproduction et d'interaction sociale génère une forme d'agrégation spatiale (chapitres 1-3). Cette agrégation spatiale a des effets perceptibles sur la dynamique écologique d'une espèce sociale. A l'échelle régionale, l'hétérogénéité spatiale est imposée par l'environnement, même si ses propriétés peuvent être dynamiques.

Notre travail montre que la compétition générée par l'hétérogénéité locale de la population n'empêche pas l'évolution d'un altruisme de reproduction fort. Ce résultat reste valide indépendamment de la structure géométrique du réseau : l'altruisme évolue plus ou moins spontanément dans un réseau structuré dans l'espace comme dans un réseau aléatoire. En fait, une géométrie régulière semble favoriser l'émergence de phénotypes plus altruistes (Figure 1). Ces différences posent la question de l'évolution conjointe du voisinage. Un modèle récent qui considère l'évolution de la distance d'interaction sociale et de la distance de dispersion sur un réseau fournit un premier élément de réponse. L'altruisme peut alors coexister avec l'égoïsme parce que les altruistes maintiennent des liens sociaux à courte distance qui les séparent dans l'espace des égoïstes qui évoluent des liens sociaux à longue distance (Koella 2000). Cependant, ce modèle repose sur des conditions restrictives d'itération du cycle de vie et sur des structures spatiales à grande échelle qui peuvent être rapidement détruites par la variabilité démographique. Lorsque l'hétérogénéité de la population est plus locale, un polymorphisme peut émerger par un processus continu de mutation-sélection autour du foyer de la dynamique adaptative des deux traits pour peu que les mutations soient orientées le long d'une corrélation génétique négative (voir Figure 5 du chapitre 3). Ce branchement évolutif amène à la coexistence entre une espèce sociale sédentaire et une espèce asociale mobile par branchement évolutif (*sensu* Geritz et al. 1998) comme prévu par van Baalen et Rand (1998).

Au contraire, **la compétition générée par la structuration régionale de la population constitue un frein à l'évolution de la socialité** que la dispersion soit globale (modèles en îles) ou locale (modèles en stepping-stone, Queller 1992; Taylor 1992a; West et al. 2002). Cependant, pour une population qui prendrait la forme d'une grille de sites voisins comme dans notre réseau structuré, Wilson et al. (1992) ont aussi observé une incapacité des altruistes à prendre le dessus sur les égoïstes. Il est donc évident que notre résultat ne traduit pas uniquement des différences d'échelle spatiale de l'hétérogénéité de la population (locale *versus* régionale). Nous discuterons plus loin plusieurs mécanismes qui peuvent contribuer à diminuer la compétition entre apparentés et expliquer l'évolution de la socialité dans notre modèle.

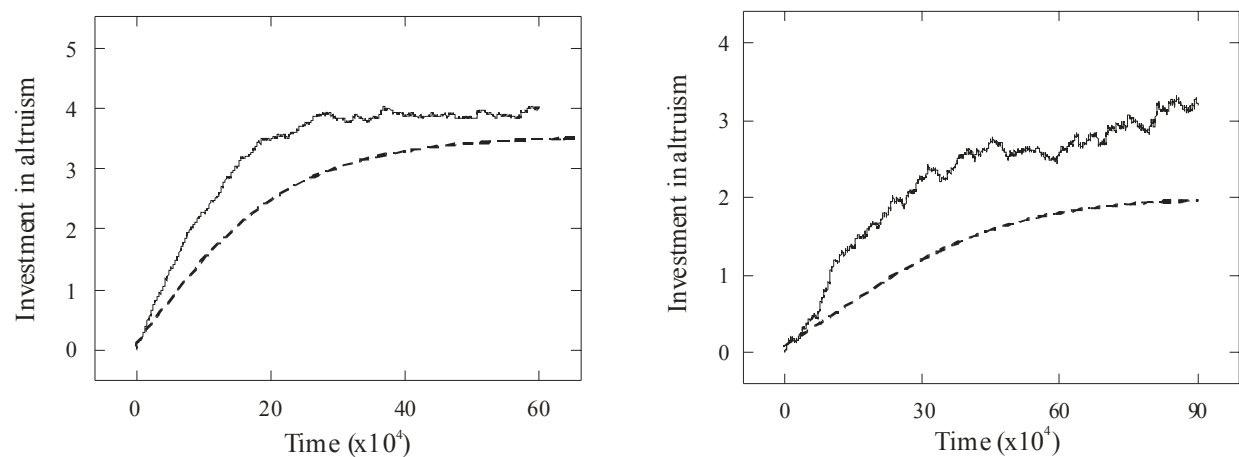


Figure 1. Evolution de la coopération dans un réseau structurée dans l'espace où les liens sont tirés entre les plus proches voisins selon une structure carrée et non aléatoire. Coûts de type accélérant selon les mêmes paramètres de simulation que la Figure 7F du chapitre 2 pour $m=0$ à gauche et $m=6$ à droite. L'altruisme évolue à des niveaux sensiblement plus élevés que dans un réseau aléatoire dans ce cas, comme pour d'autres combinaisons de paramètres.

DE L'HETEROGENEITE LOCALE AUX PRESSIONS DE SELECTION

Il n'est pas évident de prédire a priori l'effet de l'hétérogénéité locale sur les dynamiques adaptatives de l'altruisme et de la mobilité, et d'expliquer ces dynamiques à l'aide des pressions de sélection (Ferrière et Le Galliard 2001). **D'une part, l'hétérogénéité locale induit à la fois des éléments de parenté (les interactions coopératrices et compétitives se font préférentiellement entre individus apparentés) et des éléments de variabilité (la variabilité spatiale et temporelle émerge de la stochasticité des évènements démographiques).** Notre approche se situe donc à la frontière entre les modèles de sélection de parentèle, qui ignorent en général la dynamique écologique de la population, et les modèles de dynamique adaptative, qui étudient les conséquences de la structuration spatiale et démographique de la population en supposant un apparentement nul (chapitre 1). **D'autre part, la description de l'invasion de la population mutante dans une population structurée dans l'espace pose plusieurs problèmes techniques :** le mutant est globalement rare mais localement abondant et la structure spatiale de la population mutante varie lors de la dynamique d'invasion (Ferrière et Michod 1996; Rousset et Billiard 2000). En utilisant l'*approximation des paires* du processus d'invasion décrite par van Baalen (2000), nous sommes arrivés à formuler une expression analytique de la valeur sélective qui clarifie les pressions de sélection agissant sur l'altruisme et la mobilité. Cette approximation est basée sur l'hypothèse de la mise en place d'une structure transitoire d'invasion lors de la phase initiale de rareté du mutant, en considérant que la population du mutant est distribuée de façon homogène sur le réseau (Ferrière et Le Galliard 2001). Les nombreuses comparaisons que nous avons menées entre les dynamiques adaptatives et des

simulations numériques suggèrent que la distribution réellement locale du mutant induit peu de changements qualitatifs et favorise quantitativement l'altruisme (voir chapitres 1-3). La structure locale de la population mutante provoque vraisemblablement une plus forte agrégation des mutants que sous l'hypothèse de l'approximation des paires (Ellner et al. 1998). Remarquons cependant que ces approximations sont sensibles à la structure géométrique du réseau et au cycle de vie considéré (Morris 1997) : notre relatif succès n'est donc pas généralisable. Dans l'attente de nouveaux résultats analytiques, on serait donc tenter de recommander de toujours combiner l'approche analytique à une série de simulations.

Une fois considéré le processus d'invasion, la valeur sélective se dérive comme le taux de croissance exponentielle de la population mutante. **Le gradient de sélection sur l'altruisme permet d'obtenir une règle marginale de Hamilton du type $\partial B \times r > \partial C$** où ∂B indique le gain marginal indirect et ∂C le coût marginal direct (voir chapitre 2). **La mesure correcte de l'apparement est alors la probabilité qu'un voisin d'un mutant soit lui-même un mutant : $r = \bar{q}_{y|y}$.** Cet apparement est mesuré dans une phase transitoire de l'invasion où le mutant est globalement rare et établi à un pseudo-équilibre spatial. La pression de sélection liée à la diminution des sites vides dans le voisinage d'un mutant plus altruiste s'oppose à l'évolution de la coopération, mais elle quantitativement négligeable (chapitre 2). L'évolution de la coopération passe alors par une forme de sélection de parentèle impliquant la proximité spatiale des mutants. **Le gradient de sélection sur la mobilité implique une première pression de sélection pour ouvrir de l'espace dans le voisinage du mutant, modulé par un terme impliquant la saturation de l'habitat et les traits d'histoire de vie de la population résident, et une deuxième pression de sélection pour réduire les coûts de la mobilité.** L'évolution de la mobilité est donc motivée par une diminution de l'intensité de la compétition locale pour l'espace entre mutants. C'est donc *a priori* la compétition pour l'espace entre mutants qui est diminuée par l'évolution de plus forts taux de mobilité, ce qui implique que la mobilité évolue en partie par une forme de sélection de parentèle. Cependant, toutes choses étant égales par ailleurs, une plus forte saturation de l'habitat de la population résidente augmente cette pression de sélection, même si cette saturation de l'habitat n'agit pas en soit comme un moteur de l'évolution de la mobilité. De plus, la saturation de l'habitat de la population résident constitue le filtre principal des effets des traits d'histoire de vie, de la structure de l'habitat et du phénotype altruiste sur l'évolution de la mobilité. Remarquons cependant que, du fait que la pression de compétition locale ne puisse s'écrire sous une forme compacte, nous nous sommes limités à une analyse numérique des différents termes du gradient de sélection et nos explications restent qualitatives (voir chapitre 3). Cette analyse démontre de la difficulté à mettre en évidence les pressions de sélection impliqués dans l'évolution de la dispersion dans un environnement hétérogène et variable (voir aussi Cadet et al. 2003).

INTERACTIONS SOCIALES ENTRE APPARENTÉS

Les structures sociales sont menacées par un risque accru de compétition locale, et ce risque peut annuler les bénéfices à la coopération locale entre apparentés. Pourtant, de très nombreuses sociétés coopératrices existent sous la forme de populations structurées où les risques de compétition entre proches génétiques sont élevés (Annexe 1). Face à ce dilemme, deux solutions sont possibles. Pour certains auteurs, la coopération émerge de bénéfices directs liés à la réciprocité, à l'acquisition d'un territoire, à l'apprentissage ou aux avantages de la vie en groupe plutôt que de bénéfices génétiques indirects. En ce sens, la synthèse de Clutton-Brock (2002) sous-entend que les comportements sociaux reflètent un *altruisme faible*. Une telle forme d'altruisme peut émerger dans un contexte de compétition entre apparentés. Charge alors aux empiristes de nous fournir des mesures plus précises des coûts et des bénéfices de l'altruisme, une tâche qui peut s'avérer bien compliquée (Annexe 1). Pour d'autres auteurs, à la suite des synthèses de Queller (1992, 1994), il faut rechercher des mécanismes permettant de découpler la compétition et la coopération entre apparentés. Je vais donc discuter ce point dans les paragraphes qui suivent.

LA STRUCTURE DU CYCLE DE VIE

Les modèles de sélection de parentèle supposent un cycle de vie itéropare (un seul événement de reproduction) et une alternance entre stades du type « interactions sociales, reproduction, dispersion, puis compétition ». Les individus interagissent socialement, ce qui se traduit par des différences de reproduction annuelle. Après la reproduction, tous les adultes meurent et laissent la place aux juvéniles qui dispersent globalement ou localement entre les habitats. La compétition a lieu entre les juvéniles pour les places disponibles. Un bon exemple de ce cycle de vie est décrit dans les modèles en îles ou en stepping-stone de Taylor (1992a, 1992b).

Une première altération du cycle de vie consiste à **modifier la position respective des événements de dispersion et de reproduction** (Perrin et Lehmann 2001). Dans un cycle de vie où la dispersion a lieu avant la reproduction, la compétition locale entre les jeunes s'effectue dans un voisinage plus large que la coopération, et l'altruisme devrait évoluer. Un cas possible est celui d'un insecte à développement larvaire et à cycle de vie annuel (Perrin et Lehmann 2001) : la coopération a lieu entre les larves au sein d'une famille, et les adultes dispersent après la métamorphose avant de se reproduire. Une situation similaire a été analysée par Kelly (1994) pour un altruisme affectant la survie des individus.

Une deuxième modification consiste à **autoriser la survie et plusieurs événements de reproduction après le premier, ou itéroparité** (Taylor et Irwin 2000). L'itéroparité augmente l'apparentement local entre adultes, alors que la dispersion contrôle le niveau de compétition entre apparentés. L'altruisme peut alors évoluer sous certaines conditions, et une augmentation de la survie

adulte favorise la coopération (Irwin et Taylor 2001, Taylor et Irwin 2000). Le cas d'un cycle de vie itéropare permet par ailleurs d'envisager deux contextes démographiques : *l'altruisme de reproduction*, qui affecte la natalité, et *l'altruisme de survie*, qui affecte la mortalité. Les résultats de Irwin et Taylor (2000, 2001) démontrent que l'altruisme de reproduction évolue sous des conditions moins restreintes que l'altruisme de survie dans des populations fragmentées (voir aussi Nakamaru et al. 1997, 1998; van Baalen et Rand 1998). L'interprétation fournie par ces auteurs est que l'altruisme de reproduction s'exporte par la dispersion des juvéniles, alors que l'altruisme de survie augmente la compétition locale si les adultes ne dispersent pas. Le contraste évolutif entre altruisme de reproduction et altruisme de survie devrait donc être moins marquée si les adultes dispersent.

Dans notre cas, la **dynamique adaptative de l'altruisme est affectée par les conséquences démographiques des bénéfices et des coûts de l'altruisme** (chapitre 2). Des analyses préliminaires comparant un altruisme de reproduction à un altruisme de survie montrent que (i) la pression de sélection pour limiter la compétition locale entre altruistes n'est plus négligeable quand les bénéfices et les coûts de l'altruisme affectent la mortalité plutôt que la natalité, et que (ii) l'altruisme de survie évolue plus difficilement que l'altruisme de reproduction. La structure du réseau explique en partie ces résultats. En augmentant la natalité d'un voisin, on favorise la production de jeunes en dehors de son propre voisinage (pour peu que le réseau soit aléatoire). Au contraire, en diminuant la mortalité de ses congénères, on baisse l'intensité du flux démographique de son voisinage et l'évolution de l'altruisme de survie se heurte à l'effet négatif de la compétition locale (West et al. 2002). Il est intéressant de constater que l'altruisme de reproduction semble plus répandue que l'altruisme de survie, en accord avec les prédictions de tous ces modèles (Annexe 1).

LA STRUCTURE DE L'HABITAT

Dans une population structurée en îles, la compétition entre apparentés a lieu à la même échelle spatiale que la coopération. **Une façon de limiter les chevauchements entre la compétition et la coopération consiste alors à séparer les échelles spatiales de la coopération et de la compétition.** Une première alternative est d'élargir l'échelle spatiale de la compétition. On pourrait ainsi envisager une régulation de la densité de la population à l'échelle de plusieurs groupes de coopération (Kelly 1994). Par exemple, la coopération a lieu entre plusieurs membres de la même famille (des larves d'insectes qui se défendent mutuellement) et la compétition a lieu entre ces familles sur la même plante. Certains travaux montrent que ceci revient à diminuer l'effet délétère de la compétition entre les apparentés sur l'évolution de la coopération (Kelly 1994; Queller 1994 ; West et al. 2002). **Une seconde alternative repose sur le principe que « les voisins de mes voisins ne sont pas forcément mes voisins ».** Dans un réseau social, les voisinages de compétition et d'interaction se trouvent ainsi dissociés par la géométrie de l'habitat (chapitre 2, van Baalen 2000).

L'ELASTICITE DE L'ENVIRONNEMENT

La dynamique de population des modèles de sélection de parentèle conduit à une saturation de l'habitat qui annihile toute stochasticité, sauf via la dérive génétique (e.g., Frank 1998; Taylor et Frank 1996). Dans les populations naturellement fragmentées, la petite taille des populations se traduit en réalité par une variabilité démographique locale dans la composition et l'effectif de la population, et par une variabilité régionale dans l'occupation des habitats (voir chapitre 5 et Annexe 3). **Il y a ici un paradoxe à vouloir envisager la structuration génétique locale engendrée par la fragmentation de l'habitat en ignorant les conséquences démographiques de cette fragmentation.**

En terme sélectif, la saturation de l'habitat conduit à une *inélasticité* de l'environnement : les populations altruistes sont localement plus productives et elles sont donc défavorisées par une compétition locale plus forte pour un même espace disponible (e.g., Kelly 1994). Plusieurs auteurs ont suggéré **des formes d'élasticité qui permettraient à l'environnement de s'étendre pour accommoder le surplus de descendants produits par un groupe plus altruiste** (Taylor 1992b). C'est le cas dans une population en croissance exponentielle, même si cette situation ne peut pas éternellement perdurer du fait de la régulation locale par la densité. De plus, la possibilité que l'altruisme puisse évoluer parce que les groupes altruistes sont plus aptes à fonder et développer des populations pourrait être compromise par des effets de Allee. On pourrait donc s'attendre à des interactions entre la coopération locale, la compétition locale et les mécanismes démographiques. Une deuxième possibilité consiste à homogénéiser les chances d'établissement des jeunes entre les différentes populations. Kelly (1992) a ainsi construit un modèle de dispersion complète où le regroupement local alterne avec une phase de mélange complet, mais ce modèle détruit l'apparement local (voir aussi Goodnight 1992). Finalement, **l'habitat peut s'ouvrir spontanément sous l'effet de la stochasticité démographique, de la stochasticité environnementale, ou de catastrophes locales** (Ferrière et Le Galliard 2001). La capacité de l'altruisme à exploiter ces ouvertures dépendra de l'échelle de la dispersion et de la compétition, et de l'impact d'un changement adaptatif de l'altruisme sur ce processus stochastique. Dans notre modèle, l'ouverture de l'habitat est facilitée par la mortalité individuelle (chapitres 1-2). Si l'altruisme affecte uniquement la natalité, alors l'évolution de l'altruisme n'a pas d'effet sur ce processus et la capacité d'exportation de l'altruisme se maintient au cours de l'accroissement adaptatif de l'investissement altruiste. Au contraire, si l'altruisme affecte la mortalité, alors une augmentation de l'investissement altruiste agit directement contre ce processus. La stochasticité environnementale peut alors devenir nécessaire à l'évolution de la coopération (Mitteldorf et Wilson 2001). **L'effet de la stochasticité sur la diminution de la compétition locale et l'évolution de la coopération dépendrait donc du type de stochasticité et des mécanismes démographiques de la coopération.** Remarquons toutefois que cette démarcation nette entre altruisme de reproduction et de survie repose sur l'hypothèse forte de l'absence d'un trade-off entre natalité et mortalité (Roff 1992). Par ailleurs, il serait intéressant de

tester ces hypothèses pour des populations dérivées du modèle en îles de la sélection de parentèle, par exemple en utilisant un cadre théorique récemment développé pour mesurer la valeur sélective dans des métapopulations structurées (Metz et Gyllenberg 2001).

LA FLEXIBILITE DU COMPORTEMENT

Un autre découplage de la sphère de coopération et de compétition implique des processus comportementaux par lesquels un individu choisit son partenaire de coopération ou de compétition sur la base d'un critère de ressemblance corrélé avec la proximité génétique (e.g., Komdeur et Hatchwell 1999). Par exemple, une discrimination du partenaire social peut permettre de restreindre la coopération entre les résidents du même fragment d'habitat : le voisinage de compétition reste inchangé alors que le voisinage de coopération devient plus court (Perrin et Lehmann 2001, Annexe 1). On ignore cependant dans quelle mesure la discrimination des proches génétique a évolué conjointement à la structuration sociale de l'espèce, et si la discrimination est un préalable à l'évolution des organisations sociales.

Un évitement des proches génétiques pourrait aussi être impliquée dans les phénomènes de dispersion ou de choix de l'habitat (Le Galliard et al. 2003b; Sinervo et Clobert 2003). Ces choix influenceraient en retour les risques d'interférences compétitives futures entre apparentés. Contrairement au népotisme, un évitement de la compétition entre apparentés par des mécanismes de dispersion a cependant le désavantage de diminuer l'apparentement, donc de défavoriser la coopération entre apparentés. Une forte structure d'apparentement pourrait tout de même se maintenir si on considère deux étapes de dispersion : une étape de dispersion conduisant à un évitement des apparentés pendant la phase de compétition, puis une association spatiale entre les apparentés pendant la phase de coopération.

CONCLUSION

Cette synthèse entrouvre brièvement les portes des interactions complexes qui existent entre cycles de vie, structuration socio-spatiale, stochasticité, discrimination des proches génétiques, et l'évolution des comportements altruistes. Une étude plus poussée de ces interactions nécessiterait de mettre en place une hiérarchie de modèles.

Cette complexité pose aussi un certain nombre de questions générales qui restent sans réponse à l'heure actuelle. Tout d'abord, on peut se demander si la socialité évolue globalement au cours de la phylogénie en réponse à de multiples pressions de sélection venant moduler l'intensité des interactions sociales entre apparentés, ou si de nombreux comportements sociaux évoluent indépendamment en réponse spécifique à chaque pression de sélection, la socialité n'étant alors qu'une propriété émergente. De la même façon, on peut s'interroger sur la multiplicité des facteurs génétiques, écologiques et démographiques impliqués dans le maintien de la coopération : la socialité constitue t-

elle un problème avec trop de solutions ? Ainsi, pour Alexander et al. (1991), l'émergence de l'eusocialité dépend à la fois de ressources basiques qui seraient élastiques, divisibles, améliorables, persistantes, protectrices, et défendables, et du type de risques de prédation ... Une solution empirique à ce surdimensionnement est d'envisager des approches statistiques à plusieurs facteurs de l'évolution de la socialité, alors que la théorie doit se charger de mieux définir les liens causaux entre histoire de vie, environnement, génétique et socialité (Crespi et Choe 1997). Finalement, on peut s'interroger sur le rôle fondamental qu'on prête à l'altruisme dans l'apparition de la majorité des formes de socialité. Est-ce que l'altruisme est l'état ancestral ou l'état dérivé par rapport à l'organisation sociale ? La socialité ne pourrait-elle pas être le sous-produit des stratégies de mobilité, soit parce que la socialité émerge en conséquence de fortes contraintes sur la capacité d'émigration comme l'envisage la voie sub-sociale de l'évolution de la coopération (Brockmann 1997; Helms Cahan et al. 2002), ou soit parce que l'association entre partenaires sociaux résulte des processus de la sélection de l'habitat et du partenaire de reproduction, comme Danchin et Wagner (1997) l'envisagent pour la colonialité ? Cette complication oblige à adopter une approche historique et à clairement dissocier les causes de la socialité (e.g., choix de l'habitat) de ces conséquences (e.g., avantages à la vie en groupe, structuration spatiale). C'est dans cette perspective que nous avons envisagé l'effet de l'évolution de la mobilité sur l'émergence de la coopération (chapitre 3).

LES CAUSES SOCIALES DE LA DISPERSION

Cette partie illustre et discute les effets des **propriétés généalogiques et écologiques** des voisinages sociaux sur la dispersion natale et de reproduction du lézard vivipare. Les conséquences sur la dynamique locale et régionale de la population sont aussi explicitées. Ce travail est mis en rapport avec le développement récent d'approches multi-factorielles de la dispersion, et avec les travaux traitant des mécanismes de choix de l'habitat.

INTERACTIONS ENTRE PROCHES GENETIQUES

Une augmentation de la dispersion des filles et une diminution de la dispersion des fils sont observées en présence de la mère (chapitre 4). **Ceci suggère que les filles dispersent pour éviter la compétition avec la mère, alors que les fils évitent la consanguinité avec leurs sœurs.** Des calculs simples, basés sur les valeurs des paramètres du cycle de vie de l'espèce, montrent en effet que le risque d'une rencontre entre un frère et une sœur à l'âge adulte est plus élevé en moyenne que le risque de rencontre entre une mère et son fils. Dans tous les cas, cette expérience suggère qu'il n'existe pas une raison unique à la dispersion des jeunes mais que plusieurs causes sont à l'origine de la dispersion natale (Dobson et Jones 1985 ; Gandon et Michalakis 2001). Il me semble important d'insister dans cette discussion sur trois points de ces résultats et de leur interprétation.

Le premier point concerne la structure logique de l'expérience (voir aussi la discussion de l'Annexe 3). Au cours de notre manipulation, la présence de la mère a été manipulée à l'échelle de l'enclos en gardant ou en substituant toutes les mères biologiques. L'absence des mères dans l'environnement pourrait être perçue comme un signal général de mauvaise qualité de l'environnement, d'une forte prédation ou d'une émigration intense. Cette manipulation n'est donc pas absente de tout biais d'interprétation. Plus généralement, il s'avère bien souvent difficile de déconnecter un élément particulier du déterminisme du comportement de dispersion (Ims et Hjermann 2001). Les sources d'informations véhiculées par la présence de la mère sont ainsi discutées par Léna (1999) et Meylan et al. (2002) : la présence de la mère indiquerait à la fois un risque fort de compétition entre apparentés, un bénéfice par des relations de familiarité, un risque plus élevé de croisements consanguins futurs pour les fils, ou des différences de qualité de l'habitat.

Le deuxième point de discussion concerne la suggestion selon laquelle la dispersion des filles serait expliquée par un évitement de la compétition avec la mère, une suggestion qui s'accorde avec le comportement de dispersion natale du lézard vivipare (Massot et Clobert 1995; Ronce et al. 1998; Sorci et al. 1994). En présence de la mère, on prédirait une augmentation de la dispersion natale sous le contrôle de la mère, qui force des jeunes à disperser afin d'éviter de diminuer la valeur sélective de ses enfants, ou sous le contrôle des jeunes, qui se risquent dans des mouvements de dispersion afin d'éviter de diminuer la valeur sélective de leur mère (Ronce et al. 1998). Même si la structure de l'expérience ne permet pas de déterminer l'acteur qui contrôle le comportement, on peut chercher le scénario le plus vraisemblable. D'une part, les classes d'âge les plus jeunes du lézard vivipare sont les plus sensibles à la densité dépendance, via la croissance natale et l'âge à première reproduction (Le Galliard et al. 2003a; Massot et al. 1992). Ceci induit une asymétrie dans les coûts à la philopatrie : le coût à rentrer en compétition avec sa mère pour une fille est plus élevée que le coût en rentrant en compétition avec ses filles pour une mère. Par ailleurs, nous avons observé une diminution de la survie des jeunes en présence de la mère. Ceci suggère que des interactions agressives aient eu lieu entre la mère et les jeunes, et que les mères ont pu activement tenter d'expulser les jeunes des enclos (voir Annexe 3). **Ces deux observations rendent plus probables l'hypothèse selon laquelle les mères ont contrôlé la dispersion des filles après leur naissance en les incitant à disperser** (*contra* Clobert et al. 1994; de Fraipont et al. 2000).

Finalement, le troisième point de cette discussion concerne la réponse des jeunes mâles, que nous avons interprétée par l'asymétrie compétitive entre sexes et l'évitement de la consanguinité avec les sœurs (voir aussi chapitre 6). Premièrement, nous suggérons que la valeur sélective des mâles est déterminée de manière critique par leurs interactions compétitives avec des mâles adultes. Cette suggestion est en accord avec le fonctionnement et la régulation par la densité des populations naturelles (Massot et al. 1992; Pilorge 1987; Pilorge et al. 1987). Deuxièmement, nous proposons que les jeunes mâles dispersent pour éviter des appariements consanguins avec leurs sœurs. Par exemple, la sexe ratio de la ponte affecte la dispersion en dépendance du sexe : les jeunes mâles dispersent plus

des pontes riches en femelles, et inversement chez les jeunes femelles (Massot et Clobert 2000). Un déterminisme post-natal de la dispersion par l'évitement de la consanguinité pourrait être démontré par des échanges d'apparentés au sein des pontes.

COMPETITION

L'intérêt porté à la densité dépendance de la dispersion est justifié par l'importance de la dispersion comme un mécanisme régulateur de la dynamique des populations (Brown et Kodric-Brown 1977) et par le rôle de la compétition intraspécifique comme une cause ultime de la dispersion (Gadgil 1971). Le signe de densité dépendance de la dispersion des mammifères a été très controversée, en partie du fait de l'ignorance des mécanismes proximaux impliqués, des disparités entre les stades de la dispersion affectés, et de l'influence de l'échelle spatiale (Gaines et McClenaghan 1980; Ims et Hjermann 2001; Lambin et al. 2001). La densité peut agir comme un reflet de l'intensité de la compétition locale pour les ressources ou pour les partenaires (e.g., Denno et al. 1991), mais aussi comme un critère de qualité de l'habitat (Stamps 1991). La densité comme reflet de la compétition locale a un effet positif sur l'émigration (e.g., Aars et Ims 2000) mais un effet négatif sur l'immigration (e.g., Gundersen et al. 2002) : la réponse totale sur la dispersion dépend donc de deux processus antagonistes dont la balance change selon la covariance spatiale de la densité de l'habitat (Ims et Hjermann 2001). Certaines structures de covariance peuvent engendrer des différences de signe et d'intensité de la densité dépendance de la dispersion en fonction de l'échelle spatiale. Par ailleurs, l'importance de la densité dépendance par rapport à d'autres causes de dispersion dépend de la stabilité de l'habitat. Dans des habitats stables, comme ceux du lézard vivipare (Clobert et al. 1994), les causes sociales de la dispersion devraient dominer sur les causes environnementales.

En manipulant le niveau de densité de deux populations connectées, nous avons mis en évidence que **la dispersion natale a diminué dans les populations à haute densité pendant la première année suivant l'introduction** (chapitre 4), **suggérant soit une préférence pour les habitats densément peuplés soit une contrainte sur les mouvements d'exploration**. Par ailleurs, les effets de la densité de la population ne sont pas les mêmes sur les différentes classes d'âge, puisque la dispersion de reproduction est indépendante de la densité (chapitre 4). Le signe de la densité dépendance conduit à des échanges balancés entre fragments d'habitat qui contribuent à maintenir la variance de densité entre populations sur le moyen terme (Annexe 3). Dans le même temps, les paramètres démographiques affectant à court terme la dynamique de la population ne sont pas ou peu affectés par la densité de la population (Annexe 3). Au contraire, il a été montré que l'immigration, la survie, et la reproduction participent à très court terme à la régulation démographique d'un habitat naturellement continue (Massot et al. 1992). **La dispersion et la densité dépendance locale en populations fragmentées s'avèrent donc moins efficaces que dans un contexte de perturbation d'une population continue.**

En manipulant l'occupation d'un voisinage d'arrivée d'un dispersant, nous avons aussi mis en évidence que **la probabilité d'immigration d'un lézard est indépendante de l'occupation de l'habitat par des congénères** (chapitre 5). Le rôle stabilisant de la dispersion sur la dynamique régionale peut alors s'exprimer par l'intermédiaire d'un effet aléatoire de rescousse (Brown et Kodric-Brown 1977; Gundersen et al. 2002; Hanski 1999). A l'échelle de notre dispositif expérimental, la colonisation d'habitat est rapide et efficace : les populations fondatrices croissent du fait d'un afflux continu d'immigrants qui jouissent alors de conditions plus favorables pour leur croissance et leur reproduction (chapitre 5). L'effet rescousse se trouve donc renforcé par une augmentation locale du recrutement reproducteur au sein des populations récemment fondées : processus régionaux et locaux se combinent alors pour diminuer la variance entre populations au sein de la métapopulation.

Ces deux études suggèrent donc une **différence entre la densité dépendance de l'émigration et de l'immigration**. Cette différence pourrait refléter des contraintes sur le comportement d'immigration et l'exploration de l'habitat chez le lézard vivipare (chapitre 5). D'autre part, les différences d'intensité de la densité dépendance entre les deux expériences peuvent être expliquées par l'échelle de la perturbation : autour de la capacité de charge supposée dans la première expérience, et depuis une densité nulle jusqu'à la densité de charge du milieu dans la deuxième expérience. Ainsi, la relaxation compétitive observée au cours de la dynamique de colonisation traduit probablement le fort contraste initial de densité (mais voir les problèmes d'interprétation de la première expérience discutés dans l'Annexe 3). Ces deux points pourraient être éclaircis par des expériences testant les effets de la densité de la population aux différents stades de la dispersion, et en manipulant une gamme plus large de densité de population. Il serait alors intéressant d'identifier les paramètres démographiques impliqués dans la régulation des effectifs en fonction de la densité locale de la population et du contraste de densité à l'échelle régionale (voir par exemple Andreassen et Ims 2001).

Une partie des asymétries compétitives dans la population peut être expliquée par le rôle différent des mâles et des femelles dans la compétition (voir chapitre 6). Notre perturbation de la sexe ratio de la population confirme que ces asymétries jouent un rôle significatif dans les décisions de dispersion. Le biais sexuel de la dispersion natale n'est pas affecté par la sexe ratio adulte de la population, suggérant que **la compétition intrasexuelle entre les jeunes et les adultes n'est pas impliquée dans la dispersion natale**. Par contre, la perturbation de la sexe ratio adulte a affecté la dispersion de reproduction des femelles après introduction, ce qui suggère que **la compétition pour les ressources a incité à la dispersion du sexe en général philopatricque**.

DISPERSION, CHOIX D'HABITAT ET INFORMATION

Un point de vue empirique et théorique consiste à considérer que la dispersion découle de la sélection de l'habitat (Danchin et al. 2001; Doligez et al. 2003; Stamps 1991). Cette approche a l'avantage (i) d'explicitement clairement le rôle des *facteurs proximaux*, en particulier des critères de

choix de l'habitat, (ii) de considérer le processus de dispersion dans sa dimension ontogénique, et (iii) de générer des prédictions testables par l'observation du comportement de dispersion des individus (Stamps 2001). Quels sont les changements comportementaux ou physiologiques impliqués dans la réponse des jeunes à la présence de la mère ? Les effets de la densité sur la dispersion natale sont ils directs (Aars et Ims 2000), ou indirects comme chez certains rongeurs (Andreassen et Ims 2001; Nunes et al. 1998) ? Quelle est la nature de l'information véhiculée par la présence de la mère, la densité de la population, ou la sexe ratio de la population ? Ces questions resteront ici en suspens parce que nous avons pris le parti de traiter ces mécanismes physiologiques et comportementaux comme une boîte noire. Pourtant, il me semble fondamental de mieux comprendre les modes d'action des causes sociales de la dispersion décrites dans cette thèse (Dufty et al. 2002; Ims et Hjermann 2001). Un tel agenda de recherche nécessiterait dans un premier temps de retourner dans les populations naturelles afin d'étudier l'association entre ces paramètres et la qualité de l'habitat, d'en décrire la variation spatio-temporelle, et de mettre en rapport cette variabilité avec l'échelle spatiale de la dispersion.

L'approche de la sélection de l'habitat a un deuxième intérêt. En considérant l'acte de mouvement dans sa dimension d'échantillonnage, elle voit la dispersion comme un processus de recherche, de collecte et d'échange d'informations. En bougeant d'un habitat à un autre, la dispersion déplace ainsi une histoire individuelle qui peut se donner à lire par des congénères. Dans certains contextes, cette histoire pourrait être utilisée pour refuser les interactions sociales avec les immigrants (Perrin et Lehmann 2001), mais elle peut aussi être considérée comme une source d'information intéressante sur les populations voisines. **On voit donc que la dispersion n'est pas seulement un transfert d'individus et de gènes entre populations, mais aussi un transfert d'information.**

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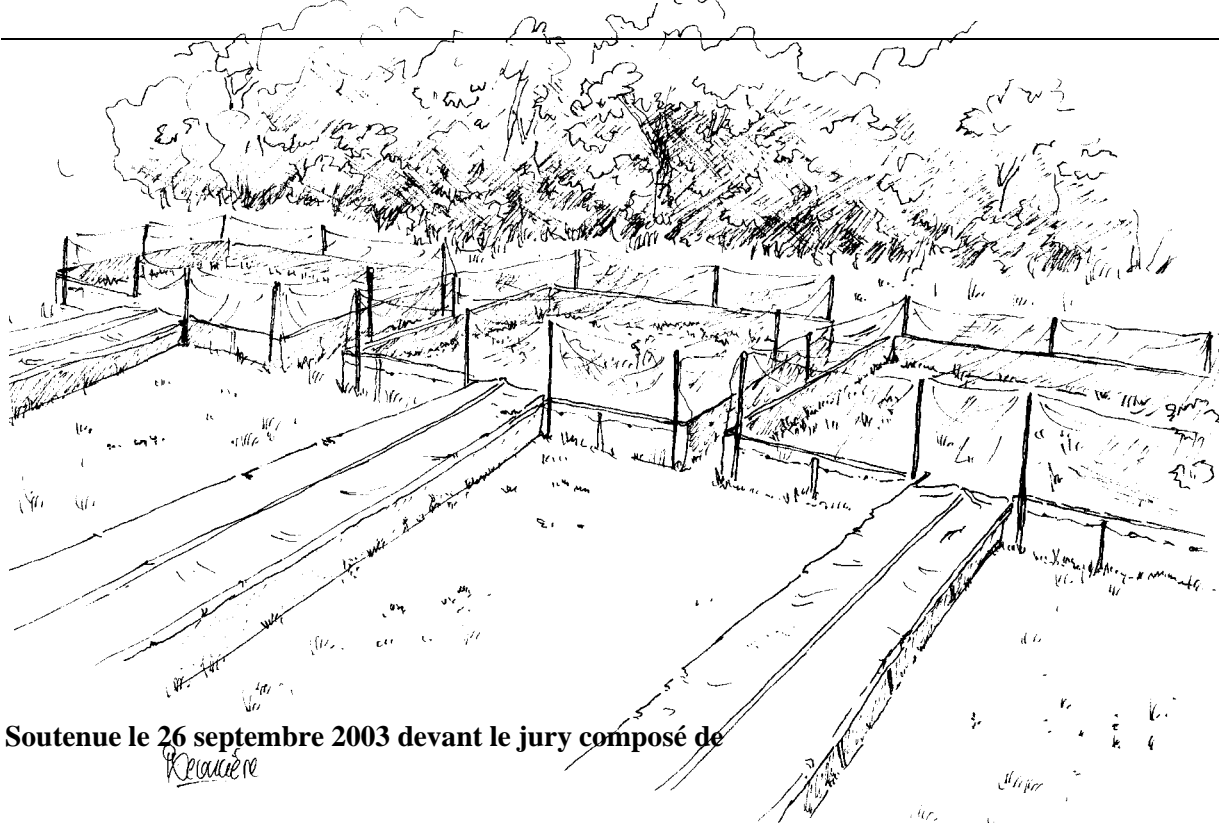
UNIVERSITE PIERRE ET MARIE CURIE - THESE DE DOCTORAT DE L'UNIVERSITE PARIS VI

SPECIALITE : ECOLOGIE

PRESENTEE PAR JEAN-FRANÇOIS LE GALLIARD

POUR OBTENIR LE GRADE DE DOCTEUR DE L'UNIVERSITE PARIS VI

INTERACTIONS SOCIALES ET DISPERSION DANS DES POPULATIONS
STRUCTUREES DANS L'ESPACE - ANNEXES



Soutenu le 26 septembre 2003 devant le jury composé de

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ANNEXE 1 – COOPERATION ET ALTRUISME



“How the workers have been rendered sterile is a difficulty ; but not much greater than that of any other striking modification of structure ; for it can be shown that some insects and articulate animals in a state of nature occasionally become sterile; and if such insects had been social, and it had been profitable to the community that a number of should have been annually born capable of work, but incapable of procreation, I can see no especial difficulty in this having been effected through natural selection”. C. Darwin dans *The origin of species*. 1859.

Attention : les appels de chapitre dans cette partie font référence aux chapitres de l’ouvrage dans lequel cette partie va a être publiée, pas aux chapitres de la thèse !

ALTRUISM AND COOPERATION

Jean-François Le Galliard & Régis Ferrière

ABSTRACT

Cooperative behaviours are widespread in human societies, but also in many other animals and in some plant species. Cooperative interactions usually involve altruistic displays where individuals engage in costly activities with positive effects on conspecifics fitness. This chapter reviews empirical and theoretical researches conducted on altruism across several systems and ecological contexts. We first define altruistic behaviours and present the evolutionary dilemma associated with these cooperative interactions. We then review proximate components of altruistic behaviours, with a specific focus on genetic determinism of complex social interactions and behavioural plasticity. We interpret the costs and benefits of altruism as selective pressures acting on the adaptive evolution of cooperative interactions. This allows us to present several theoretical explanations for the evolution and maintenance of unconditional and conditional altruism. We broaden the scope of our review, and consider how higher-level cooperative structures (e.g., colonies) emerge from competitive interactions among lower-level units (e.g., individuals). We review three mechanisms that can regulate conflicts within animal societies: integration costs, task sharing, and dominant control. We also illustrate the evolutionary fragility of cooperative associations by discussing when and how cooperative breeding and eusociality have been lost repeatedly during evolution.

Chapter 14 of « Introduction à l'écologie comportementale » textbook edited by E. Danchin, L.-A. Giraldeau and F. Cézilly.

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Key-words: cooperation, altruism, sociality, costs and benefits, game theory, kin selection, reproductive sharing, kin recognition, phylogeny.

ALTRUISME ET COOPERATION

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RESUME

Les comportements de coopération sont caractéristiques des sociétés humaines, mais aussi de nombreuses autres espèces animales et de certaines espèces de plantes. Les interactions coopératrices impliquent fréquemment des actes altruistes où les individus s'engagent dans des comportements coûteux au profit de leurs congénères. Ce chapitre présente une revue des travaux empiriques et théoriques menés sur l'altruisme dans divers contextes écologiques. Nous commençons par définir les comportements altruistes et par poser les problèmes évolutifs associés à l'existence de ces traits. Nous faisons ensuite une brève revue des mécanismes proximaux contrôlant l'expression de ces comportements, en particulier du déterminisme génétique et de la plasticité comportementale. Nous interprétons ensuite les coûts et les bénéfices de l'altruisme comme des pressions de sélection agissant sur l'évolution adaptative de ces comportements. Nous présentons alors différentes explications théoriques pour l'évolution de l'altruisme inconditionnel et conditionnel. Nous élargissons ensuite le sujet de notre chapitre pour considérer comment des structures coopératrices intégrées, comme une colonie, peuvent émerger d'interactions compétitives entre des entités indépendantes d'un niveau biologique inférieur, comme les individus. Nous discutons trois éléments de régulation des conflits opérant dans les sociétés animales : les coûts à l'intégration, le partage des tâches, et le contrôle. Nous illustrons finalement la fragilité des associations coopératives à l'aide d'exemples de pertes de la reproduction coopérative et de l'eusocialité au cours de l'évolution.

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Mots-clés: coopération, altruisme, socialité, coûts et bénéfices, théorie des jeux, sélection de parentèle, partage de la reproduction, reconnaissance des apparentés, phylogénie

1. INTRODUCTION

Dans la litière d'une forêt tempérée, les cellules solitaires du microorganisme *Dictyostelium discoideum* initient un lent processus d'agrégation depuis que les ressources ont commencé à manquer. De plus en plus dense, la colonie cellulaire devient vite une masse cohérente qui produit un corps de fructification à la suite d'une intense communication chimique. Un pédicelle se différencie à la base et une capsule de spores se développe au sommet (Fig. 1). Les cellules du pédicelle se vident progressivement de leur contenu, puis meurent. Les cellules de la capsule donnent des spores résistantes, dont la dispersion et la protection face aux prédateurs sont garanties par le sacrifice des cellules du pédicelle. Pourquoi certaines cellules sacrifient-elles leur reproduction au profit de la multiplication et de la dispersion efficace d'autres cellules ?

Dans cette même forêt, des insectes herbivores consomment une jeune plante en cours de germination. La plante agressée émet des substances chimiques produites à la suite d'un coûteux processus physiologique. Cette substance ne participera pas à la défense individuelle de la plante contre les prédateurs, mais informera les plantes voisines du danger imminent. Alarmées, les plantes voisines vont mettre en place des réactions de défense préventive. Au même moment, un jeune Campagnol roussâtre *Clethrionomys glareolus*, mammifère social d'Europe, est surpris par un Renard roux et émet un cri pour avertir les membres de sa famille de la présence du dangereux prédateur. Mais, ce même cri favorise la détection du rongeur qui est capturé par le renard. Pourquoi un individu informe-t-il ses congénères de la présence d'un danger à ses propres dépens ?

Dans la canopée, deux oiseaux s'engagent dans un épouillage mutuel au cours duquel chaque individu retire patiemment et séquentiellement les puces de son partenaire. Ces deux individus investissent dans une forme de coopération mutuelle qui implique une suite de comportements orientés vers le seul profit du partenaire. De telles activités coopératives réciproques s'observent chez les oiseaux, les mammifères et certains poissons, mais aussi au sein des sociétés de primates dont l'homme. Qu'est-ce qui garantit la stabilité d'une coopération réciproque face à une stratégie consistant à tirer avantage de son partenaire sans jamais lui retourner la faveur ?

Tous ces comportements relèvent d'une *coopération* entre individus *altruistes* de la même espèce. L'origine et l'évolution de la coopération entre altruistes pose un problème fondamental à l'écologie comportementale, dont l'analyse par des approches théoriques et empiriques fait l'objet de ce chapitre.

2. POSITION DES PROBLEMES

Dans cette section, nous posons les définitions qui seront utilisées dans ce chapitre : comportement altruiste, interaction coopérative, structure sociale. Ces notions conduisent aux principaux problèmes abordés dans les sections suivantes : mise en évidence d'un déterminisme

génétique, identification et mesure des pressions de sélection, dynamique adaptative et évolution conjointe d'autres caractères du comportement et du cycle de vie.

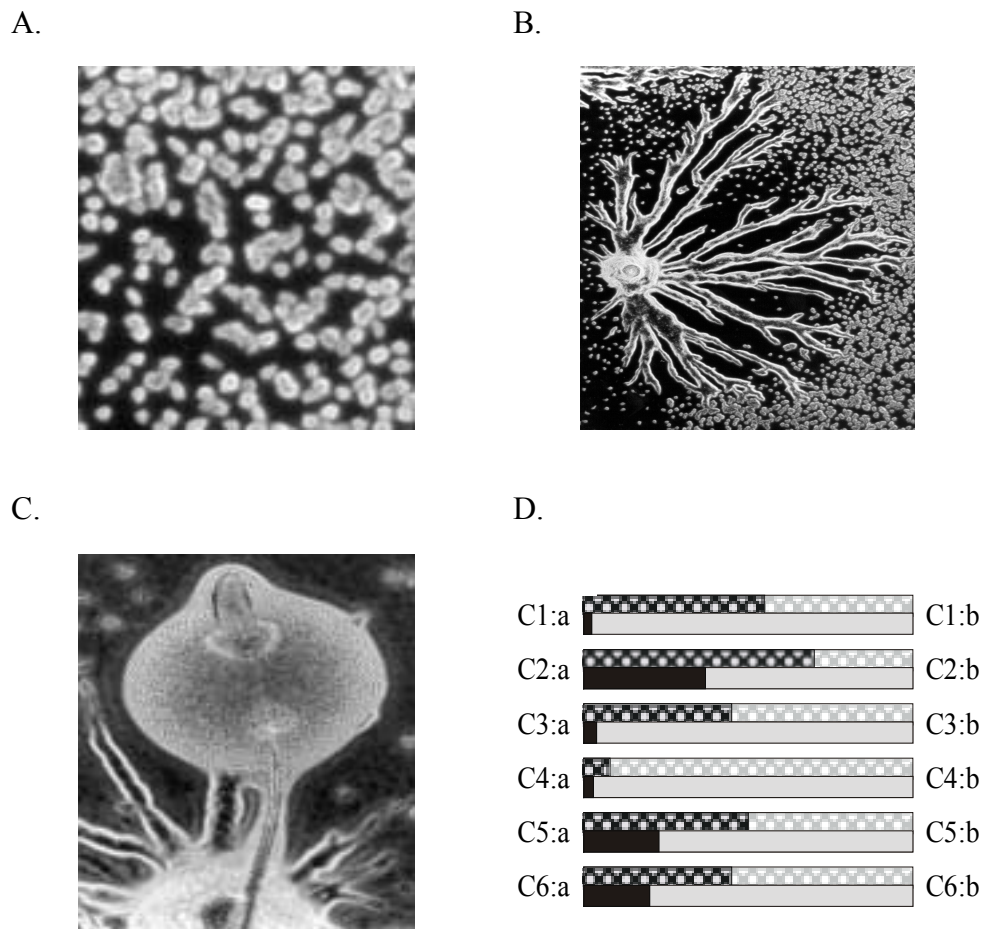


Figure 1. L'organisation sociale de l'amibe *Dictyostelium discoideum* dépend des conditions environnementales. A. Forme solitaire. Les cellules sont dispersées. B. Limace. Elle se met en place par l'agrégation des cellules solitaires en réponse à un appauvrissement de la qualité nutritive de l'habitat. C. Corps de fructification. Cette structure résulte de la différenciation de la limace en un pédicelle, structure longue et étirée faite de cellules en apoptose, et en un sore de spores résistantes dispersives. Photographies de T. Tully. D. Proportion des cellules dans le pédicelle (ligne basse) et le corps de fructification (ligne haute) pour deux clones (clone de gauche, noir ; clone de droite, gris) dans une construction chimérique. Les cellules de certains clones ne sont pas équitablement réparties entre la lignée somatique du pédicelle et la lignée germinale du corps de fructification (d'après la Figure 1 dans Strassmann et al. 2000).

2.1. Altruisme, coopération, socialité : définitions

On parle de comportement individuel *altruiste* et d'une activité collective de *coopération* dans une population de l'espèce considérée lorsque, toutes choses égales par ailleurs :

- Chez un individu isolé, l'expression du comportement se traduit par un effet net négatif sur le succès reproducteur. On parle d'effet direct négatif.

- En société, définie comme l'ensemble des congénères en interaction, l'expression du comportement se traduit par un effet net positif sur le succès reproducteur des congénères. On parle d'effet indirect positif.

La coopération altruiste suppose donc une activité collective dont bénéficient certains partenaires (Connor 1995). Notons que si l'altruisme individuel établit *de facto* une forme de coopération au niveau du groupe, la coopération peut aussi émerger d'autres types de comportements individuels qui ne seront pas considérés dans ce chapitre. Une classification fonctionnelle des comportements de coopération altruiste est présentée dans le Tableau 1. On parle de coopération symétrique (versus asymétrique) si l'effet net positif est distribué équitablement (ou non) entre individus du groupe. Par exemple, la division des activités de défense, d'alimentation, de soins aux jeunes et de reproduction au sein d'une colonie d'Abeilles mellifères (*Apis mellifera*) traduit une coopération asymétrique au sein de la colonie. Par contre, le nettoyage mutuel chez l'Impala *Aepyceros melampus*, un Ongulé africain, s'effectue par la succession d'actes d'épouillages réciproques et fournit un exemple de coopération symétrique.

Tableau 1. Typologie fonctionnelle des comportements altruistes

<i>Effet indirect positif sur le congénère</i>	<i>Effet direct négatif sur l'individu</i>	<i>Exemples</i>
	<i>Soins corporels</i>	
Diminution de l'ectoparasitisme	Augmentation risque d'infection Diminution vigilance	<i>Nettoyage réciproque chez l'impala</i> <i>Epouillage chez les abeilles</i>
	<i>Vigilance et alarme</i>	
Diminution de la prédation	Exposition au prédateur Diminution nourrissage individuel Dépense énergétique	<i>Sentinelle des marmottes</i> <i>Cris d'alarme chez les oiseaux</i> <i>Signaux d'alarme des plantes</i>
	<i>Défense des partenaires</i>	
Diminution de la prédation	Exposition au prédateur Diminution nourrissage individuel Dépense énergétique	<i>Soldats des espèces eusociales</i> <i>Attaque collective chez les oiseaux</i>
	<i>Nourrissage collectif</i>	
Succès alimentaire du groupe	Diminution nourrissage individuel Exposition aux prédateurs et parasites	<i>Nourrissage collectif des carnivores</i> <i>Agrégation de microorganismes</i>
	<i>Nourrissage individuel</i>	
Nourrissage du partenaire	Diminution nourrissage individuel Exposition aux prédateurs et parasites	<i>Dons de sang chez des chauve-souris</i> <i>Trophallaxie chez les insectes</i>
	<i>Soins à la reproduction</i>	
Reproduction des partenaires	Succès reproducteur présent diminué Coûts futurs à l'assistance	<i>Ouvrières des colonies d'insectes</i> <i>Auxiliaires des sociétés coopératives</i>

La population est ainsi structurée en *groupes sociaux* d'individus coopérant, et différentes structures de groupes sociaux sont associées aux interactions coopératives. Notons que la seule

agrégation des individus d'une même population ne suffit pas à définir un groupe social. Par exemple, un regroupement d'Etourneaux *Sturnus vulgaris* qui s'alimentent collectivement peut être le résultat du rapprochement d'individus solitaires sur une ressource attractive, sans interaction ni *a fortiori* activité coopérative : on ne parlera pas de groupe social dans ce cas. En revanche, la colonie du microorganisme décrite en introduction peut être qualifiée de société du fait de sa structuration, de l'interaction chimique entre cellules et de l'altruisme de certaines cellules (Crespi 2001).

Chez les oiseaux, différentes structures sociales se distinguent selon le système de reproduction, le partage du nid et des soins aux jeunes (Cockburn 1998). Le mode de reproduction solitaire traduit une coopération pour la reproduction au sein de la sphère parentale. Un partage du nid peut aussi se faire entre duos de femelles associées à des mâles, selon un système de polygynie coopérative. La reproduction dite coopérative implique le partage du nid et la coopération pour l'élevage des jeunes par des individus extérieurs au couple parental. Elle concerne environ 3% des espèces connues d'oiseaux et se décline sous trois formes principales (Brown 1987). Chez les espèces à reproduction dite plurielle, plusieurs couples coopèrent sur le même territoire ou plus rarement sur le même nid, ce qui est le cas du pic à glands *Melanerpes formicivorus*. Chez les espèces à reproduction polygynandrique, plusieurs femelles pondent dans un nid partagé, dont l'incubation et les soins sont assurés par le mâle. Enfin, chez les oiseaux à reproduction coopérative, un couple parental est assisté par des auxiliaires non reproducteurs, comme chez la fauvette des Seychelles *Acrocephalus sechellensis*. Cette variabilité étonnante observée chez les oiseaux a rendu nécessaire le développement d'une classification hiérarchique générale des systèmes sociaux qui reconnaisse cinq formes typiques de socialité (Tableau 2, voir aussi Encadré 1).

Tableau 2. Typologie des systèmes sociaux

Type de société	Soins parentaux aux jeunes	Partage du site de reproduction	Coopération symétrique	Coopération asymétrique	Castes spécialisées
Solitaire	Oui	Non	Non	Non	Non
Colonial	Oui	Oui	Non	Non	Non
Communautaire	Oui	Oui / Non	Oui	Non	Non
Reproduction coopérative	Oui / Non	Oui	Oui	Oui	Non
Eusocial	Oui / Non	Oui	Oui	Oui	Oui

Dans les systèmes à reproduction coopérative ou eusocial, la coopération peut prendre des formes symétriques et asymétriques selon le groupe social considéré (construit d'après Crespi et Yanega 1995 et d'après Crespi et Choe 1997.)

2.2. Pressions de sélection

De manière générale, la démonstration de la nature altruiste d'un comportement requiert une évaluation des coûts et des bénéfices associés, dont la section 4 de ce chapitre détaille des exemples empiriques. L'identification des composantes potentiellement coûteuses ou bénéfiques peut s'avérer problématique, comme en témoigne le cas du comportement d'alarme chez les oiseaux. Le signal

d'alarme d'une proie en présence d'un prédateur est un comportement altruiste si le signal permet la fuite efficace des partenaires et expose l'acteur au prédateur (Hamilton 1964b). Cependant, plusieurs alternatives sont concevables :

- Le cri d'alarme d'un oiseau pourrait n'avoir aucune fonction adaptative (Kitchen et Packer 1999).
- Le cri d'alarme pourrait avantager directement l'acteur en déconcentrant le prédateur ou en diluant son impact sur l'ensemble du groupe (FitzGibbon 1989). Cette possibilité a été corroborée chez une espèce où la surveillance d'un groupe est assurée par des sentinelles (Clutton-Brock et al. 1999b). Ces sentinelles sont en effet des individus à satiété qui bénéficient directement de leur position de vigilance, en étant les premiers à détecter le prédateur ou en étant plus proches d'une retraite potentielle (Rasa 1989; Bednekoff 1997).
- Le cri d'alarme pourrait correspondre à une supercherie de la part de l'acteur pour s'approprier les ressources de ses partenaires en les faisant fuir (Charnov et Krebs 1975).

Avant de prétendre à l'altruisme du cri d'alarme, il faut donc exclure ces trois hypothèses alternatives.

Encadré 1 – Classification des structures sociales

La classification des structures sociales proposée par Crespi et Yanega (1995) et Crespi et Choe (1997) distingue cinq formes typiques de socialité (pour une critique de cette division en échelle voir Sherman et al. 1995; Weislo 1997).

Structure solitaire. La vie solitaire est caractérisée par un partage des soins aux jeunes entre les parents au sein de sites de reproduction distincts entre couples (voir chapitre 11). L'exemple typique de cette structure solitaire est une espèce dont les territoires sont défendus par des couples.

Structure coloniale. La vie coloniale fait intervenir un partage du même site de reproduction sans coopération entre les individus (Danchin et Wagner 1997, voir chapitre 12). Les grandes colonies de reproduction d'oiseaux marins constituent des structures coloniales typiques.

Structure communautaire. La vie en communauté implique une coopération symétrique entre individus au sein de colonies, de sorte que les membres du groupe sont impliqués dans toutes les activités de la colonie. Des sociétés communautaires sont observées temporairement chez certaines espèces de guêpes ou de fourmis lors de la fondation d'une colonie. Par exemple, plusieurs reines non apparentées peuvent participer aux activités de la colonie fondatrice chez certaines fourmis.

Structure de reproduction coopérative. La reproduction coopérative est caractérisée par un partage des tâches entre des individus spécialisés dans la coopération au bénéfice d'autres individus spécialisés dans la reproduction. Cette spécialisation est de nature comportementale et est réversible, comme chez les oiseaux à reproduction coopérative avec des auxiliaires.

Structure eusociale. Les groupes dits eusociaux sont caractérisés par le plus haut niveau de spécialisation entre les partenaires engagés dans la coopération (Wilson 1971; Crespi et Yanega 1995; Weislo 1997). Premièrement, il existe une division de la reproduction, définissant un groupe d'individus accédant à la reproduction (caste reproductrice) et un groupe d'individus dont la reproduction est irréversiblement inhibée (caste non reproductrice). Deuxièmement, il y a une division du travail au sein de la caste non reproductrice. Certains individus participent aux soins envers la descendance ou au nourrissage (ouvriers), et d'autres assurent la défense du groupe (soldats). Des organisations eusociales sont connues chez de nombreuses espèces de l'ordre des Hyménoptères (guêpes, abeilles, fourmis ; Hamilton 1964b, 1975) et des Isoptères (termites ; Shellman Reeve 1997; Thorne 1997), mais aussi chez un Coléoptère (le scarabée *Austroplatypus incompertus*), chez des Thysanoptères (Crespi 1992) ou chez des Hémiptères (Benton et Foster 1992). On connaît aussi des espèces eusociales chez certains Crustacés (crevettes du genre *Synalpheus* ; Duffy 1996) et deux espèces eusociales de vertébrés, appartenant à la famille des Bathyergidae (mammifères rat-taupe ; Jarvis et al. 1994).

L'estimation des coûts et bénéfices associés à un comportement altruiste fournit la base d'une évaluation des pressions de sélection qui peuvent s'exercer sur ce caractère, dont la nature quantitative ne peut être ignorée. Ainsi, différents individus d'une même population peuvent manifester des comportements altruistes plus ou moins marqués. Chez l'impala par exemple, il existe une forte variabilité interindividuelle dans le temps dévolu à l'épouillage. Lorsqu'un individu s'engage dans un comportement d'épouillage collectif, des séries d'actes de nettoyage réciproques sont entreprises pendant plusieurs minutes. Des individus 'tricheurs' car moins altruistes participent moins efficacement au nettoyage de leur partenaire, et des individus strictement 'égoïstes' profitent du nettoyage du partenaire sans en retourner le geste (Hart et Hart 1992; Roberts et Sherratt 1998). La question du déterminisme génétique d'une telle variabilité, fondamentale pour une analyse adaptative de l'altruisme, est posée dans la section 3.

2.3. Origine et stabilité évolutives

La variabilité génétique des comportements altruistes soulève un double problème en écologie comportementale :

- Comment expliquer la sélection d'un phénotype altruiste dans une population ancestrale composée exclusivement d'égoïstes ?
- Comment expliquer la persistance de l'altruisme face à la menace de phénotypes tricheurs produits par mutation ?

Le *dilemme des prisonniers*, un cas d'école de la théorie des jeux (voir chapitres 2 et 7), offre un cadre conceptuel pour aborder ces questions. Ce jeu oppose deux adversaires par des règles qui spécifient les gains remportés selon leur propre stratégie et la stratégie de l'adversaire. Dans le contexte évolutionniste, une partie du jeu correspond à une interaction entre deux individus, la stratégie d'un individu décrit son comportement (supposé héritable), et les gains sont traduits en succès reproducteur. La version originale du dilemme met en scène deux prisonniers coupables d'un larcin. Chaque prisonnier est interrogé séparément par un juge qui détermine la sévérité de leur peine selon leur attitude. Comparée au cas d'un aveu bilatéral, la peine est plus légère si les deux prisonniers nient leur forfait, mais un prisonnier qui nie alors que son complice avoue est beaucoup plus lourdement sanctionné, le compère étant quant à lui récompensé de son aveu par la relaxe (voir Encadré 2).

Le silence et l'aveu des prisonniers symbolisent les notions d'altruisme et d'égoïsme. Notons R le succès reproducteur d'un individu égoïste en interaction avec un autre égoïste. L'égoïsme ne coûte rien à son auteur et ne rapporte rien au partenaire. L'interaction de deux individus altruistes se traduit pour chacun par le coût direct $-c$ et le bénéfice $+b$ reçu de l'altruisme, d'où le succès reproducteur $R + b - c$ pour chacun. Lorsque l'interaction met en jeu deux individus aux comportements différents, le succès reproducteur de l'égoïste et de l'altruiste se montent respectivement à $R + b$ (l'égoïste reçoit le

bénéfice sans payer le coût) et $R - c$ (l'altruiste paye le coût sans recevoir de bénéfice). Ainsi, selon que le partenaire est altruiste ou égoïste, le succès reproducteur d'un égoïste s'élève respectivement à $R + b$ ou R , dans les deux cas supérieur au $R + b - c$ ou $R - c$ correspondant pour un altruiste. Le comportement égoïste se trouve donc immanquablement favorisé. De façon plus précise, si un individu mutant altruiste apparaît dans une très grande population stationnaire ($R = 1$) et 'bien mélangée' (c'est à dire que chaque interaction met en jeu deux individus tirés au hasard dans l'ensemble de la population) où le génotype égoïste domine, le succès reproducteur du mutant n'est que de $1 - c$: la population mutante s'éteint. Si un individu mutant égoïste apparaît dans une telle population ($R + b - c = 1$ et mélange homogène) où le génotype altruiste domine, le succès reproducteur du mutant s'élève à $1 + c$, si bien que la population mutante envahit le système. Ainsi, origine et maintien de l'altruisme posent une énigme dont les sections 5 à 7 de ce chapitre exposent les trois clés :

- l'hétérogénéité naturelle de la population,
- le conditionnement du comportement,
- la hiérarchisation des niveaux de sélection.

La section 8 remet finalement en cause l'idée d'une évolution irréversible de la coopération, en montrant que les mécanismes sélectifs qui sont à l'origine même de l'évolution de l'altruisme peuvent conduire à sa perte adaptative, voire à l'extinction de la population qui en fut le théâtre.

3. GENETIQUE ET PLASTICITE DE LA COOPERATION

L'évolution de tout comportement requiert une variabilité entre individus, une héritabilité de ces variations phénotypiques, et une relation entre comportement et valeur sélective (Endler 1986; Cockburn 1991). Avant d'analyser les coûts et bénéfices associés à l'altruisme (section 4), nous examinons ici le déterminisme génétique et la plasticité phénotypique des comportements altruistes.

3.1. Déterminisme génétique

Alors que le déterminisme génétique du comportement est une hypothèse fondamentale des modèles évolutifs, les données génétiques concernant les comportement altruistes sont très parcellaires, notamment chez les vertébrés.

Bactériophages. Les phages sont des virus qui infectent les bactéries et dont la réplication nécessite la production de substances catalytiques qu'ils produisent eux-mêmes. Turner et Chao (1999) ont comparé les comportements métaboliques du phage $\phi 6$ et de son mutant $\phi H2$. Dans une même bactérie, les substances métaboliques produites par les phages profitent à chacun, mais $\phi H2$ se comporte en égoïste car son taux de production des métabolites est inférieur. La configuration d'un dilemme des prisonniers est confirmée par la mesure expérimentale du taux de renouvellement de

chaque clone. Ainsi, en prenant comme référence la valeur du taux de renouvellement de ϕ_6 dans une bactérie infectée par ϕ_6 exclusivement (avec les notations du dilemme des prisonniers de l'encadré 2, $R = 1$), ce taux pour ϕ_{H2} dans une cellule où ϕ_6 prédomine est presque doublé ($T = 1.99$). Dans une cellule où l'égoïste ϕ_{H2} est seul présent, le taux de renouvellement de ϕ_{H2} lui-même est réduit à $P = 0.83$, et celui de ϕ_6 , à $S = 0.65$. Ainsi les phages présentent des phénotypes altruistes et égoïstes génétiquement déterminés, et dont le bilan des interactions se conforme au dilemme des prisonniers.

Encadré 2 – Tournoi de coopération à un tour entre non-apparentés

On considère un jeu simple entre deux partenaires qui implique deux stratégies, qui sont la coopération C et l'égoïsme D. Les interactions possibles entre deux partenaires C et D peuvent être formulées sous la forme d'une matrice, qu'on appelle aussi matrice des gains du jeu. Dans notre cas, la matrice de ces gains s'écrit :

Gains de l'interaction	Partenaire C	Partenaire D
Acteur C	R	S
Acteur D	T	P

où R est la Récompense de la coopération avec un coopérateur, S est la Supercherie de la coopération avec un égoïste, T est la Tentation de la tricherie avec un coopérateur et P la Punition de l'égoïsme face à un égoïste (Axelrod et Hamilton 1981). On peut directement noter que la formulation du jeu implique les relations de rang $R > S$, $T > P$, $T > S$, $R > P$ et $P = 0$. On va reconstruire la valeur des gains de la matrice sur la base d'hypothèses réalistes et en déduire le résultat évolutif du jeu.

Première situation : coopération non coûteuse et effets additifs. On suppose ici que la coopération est exprimée par un gain a sans coût pour l'individu coopérateur et qu'elle a des effets additifs. Donc, on obtient $R = T = a$ et $S = P = 0$: il n'existe pas de stratégie évolutivement stable du jeu. L'équation aux réplicateurs prédit une ligne d'équilibres neutres en tout point. Cependant, comme une population pure de coopérateurs assure des gains supérieurs à une population pure d'égoïstes, la coopération est avantageuse dans des populations où l'extinction et la dérive sont possibles.

Deuxième situation : coopération non coûteuse et effets synergiques. On suppose ici que la coopération est exprimée par un gain a sans coût pour l'individu ($S = P = 0$) et dont les effets sont synergiques : si le partenaire est un égoïste $T = a$ et si le partenaire est un coopérateur $R = f(a) > a$. Dans cette situation, la coopération est une stratégie évolutivement stable et l'égoïsme est évolutivement neutre : il y a émergence de la coopération à partir d'un seuil d'abondance initiale des coopérateurs.

Troisième situation : altruisme à effet additif. On suppose ici que la coopération résulte en un gain a à effets additifs pour un coût individuel c , ce qui conduit à $R = a - c$, $S = -c$, $T = a$ et $P = 0$. Dans ces conditions, la stratégie C est envahissable par un égoïste D, alors que la stratégie égoïste est évolutivement stable. On prédit donc l'évolution de l'égoïsme dans une population homogène des deux stratégies. On remarquera que si $R > P$, ce jeu correspond précisément à une situation de dilemme du prisonnier (voir texte), ce qui signifie que la coopération peut évoluer si le jeu est itéré.

Quatrième situation : altruisme à effet synergique. On suppose dans cette dernière situation que la coopération résulte en un gain a à effets synergiques et avec un coût c , ce qui conduit à $R = f(a) - c$, $S = -c$, $T = a$ et $P = 0$. On peut distinguer deux cas selon la hiérarchie des gains de la matrice du jeu. Lorsque l'interaction synergique est trop faible ($f(a) - c < a$), on retrouve la situation précédente avec le cas du dilemme du prisonnier si $0 < f(a) - c < a$. Lorsque $f(a) - c > a$, alors la coopération comme l'égoïsme sont des stratégies évolutivement stables : il y a bistabilité. La coopération se fixe quand la population des coopérateurs est suffisamment abondante.

Amibes sociales. L'amibe *Dictyostelium discoideum* est un microorganisme de la famille des Acrasiales qui possède un comportement social. Le cycle de vie de l'espèce fait alterner des phases solitaires, lorsque les conditions sont favorables pour la croissance individuelle de l'amibe, avec des phases sociales en conditions défavorables. Au cours de cette phase sociale, un agrégat de plusieurs milliers de cellules se forme à partir des cellules solitaires du voisinage et de leurs descendants, puis se différencie dans un corps de fructification (Fig. 1). En moyenne, 20 % des cellules originales contribuent à une lignée somatique du corps de fructification, le pédicelle, alors que 80 % des cellules se différencient en spores. Cette description moyenne de la coopération cache un conflit intense entre les clones pour l'accès à la reproduction. En réalisant des agrégats chimériques à partir de plusieurs clones échantillonnés dans des populations naturelles, Strassmann et al. (2000) ont en effet mis en évidence un polymorphisme génétique du comportement altruiste. D'après ces expériences, la moitié des chimères construites révèlent un clone altruiste sur-représenté dans la lignée somatique par rapport à la lignée germinale et un clone égoïste sur-représenté dans la lignée germinale par rapport à la lignée somatique (Fig. 1D). De tels tricheurs ont aussi été obtenus en laboratoire à l'aide de mutations dirigées, permettant d'identifier des gènes de motilité cellulaire contrôlant génétiquement le comportement social (Ennis et al. 2000).

Insectes sociaux. Une composante génétique a été décrite pour certains comportements sociaux chez des insectes (Moritz et al. 1996; Olroyd et al. 1994; Keller et Ross 1998; Ross et Keller 1998). Chez l'Abeille mellifère *Apis mellifera*, les croisements contrôlés montrent que le comportement de nettoyage du nid et des couvains est soumis à un déterminisme simple impliquant deux gènes dialléliques (Rothenbuhler 1964). La structure sociale polygyne facultative de la fourmi *Solenopsis invicta* est contrôlée par un gène ou un ensemble de gènes au voisinage d'un locus polymorphe connu (Ross et Keller 1998).

3.2. Interaction gène et environnement

Chez certains insectes sociaux, le statut d'ouvrier est déterminé par le contrôle dominant de la reine (Keller et Nonacs 1993), par la nourriture des larves (Wilson 1971) ou par l'âge de l'individu (Stern et Foster 1997). Cette flexibilité de l'altruisme de reproduction illustre de manière générale la dépendance de l'altruisme aux conditions physiologiques, sociales ou écologiques, ou *plasticité*. Parmi les études ayant mis en évidence une telle dépendance, le cas du puceron *Pemphigus obesinymphae* est exemplaire. Le cycle de vie de cette espèce alterne une phase de reproduction parthénogénétique mettant en place des colonies composées de formes reproductrices (larves jeunes) et de soldats non reproducteurs (larves âgées), et une phase de reproduction sexuée associée à la production de formes ailées fondatrices. Le partage équitable entre reproducteurs et soldats est possible si l'homogénéité génétique assure un parallélisme des intérêts individuels (Hamilton 1972). Cependant, des individus non apparentés immigreront dans ces colonies. Dans ce cas, le clone immigrant adopte un comportement

égoïste en participant de façon disproportionnée à la reproduction (Abbot et al. 2001). Cette observation démontre une plasticité de la coopération en fonction du contexte social.

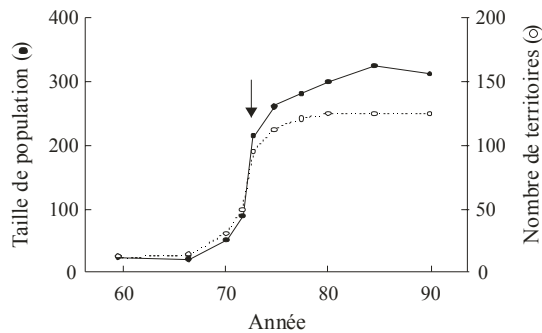


Figure 2. La saturation du nombre de territoires de l'habitat provoque la formation de structures familiales coopératives (flèche) chez la Fauvette des Seychelles pendant un programme de restauration de la population (d'après la Figure 1A dans Komdeur 1992).

Un autre exemple de l'influence de l'environnement sur l'expression d'un comportement altruiste provient de l'étude des sociétés familiales d'une espèce rare et endémique des Seychelles, la Fauvette des Seychelles *Acrocephalus sechellensis* (Komdeur 1992). Il s'agit dans ce cas de la réponse du mode de reproduction – solitaire ou coopératif – à la saturation de l'habitat. Chez ce passereau confiné à quelques îles de l'archipel des Seychelles, au nord de Madagascar, une certaine proportion des jeunes demeure sur le territoire parental pendant plusieurs années, alors que la maturité sexuelle est atteinte dès l'âge d'un an. Les groupes familiaux sont formés par un couple reproducteur et des auxiliaires qui participent à la défense du territoire, à la construction du nid, à l'incubation et au nourrissage des jeunes. Une dynastie familiale se maintient sur le même territoire, du fait de la faible mortalité des adultes, de la fidélité des couples, et de la philopatrie des jeunes (Komdeur 1992). Sur l'île de Cousin, les populations ont fait l'objet d'un programme de conservation et de restauration depuis le début des années 1960. A partir d'une population initiale de 26 individus à reproduction solitaire, la taille de la population a augmenté progressivement pour atteindre environ 300 individus à partir de 1980. Dès 1973, des familles à reproduction coopérative ont été observées sur quelques territoires de bonne qualité, puis sur l'entièreté de l'île à partir de 1982 (Fig. 2). L'apparition de la reproduction coopérative a coïncidé avec la saturation de l'habitat. Des transferts d'auxiliaires dans deux îles voisines ont été réalisés pour tester expérimentalement cette hypothèse. Ces transferts ont provoqué la reproduction solitaire des auxiliaires transférés, ce qui suggère que leur reproduction était inhibée dans l'habitat d'origine, et la saturation des habitats de bonne qualité a rétabli la reproduction coopérative une année après le transfert (Komdeur 1992).

4. COÛTS ET BÉNÉFICES DE L'ALTRUISME : EVALUATION EMPIRIQUE

Toute interaction comportementale correspond à une chaîne de type émission, réception et réaction (Sherman et al. 1997). La production et la réception d'un signal comportent des coûts physiologiques pour le maintien et l'usage des voies de communication. La composante réactive de l'interaction comportementale implique des coûts et des bénéfices pour l'acteur et pour les partenaires.

Ceux-ci dépendent du comportement de l'acteur, de la réponse des partenaires, et du contexte écologique de l'interaction. Ces coûts et bénéfices du comportement peuvent être séparés en *effets directs*, qui affectent directement la valeur sélective de l'acteur, et en *effets indirects*, qui affectent la valeur sélective de l'acteur par l'intermédiaire de son effet sur les partenaires (Fig. 3). Un comportement de coopération altruiste est caractérisé par un gain direct négatif et un gain indirect positif (section 2.1).

A. *Effets directs.*

B. *Effets indirects.*

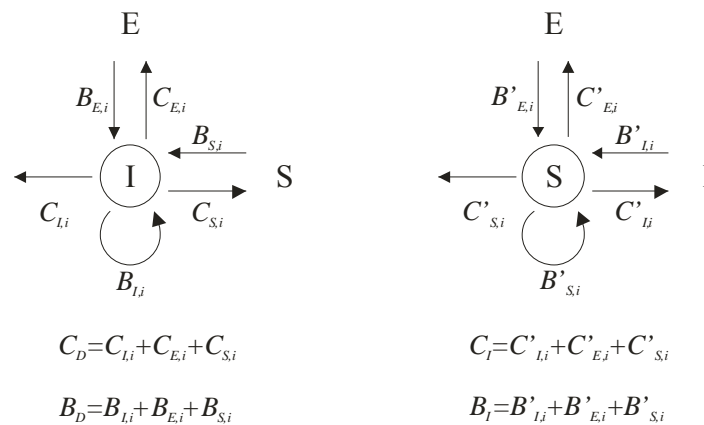


Figure 3. Modèle économique d'une interaction comportementale impliquant un acteur, désigné par I , et des partenaires S dans un contexte environnemental E . Un comportement du type i est caractérisé par des coûts et des bénéfices directs pour un acteur qui dépendent de ses partenaires et de l'environnement. Les coûts et les bénéfices sont définis en référence à l'individu I : les flux sortants sont des coûts et les flux entrants sont des bénéfices. A. Le coût direct C_D d'un comportement se mesure comme le coût individuel du comportement, plus les effets additifs des partenaires sociaux et de l'environnement (respectivement pour le bénéfice direct). Le gain direct de l'interaction correspond à la différence entre le bénéfice direct et le coût direct. B. Le coût indirect C_I d'un comportement se mesure chez les partenaires de l'acteur. Ce coût est la somme du coût à la réception du comportement, plus les effets additifs de l'acteur et de l'environnement (respectivement pour le bénéfice indirect). Le gain indirect de l'interaction correspond alors à la différence entre bénéfice et coût indirect.

Les oiseaux sociaux à reproduction coopérative fournissent un modèle de choix pour l'étude des bénéfices et des coûts associés à l'altruisme de reproduction (Cockburn 1998; Heinsohn et Legge 1999). Les individus altruistes constituent un groupe distinct d'auxiliaires au nid, dont le comportement de nourrissage et de défense du territoire peut être quantifié. Les conséquences physiologiques à court terme peuvent être estimées, de même que les effets à moyen et à long terme sur la valeur sélective des auxiliaires.

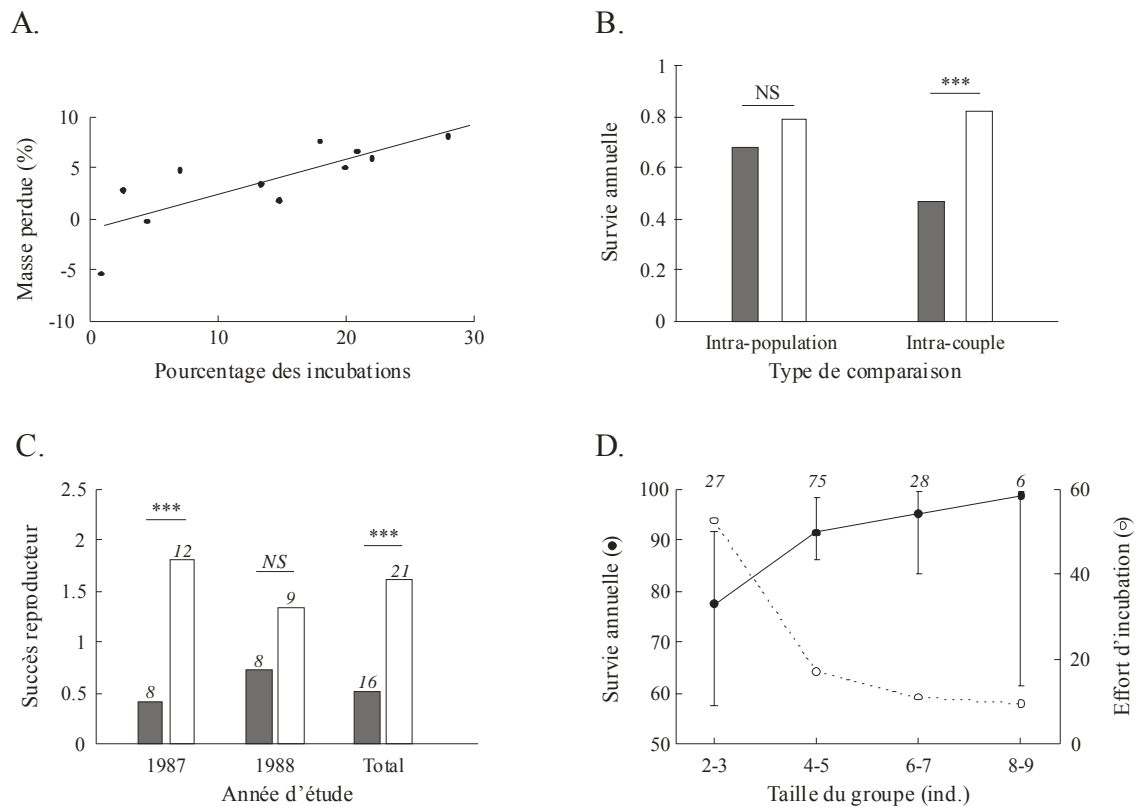


Figure 4. Coûts et bénéfices de l'assistance chez les oiseaux à reproduction coopérative. A. Une augmentation de l'effort de l'assistance chez le Tousseur à ailes blanches se traduit par une diminution de la masse corporelle des auxiliaires, alors que le couple parental ne perd pas de masse pendant l'incubation (d'après la Figure 2D dans Heinsohn et Cockburn 1994). B. Les auxiliaires avec un important investissement altruiste chez le Troglodyte à dos rayé ont une survie réduite (d'après Rabenold 1990, barre pleine : investissement important). C. Une manipulation expérimentale de la présence des auxiliaires chez le Geai des buissons révèle des bénéfices immédiats à l'assistance pendant deux années. Le succès de l'élevage des jeunes jusqu'à 60 jours est plus faible dans les groupes manipulés (barre pleine) que dans les groupes contrôles (d'après la Figure 1B dans Mumme 1992). D. Chez l'Ani à bec cannelé, la femelle reproductrice participe moins intensément à l'incubation des œufs et à l'élevage des jeunes dans les groupes de grande taille, et elle a alors une survie annuelle plus forte (d'après la Figure 19.3 et données de Vehrencamp et al. 1988).

4.1. Coûts directs

L'estimation des coûts à l'assistance repose uniquement sur des données corrélatives. Chez le Tousseur à ailes blanches *Corcorax melanorhamphos*, les auxiliaires sont de jeunes individus inexpérimentés qui contribuent à la construction du nid, à l'incubation et à l'élevage des jeunes (Heinsohn et Cockburn 1994). Les auxiliaires d'un an subissent une diminution de masse proportionnelle à l'effort d'assistance, alors que les individus reproducteurs conservent une masse stable pendant la reproduction (Fig. 4A). Si cette corrélation suggère un coût physiologique direct à l'effort d'assistance chez les jeunes individus, un détrimement sur le long terme est aussi possible. Par

exemple, chez le Troglodyte à dos rayé *Campylorhynchus nuchalis*, l'effort d'assistance est négativement corrélé négativement à la survie de l'individu (Rabenold 1990). Les individus du même sexe et du même groupe ont une survie plus faible quand leur effort d'assistance est intense (Fig. 4B).

4.2. Bénéfices directs

Le coût direct engagé dans le comportement altruiste peut être compensé par des bénéfices directs futurs de ce comportement. En ce sens, le comportement est égoïste sur l'ensemble de l'histoire de vie de l'individu, les bénéfices du comportement étant simplement décalés dans le temps. Ces bénéfices directs peuvent s'obtenir par la réciprocité comportementale du partenaire, mais aussi sans réciprocité. Par exemple, chez les oiseaux à reproduction coopérative, les bénéfices directs futurs peuvent être la possibilité d'hériter le territoire parental (Stacey et Ligon 1991; Cockburn 1998) ou de remplacer un membre du couple (Rabenold et al. 1990; Sherley 1990), l'apprentissage du comportement de reproduction (Heinsohn 1991b; Komdeur 1996), la formation de liens sociaux sous la forme d'alliances (Zahavi 1990) ou un prestige social accru (Zahavi 1995, Encadré 3).

4.3. Coûts indirects

En contribuant directement à l'augmentation du succès reproducteur de son partenaire, un individu altruiste risque d'exacerber les conditions de concurrence locale à son propre détriment (Griffin et West 2002). Des travaux théoriques ont montré que ce coût indirect lié à la compétition entre apparentés pouvait contrebalancer les bénéfices de l'altruisme, ce dont l'exemple des combats entre mâles chez les guêpes du figuier a donné une possible confirmation. Dans ce groupe, les mâles émergeant d'une figue rentrent en compétition plus ou moins intensément pour l'accès aux femelles de la même figue, indépendamment de l'apparentement entre mâles (West et al. 2001). Un coût indirect de concurrence est probablement présent chez les mammifères et les oiseaux à reproduction coopérative (concurrence pour la position dominante ou pour les opportunités de reproduction), ainsi que chez des insectes sociaux, où la concurrence est susceptible de s'exercer entre colonies produites par 'bourgeoisement' (Thorne 1997).

4.4. Bénéfices indirects

Les méthodes expérimentales d'estimation des bénéfices indirects consistent à retirer ou à ajouter des individus au sein des groupes sociaux. Un bénéfice indirect à l'assistance au nid a ainsi été démontré pour le Geai des buissons de Floride *Aphelocoma c. coerulescens* (Mumme 1992). Chez cette espèce, un couple parental est assisté sur son territoire par des jeunes participant à l'élevage des poussins. Le retrait de tous les individus non reproducteurs de plusieurs groupes a permis de mettre en évidence un bénéfice à la présence des auxiliaires pour la survie des oisillons au nid (Fig. 4C). Cet effet a été attribué à une diminution de la prédation des poussins et à une augmentation du nourrissage des jeunes en présence des auxiliaires (Mumme 1992). En réduisant les efforts reproducteurs du

couple parental, les auxiliaires peuvent aussi générer des bénéfices indirects futurs comme une mortalité réduite ou une meilleure reproduction future du couple parental. Chez l'Ani à bec cannelé *Crotophaga sulcirostris*, une espèce où plusieurs femelles pondent leurs œufs dans le même nid, une femelle peut investir moins dans la reproduction au sein des groupes sociaux de grande taille et voit alors sa mortalité annuelle réduite (Vehrencamp et al. 1988, Fig. 4D).

Encadré 3 - Prestige social chez le cratérope écaillé : applications et limites

Zahavi propose la théorie du handicap pour rendre compte de l'évolution de l'altruisme (Zahavi 1995). Selon cette théorie (voir chapitres 10 et 15), un comportement individuel reflète avec honnêteté la qualité génétique d'un individu si il est différentiellement coûteux. Ces deux hypothèses peuvent valoir pour un comportement altruiste en général : l'acte altruiste est coûteux par définition, et le coût d'un acte altruiste pourrait être plus faible pour un individu de bonne qualité. On peut donc considérer l'altruisme comme un signal honnête de la qualité de l'individu, ce que Zahavi nomme le 'prestige social' dans ce contexte (Zahavi 1990). Ce prestige social indiquerait la qualité de l'individu comme futur partenaire pour la coopération (réciprocité indirecte, voir section 6.2) ou comme futur conjoint pour la reproduction (Zahavi et Zahavi 1997; Nowak et Sigmund 1998).

Dans les groupes du cratérope écaillé *Turdoides squamiceps*, une espèce d'oiseau étudiée depuis 1970 au sein d'une population israélienne, les adultes rentrent en compétition pour l'accomplissement des actes altruistes, en interférant pour le nourrissage des jeunes ou d'autres adultes. Les interactions altruistes procèdent selon une hiérarchie sociale compétitive. Les dominants défendent un accès privilégié à l'altruisme et refusent les bénéfices d'une coopération avec les subordonnés (Carlisle et Zahavi 1986; Zahavi et Zahavi 1997). De plus, les interactions altruistes ne se feraient pas de façon discriminante en fonction de l'apparentement ou du comportement passé des partenaires (Zahavi et Zahavi 1997). La théorie du prestige social semble seule capable de rendre compte de ce faisceau d'observations, mais elle pose cependant une série de problèmes :

- Les observations ont été obtenues au sein de structures sociales atypiques. Des travaux plus récents suggèrent que l'assistance fournie aux jeunes est compatible avec un modèle d'optimisation du succès de la ponte plutôt qu'avec un modèle de compétition pour le prestige (Wright 1997).
- La majorité des interactions sociales ont tout de même lieu entre apparentés, au sein de familles étendues (Wright 1999). La possibilité d'une sélection de parentèle pour l'émergence de la coopération n'est donc pas à exclure.

Les interférences entre individus pour la coopération ont été rarement observées chez d'autres espèces (Reyer 1984; Boland et al. 1997; Wright 1999). Chez les tousseurs à ailes blanches *Corcorax melanorhamphos*, les jeunes auxiliaires font état de leur caractère altruiste en nourrissant préférentiellement les poussins en présence de congénères (Boland et al. 1997).

5. ORIGINE DE L'ALTRUISME INCONDITIONNEL

L'analyse du dilemme des prisonniers résumée en section 2.2 se fonde sur l'hypothèse cruciale d'une population homogène. Ainsi, pour chaque individu la probabilité d'interagir avec un partenaire d'un génotype donné est donnée par la fréquence de ce dernier dans la population tout entière. Dans une très grande population, un mutant n'a donc pratiquement aucune chance d'interagir avec un

semblable. L'hypothèse d'homogénéité est cependant peu réaliste. Il existe des facteurs 'spontanés' d'interactions préférentielles : une mobilité individuelle limitée, l'interaction favorisée par la proximité spatiale ou, plus généralement, une structuration préexistante du tissu social de la population. Dans ces conditions, la probabilité d'interaction d'individus issus d'un groupe très minoritaire peut néanmoins atteindre de fortes valeurs.

5.1. Sélection de parentèle et règle de Hamilton

Dans une très grande population stationnaire initialement dominée par l'égoïsme, notons r la probabilité moyenne qu'un individu altruiste interagisse avec un semblable. Le succès reproducteur moyen d'une population altruiste est donc $1 - c + r \times b$, tandis qu'il vaut 1 en première approximation pour un égoïste si l'on néglige les interactions des résidents égoïstes avec les mutants altruistes, initialement rares. On voit alors que le phénotype altruiste est à même d'envahir la population si $1 - c + r \times b > 1$, c'est-à-dire que la probabilité d'interaction de deux mutants altruistes soit supérieure au rapport du coût sur le bénéfice de l'altruisme : $r > c / b$.

C'est par une approche théorique un peu différente que cette condition de l'origine de l'altruisme fut établie pour la première fois par William D. Hamilton (voir aussi chapitre 3). Pour Hamilton (1964a), la structure familiale d'une population lui confère une forme d'hétérogénéité intrinsèque. Un groupe familial peut être caractérisé par son degré d'apparentement moyen que nous notons encore r . La valeur sélective d'une famille fondée par un individu altruiste est donc égale à $1 - c + r \times b$, où $r \times b$ mesure l'aide distribuée par l'individu focal à ses apparentés. Cette valeur sélective qui mesure le taux de multiplication familial est qualifiée d'inclusive (*inclusive fitness*). Par contraste, la valeur sélective d'une famille fondée par un égoïste vaut simplement 1 (car la population est stationnaire). Ainsi la population familiale fondée par des altruistes se multiplie au point d'envahir le système à condition que la règle de Hamilton s'applique : $r > c / b$. Le mécanisme sélectif mis en jeu procède à un tri au niveau des familles : c'est la sélection de parentèle (*kin selection*). Il est intéressant de remarquer que des calculs effectués dans les contextes de la sélection individuelle ou de la sélection de parentèle conduisent au même résultat – une coïncidence analysée en détail par Taylor et Frank (1996). Il y a donc équivalence entre la mesure de valeur sélective individuelle d'un caractère qui comptabilise ce que reçoit l'individu (et de qui il reçoit), et la mesure de valeur sélective inclusive qui comptabilise ce que donne l'individu (et à qui il donne). Pour un système génétique haploïde, Day et Taylor (1998) ont de plus montré que l'apparentement correspondait à la probabilité qu'un mutant interagisse avec un autre mutant.

Le mérite de la règle de Hamilton est avant tout de démystifier l'avantage sélectif de l'altruisme entre apparentés : des gènes favorisant un comportement altruiste voient le dommage (coût – c) qu'ils causent à leur propre 'véhicule' (l'individu) contrecarré par le bénéfice reçu par les mêmes gènes dans leurs autres véhicules (Dawkins 1976). Cette règle est néanmoins sous-tendue par des approximations drastiques : très grande population, apparentement r constant, et surtout la non prise en compte de

l'ensemble des frictions entre altruistes et égoïstes (Ferrière et Michod 1995, 1996). Imaginons en effet la population dans son contexte spatial. Un petit groupe d'altruistes apparaît dans un ensemble d'égoïstes. L'expansion de ce groupe dépend de la dynamique du noyau du groupe constitué seulement d'altruistes et de la dynamique du bord. On voit ainsi que r possède une forte hétérogénéité : proche de 1 dans le noyau, l'apparentement est variable au bord. De plus, sur ce bord, on ne peut négliger les interactions avec les altruistes pour calculer le succès reproducteur des égoïstes. Axelrod et Hamilton (1981) s'attaquèrent déjà à cette difficulté, mais leurs calculs sont incomplets et reflètent mal la dynamique spatio-temporelle inhérente au processus d'invasion. C'est l'étude numérique de Nowak et May (1992) qui confirma les prédictions de Hamilton : placés sur une grille régulière où les interactions prennent place entre proches voisins, un petit groupe d'altruistes inconditionnels peut envahir une population d'égoïstes, une coexistence durable s'instaurant entre les deux phénotypes. Les expériences mathématiques de Nowak et May (1992) mettent cependant l'accent sur le fait que la *viscosité* de la population – adultes immobiles et dispersion natale restreinte au minimum – peut garantir le fort apparentement requis par la règle de Hamilton.

5.2. Contexte écologique

L'approche de la sélection de parentèle se heurte au 'paradoxe écologique' de l'altruisme soulevé par Taylor (1992b), Queller (1992, 1994) et Wilson et al. (1992). La mobilité individuelle réduite favorise l'évolution de l'altruisme entre apparentés, mais les performances reproductives accrues des altruistes conduisent à une intense concurrence entre apparentés pour des ressources limitées (voir section 4.4). Les modèles suggèrent que l'évolution de l'altruisme demeure possible face à ce coût indirect si la portée des interactions concurrentielles est plus longue que la portée des interactions coopératrices (Queller 1992), si compétition et coopération sont décalées dans le temps (West et al. 2002), ou si les ressources limitées sont mises à disposition par la variation temporelle de l'environnement (Mitteldorf et Wilson 2001; Le Galliard et al. 2003). Ainsi, l'apparentement entre individus bénéficiant du comportement altruiste resterait plus élevé que l'apparentement des individus qui en subissent le coût indirect. Le sort du phénotype altruiste serait alors déterminé par une règle de Hamilton amendée, faisant intervenir ces deux degrés d'apparentement (Frank 1998; Queller 1994).

Cependant, la mobilité individuelle est aussi sensible aux pressions de sélection qui affectent l'altruisme, en particulier à la compétition de parentèle. L'évolution et le maintien de la coopération dépendent donc de l'évolution conjointe de la mobilité, en particulier (Le Galliard et al. en préparation) :

- L'existence d'un coût à la mobilité est cruciale pour expliquer l'origine évolutive de l'altruisme et le maintien d'un degré significatif d'altruisme requiert un coût à la mobilité suffisamment élevé. Entre les valeurs faibles et hautes du coût à la mobilité, on passe d'un état asocial et mobile à un état social et sédentaire.

- Au cours d'une évolution d'un état ancestral solitaire et mobile vers un état social et sédentaire, la dynamique adaptative d'une population passe par une première phase de sélection de la philopatrie préservant l'état asocial, suivie dans un deuxième temps par l'évolution de l'altruisme.

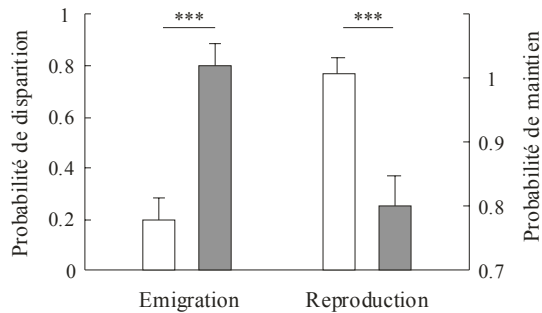


Figure 5. Différence de dispersion et de structure sociale entre un habitat semi-aride (barre pleine) et un habitat non aride (barre vide) chez le Rat-taupe commun. L'intensité de l'émigration est mesurée par la probabilité de disparition d'un individu entre deux sessions de capture. La stabilité sociale des individus reproducteurs (en général un couple) est mesurée par la probabilité de se maintenir à l'état reproducteur dans la même colonie. Dans les habitats semi-arides, l'émigration est plus faible et les couples reproducteurs sont très stables (d'après Spinks et al. 2000).

Le groupe des rats-taupes africains, ou Bathyergidae, définit un niveau taxonomique cohérent pour analyser l'évolution de l'altruisme dans son contexte écologique et mettre à l'épreuve les prédictions théoriques que nous venons de résumer. Les rats-taupes sont des mammifères fouisseurs vivant en couples ou en colonies dans des cavités souterraines qu'ils utilisent pour défendre et exploiter leurs ressources alimentaires (Bennett et Faulkes 2000). Ce groupe comprend un total de 18 espèces dont quatre ont une reproduction solitaire et 14 une reproduction coopérative. Dans chacun des deux genres *Heterocephalus* et *Cryptomys*, il existe une espèce qui peut être considérée comme eusociale : le rat-taupe glabre, *Heterocephalus glaber* (Jarvis 1981), et le rat-taupe de Damaraland, *Cryptomys damarensis* (Jarvis et al. 1994). L'évolution de la reproduction coopérative chez les rats-taupes est associée aux milieux arides. Dans ces habitats, les coûts à la dispersion sont élevés, les opportunités de reproduction indépendante sont limitées et les bénéfices à la vie en groupe sont élevés (Jarvis et al. 1994). Ces espèces semblent se distribuer régulièrement le long d'un gradient d'aridité, l'eusocialité s'observant au sein des milieux les plus arides où la dispersion est la plus faible (Jarvis et al. 1994, 1998; Faulkes et Bennett 2001). Par ailleurs, chez le rat-taupe commun *Cryptomys hottentotus hottentotus*, Spinks et al. (2000) ont observé que la philopatrie est plus forte, la reproduction plurielle est plus rare et les couples reproducteurs sont plus stables dans un milieu semi-aride que dans un milieu non aride (Fig. 5).

Le cas de la reproduction coopérative chez les oiseaux jette aussi un éclairage empirique sur la dynamique adaptative de l'altruisme et de la dispersion. L'hypothèse de la 'saturation de l'habitat' (Brown 1978; Emlen 1982) propose que les individus auxiliaires décalent leur propre reproduction et s'installent sur le territoire parental lorsque les sites de reproduction sont limités. Les individus philopatriques ont alors la possibilité de participer à la défense du territoire parental et de la nichée. Le

comportement d'assistance évoluerait du fait des bénéfices génétiques indirects (Emlen 1997) et des bénéfices directs (acquisition du territoire facilitée) décalés dans le temps (Cockburn 1998). Ce scénario s'accorderait donc à la dynamique adaptative prédite : l'évolution préliminaire de la philopatrie et d'une maturité retardée sous la pression de sélection imposée par la saturation de l'habitat, puis l'évolution de l'assistance à la reproduction.

5.3 Contexte génétique

L'impact de la structure d'apparement sur les coûts et bénéfices de l'altruisme ne peut s'évaluer non plus hors du contexte fixé par le système de reproduction de l'espèce. Un exemple de choix nous est fourni par les Hyménoptères sociaux (guêpes, abeilles, fourmis), caractérisés par un altruisme reproducteur entre femelles. Dans les sociétés les plus simples, la colonie est composée de quelques femelles, souvent des sœurs, partageant le même nid et la protection des œufs (Peeters 1997). Dans les sociétés plus complexes, la colonie est composée d'une seule femelle reproductrice et de très nombreuses ouvrières qui ont parfois complètement perdu la capacité de se reproduire. L'altruisme de reproduction entre sœurs des Hyménoptères est classiquement interprété par leur caryotype particulier (Hamilton 1964a, 1964b, 1972). Les Hyménoptères sont tous caractérisés par des mâles haploïdes, issus du développement d'œufs non fécondés, et des femelles diploïdes, issues du développement d'œufs fécondés. Le sexe de la descendance est sous un double contrôle. Les reines peuvent assurer volontairement la fécondation d'un ovule pondu par le sperme stocké dans une spermathèque abdominale. Les ouvrières participent au nourrissage des différents types d'œufs et peuvent pondre leurs propres œufs non fécondés.

On considère ici une société où toutes les femelles sont capables de s'accoupler et produisent uniquement des filles (voir section 8.4 pour le rôle des mâles). Au sein d'une société monogynandrique, l'apparement moyen d'une femelle avec ses sœurs ($r = 0.75$) est plus élevé que l'apparement de cette même femelle avec ses filles ($r = 0.5$, Fig. 6A). Selon la règle de Hamilton, cette asymétrie biaise le comportement des femelles en faveur d'une participation altruiste à l'élevage de sœurs plutôt que de leurs propres filles (Hamilton 1964a). Dans une colonie polygyne, plusieurs reines partagent la reproduction (jusqu'à plus de 100 reines chez certaines espèces de fourmis), ce qui diminue l'apparement entre sœurs au sein de la colonie. Quand la colonie consiste de trois reines sœurs accouplées à des mâles non apparentés et participant équitablement à la reproduction, l'apparement moyen entre les sœurs chute à $r = 0.375$ (Fig. 6B, Pamilo 1991). Dans une colonie polyandrique, plusieurs mâles participent à la descendance (jusqu'à 17 mâles chez l'Abeille mellifère). Si la colonie consiste d'une seule reine accouplée à trois mâles non apparentés qui contribuent équitablement à la descendance, l'apparement moyen entre les sœurs chute à $r = 0.42$. Ainsi, l'haplodiploïdie n'est pas suffisante pour permettre le maintien de l'altruisme de reproduction chez de nombreuses espèces d'Hyménoptères caractérisées par un faible apparement entre sœurs. La stabilité de l'altruisme reproducteur entre femelles dans ce contexte pourrait s'expliquer par de plus

forts bénéfiques à la coopération, par un contrôle maternel dominant ou par la stérilité irréversible des ouvrières (Keller 1995). Bien que l'haplodiploïdie favorise la coopération entre femelles, elle n'est plus reconnue comme le facteur unique expliquant l'évolution de l'eusocialité dans ce groupe taxonomique (Choe et Crespi 1997).

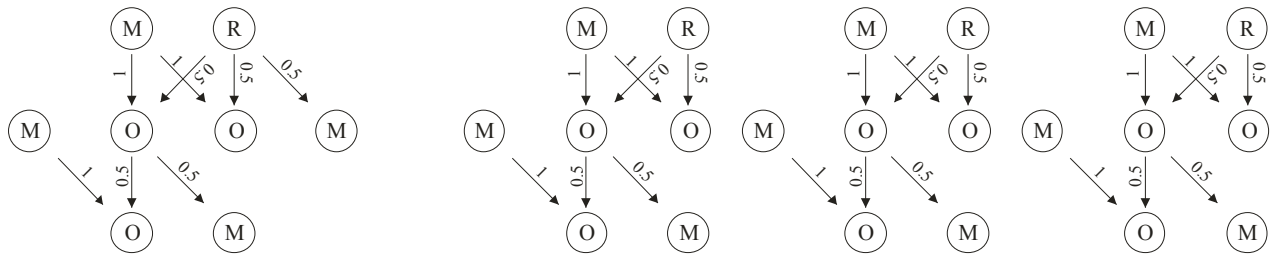
A. *Société monogynandrique.*B. *Société polygyne.*

Figure 6. Effet de l'asymétrie génétique sur l'altruisme de reproduction entre sœurs chez les Hyménoptères. Règles d'apparentement dans une société monogynandrique (A) et polygyne (B, trois reines). La valeur associée à chaque flèche correspond à l'espérance de la proportion des gènes du parent transmis à un descendant (identité génétique par descendance). Les lettres désignent les reines (R), les ouvrières (O), et les mâles (M).

5.4. La facilitation par effet de groupe

La 'facilitation par effet de groupe' est parfois proposée comme alternative à la sélection de parentèle pour expliquer l'origine et le maintien de certaines formes de coopération entre altruistes (Jarvis et al. 1994; Emlen 1997; Bernasconi et Strassmann 1999; Clutton-Brock 2002). Clutton-Brock (2002) souligne que l'effet de groupe (augmentation du bénéfice indirect de l'altruisme avec la taille du groupe social) pourrait opérer dans les sociétés de vertébrés et d'invertébrés à reproduction coopérative, où une plus grande taille de groupe est associée à un plus grand succès individuel dans l'acquisition des ressources (Wilson 1971), l'évitement de la prédation (Queller et Strassmann 1998), la dispersion (Ligon et Ligon 1978), ou l'élevage des jeunes (Brown 1987). Il en va ainsi de la coopération entre reines non apparentées lors de la fondation des colonies chez certaines fourmis (Bernasconi et Strassmann 1999). Pendant cette période, les reines mobilisent les réserves énergétiques stockées dans leurs muscles alaires pour pondre et nourrir une première portée d'ouvrières. Comparées à des fondatrices solitaires, les reines qui s'associent lors de cette phase critique sont avantagées par des dates de ponte plus précoces et des contingents d'ouvriers plus importants (Bernasconi et Strassmann 1999). Par ailleurs, les effets de groupe peuvent aussi augmenter les bénéfices directs futurs, par exemple l'héritage d'un groupe de grande taille et avec une productivité élevée. Des modèles récents ont ainsi suggéré que si les individus partagent équitablement les bénéfices induits par l'augmentation de la taille de groupe, les pressions de sélection induites

conjointement par la structure de parentèle et l'effet de groupe favorisent l'évolution d'un niveau plus élevé d'investissement individuel dans la fonction altruiste (Roberts 1998; Kokko et al. 2001).

Cette facilitation par effet de groupe pourrait fonctionner par des mécanismes de compétition entre groupes sociaux, comme ceux observés chez certains oiseaux à reproduction coopérative (Cockburn 1998) ou chez certaines fourmis (Wilson 1971). Cette compétition peut s'exprimer par le phénomène étrange du rapt décrit chez un oiseau à reproduction coopérative d'Australie, le Tousseur à ailes blanches. Ce phénomène implique une participation coopérative à l'élevage de la portée de jeunes individus non-apparentés qui ont été détournés de leur propre nichée (Connor et Curry 1995). Plusieurs études ont démontré que la présence d'un minimum de cinq auxiliaires est nécessaire au succès de la ponte, de l'élevage et du premier hivernage de la couvée du groupe chez cette espèce (Heinsohn et Legge 1999). La viabilité des petits groupes s'en trouve fortement compromise. L'enlèvement offre une solution adaptative, car les jeunes détournés peuvent recruter au sein de leur famille d'élevage (Heinsohn 1991a, 1991b). En quatre années de suivi, Heinsohn (1991a) a ainsi décrit 14 cas de transferts de jeunes oiseaux dépendants vers des groupes non apparentés, dont quatre ont été attribués directement à de l'enlèvement.

L'argument de la facilitation par effet de groupe s'avère moins convaincant dans d'autres cas où les individus semblent ajuster leur investissement à la taille du groupe (Kitchen et Packer 1999). Par ailleurs, ces bénéfices ne constituent pas une condition suffisante pour assurer la stabilité évolutive de l'association altruiste. Comme nous le suggérons dans l'Encadré 2 pour un cas simple, il est important que le bénéfice de l'association soit une fonction disproportionnée de l'investissement individuel. Et même dans ce cas, le bénéfice de la coopération n'est pas suffisant pour permettre l'évolution de l'altruisme dans une population initiale d'individus égoïstes. La portée théorique du seul mécanisme évolutif de facilitation par effet de groupe semble donc limitée (*contra* Clutton-Brock 2002).

6. ÉVOLUTION DE L'ALTRUISME CONDITIONNEL

Si la sélection de parentèle offre une explication générale de l'origine adaptative de la coopération, le problème de la stabilité évolutive d'un investissement élevé dans un comportement altruiste ne se trouve résolu que dans certains cas, notamment lorsque la mobilité individuelle est limitée (Le Galliard et al. 2003). Houston (1993), à la suite des travaux de Dugatkin et Wilson (1991) et de Enquist et Leimar (1993), a souligné qu'un phénotype tricheur mobile éviterait de multiplier les interactions peu avantageuses au sein de son propre clan et serait susceptible de mettre en péril la pérennité d'une population altruiste sédentaire. Face à ce danger, le conditionnement de l'altruisme – ne coopérer qu'à certaines conditions – offre une possible garantie de stabilité. Dans cette section, nous considérons les mécanismes individuels et les conséquences évolutives du conditionnement comportemental, selon qu'il implique l'état de l'agent ou l'état du partenaire.

6.1. Conditionnement à l'état de l'agent

Dans le cas où l'interaction entre partenaires est répétée, un individu peut conditionner son comportement altruiste aux interactions précédentes. A la fin des années 1970, Robert Axelrod exécuta des tournois informatiques d'un dilemme des prisonniers itéré opposant différentes stratégies conditionnelles – certaines très complexes utilisant l'information tirée des interactions passées pour prédire le comportement futur du partenaire et ajuster leur propre comportement (Axelrod et Hamilton 1981). Le vainqueur quasi-systématique sortit pourtant des stratégies les plus simples : il s'agit de 'donnant-donnant' (*Tit-For-Tat*, TFT), qui coopère lors de la première interaction, puis imite le dernier coup du partenaire. TFT est donc prompt à la vengeance, mais dans une population pure du phénotype TFT un observateur extérieur ne perçoit que le comportement coopérateur des individus.

Un calcul simple montre qu'une population du phénotype TFT résiste au parasitisme de mutants égoïstes si la probabilité que l'interaction se répète entre les mêmes individus est suffisamment élevée (Axelrod et Hamilton 1981). Différents facteurs peuvent s'y opposer, comme une mortalité ou une mobilité différentielle des individus altruistes et égoïstes. Ainsi, TFT est incapable d'envahir l'égoïsme ambiant dans une population homogénéisée entre chaque génération (Ferrière et Michod 1995). L'invasion initiale et le maintien de TFT sont néanmoins possibles pour des niveaux de mobilité suffisants et comparables des altruistes et des égoïstes. La mobilité confère à TFT la capacité d'étendre sa répartition à partir d'un foyer initial, et préserve son pouvoir de vengeance à l'encontre d'individus parasites mobiles (Ferrière et Michod 1995, 1996). Le risque d'erreur est aussi facteur de déstabilisation de la coopération par réciprocité car une erreur entraîne une rafale d'égoïsme dans une interaction répétée entre deux individus jouant TFT. Nowak et Sigmund (1993) ont à cet égard découvert une stratégie plus robuste que TFT, dénommée PAVLOV, qui rejoue son propre coup précédent ou son contraire selon que son gain est positif ou au plus nul, respectivement. Ainsi, des actions égoïstes accomplies par erreur entre deux PAVLOV conduisent à l'égoïsme réciproque au coup suivant, puis à la reprise bilatérale de la coopération. La stratégie PAVLOV apparaît très résistante aux erreurs, mais peu apte à s'établir dans une population ancestrale égoïste. Sa supériorité compétitive n'est mise en valeur que lorsque des stratégies plus sévères, sans concessions (telle TFT), ont ouvert la voie en éliminant les égoïstes inconditionnels.

De manière générale, le conditionnement d'un comportement requiert une capacité cognitive minimale de prise et de traitement d'une information (Stephens et al. 2002). La stratégie TFT peut se redéfinir comme conditionnelle à l'état de l'agent à l'issue de l'interaction : si son gain est positif, il se comportera en altruiste ; si son gain est nul ou négatif, il jouera l'égoïsme. Dans une interaction soudée entre partenaires, aucune capacité de mémorisation n'est donc requise. Au contraire, dans un jeu où les paires d'individus en interaction se renouvellent, la mise en œuvre de cette stratégie nécessite une mémoire individuelle. Il peut s'agir du souvenir des partenaires rencontrés à l'occasion d'une ou plusieurs interactions précédentes (Brown et al. 1982; Ferrière et Michod 1996), ou de la

seule aptitude à ‘garder un œil sur ses voisins’ – un individu est alors oublié dès lors qu’il sort du cercle des connaissances (Hutson et Vickers 1995). L’influence des capacités de mémorisation sur l’évolution de stratégies conditionnelles a donné lieu à de multiples expériences informatiques que l’on trouvera résumées chez Lindgren et Nordahl (1994).

La pertinence empirique du conditionnement de l’altruisme et de l’avantage de la coopération à long terme face à un gain immédiat est très discutée. Les stratégies décrites ci-dessus conduisent à l’établissement d’une forme symétrique de coopération, sans doute limitée à certains marchés de biens et services comme l’accès aux ressources alimentaires ou l’épouillage. Par ailleurs, les données appuyant l’hypothèse d’une capacité de vengeance sont peu nombreuses (Clutton-Brock 2002). Ainsi, la même poignée d’exemples continue de circuler dans la littérature de comportement animal (voir Dugatkin 1997) :

- les inspections anti-prédateurs chez les poissons, où par exemple deux épinoches s’entraident pour tester l’agressivité d’un brochet ;
- le commerce des œufs chez les poissons hermaphrodites, qui s’échangent le rôle du mâle et celui, plus coûteux, de la femelle ;
- l’échange de sang entre chauve-souris vampires *Desmodus rotundus*, où des dons réciproques de sang permettent de pallier un manque fatal de nourriture.

La réciprocité n’en demeure pas moins une composante certainement fondamentale de l’organisation des sociétés humaines (Sigmund et Nowak 1999). Ainsi, des expérimentations contrôlées chez l’homme en situation de dilemme des prisonniers confirment l’utilisation prédominante d’une stratégie de type PAVLOV (Wedekind et Milinski 1996) dont la performance est modulée par les capacités de mémorisation des agents, conformément à la théorie (Milinski et Wedekind 1998).

6.2. Conditionnement à l’état du partenaire

Le conditionnement à l’état du partenaire présente une alternative non exclusive qu’envisageaient déjà Eshel et Cavalli-Sforza (1982) sous la forme d’une interaction préférentielle des individus selon leur degré d’altruisme. Un signal direct a été mis en évidence récemment dans certaines sociétés de fourmis, sous la forme d’un gène ‘barbe verte’ déterminant conjointement la reconnaissance de la reine par ses filles ouvrières et la coopération des ouvrières à la reproduction de la reine (Keller et Ross 1998, voir aussi chapitre 2). Un tel conditionnement impliquant une signalisation primaire du caractère altruiste (ici vraisemblablement par un marqueur cuticulaire) est peut-être exceptionnelle, mais deux alternatives mettant en jeu des signaux secondaires ont été envisagées :

- Le conditionnement au signal génétique de l’apparentement (Encadré 4).
- Le conditionnement au signal social de ‘l’image de marque’.

Encadré 4 – Reconnaissance des apparentés

Fonctions. La reconnaissance des apparentés permet quatre formes de discriminations :

- l'évitement de la transmission de maladies par les contacts avec les congénères,
- l'évitement de la compétition avec les apparentés (Hamilton et May 1977, chapitre 9),
- la distribution préférentielle de la coopération vers les individus les plus apparentés (Hamilton 1964a),
- et l'évitement de la consanguinité lors de la reproduction (Bateson 1978, 1983).

Mécanismes. Trois modes majeurs de reconnaissance des apparentés sont reconnus, dont un seul peut être défini comme un mécanisme *sensu stricto* de reconnaissance des apparentés (Grafen 1990; Hepper 1991; Sherman et al. 1997). Cette reconnaissance au sens strict des apparentés fait appel à des *allèles de reconnaissance* : elle passe par une reconnaissance directe de la proximité génétique (Grafen 1990). Par exemple, chez l'ascidie coloniale marine *Botryllus schlosseri* la fusion entre colonies est contrôlée par les allèles du complexe majeur d'histocompatibilité (Grosberg et Quinn 1986). La reconnaissance au sens large assure la même fonction par un mode de reconnaissance indirect. Le premier mécanisme est une *comparaison phénotypique* : l'apparement est évalué par la différence entre la valeur d'un marqueur phénotypique du partenaire et de l'acteur (Lacy et Sherman 1983). Lorsque ce mécanisme utilise une référence phénotypique qui se met en place au cours du développement de l'individu, on dit que l'apparement est estimé par un *apprentissage associatif*. Par exemple, la familiarité est la composante principale de la discrimination entre individus pendant les interactions agonistes chez les écureuils terrestres de Belding (Holmes 1986a). Le second mécanisme est un processus minimaliste qui utilise simplement la *proximité spatiale* comme un indice de l'apparement.

Evolution de la reconnaissance des apparentés et coopération. Les données obtenues chez les vertébrés et les invertébrés suggèrent que la reconnaissance des apparentés est répandue chez des espèces solitaires ou coloniales (Waldman 1988; Hepper 1991). Par exemple, chez les amphibiens, cette reconnaissance affecte le comportement cannibale des têtards (Pfennig et al. 1993; Pfennig et al. 1994). La capacité à discriminer les apparentés semble donc préexister à la socialité et ne fournit donc pas *a priori* une limite à l'évolution de la coopération. Cependant, la socialité a pu favoriser la régression ou l'évolution de certaines formes de reconnaissance. En permettant le contact sur de longues durées entre plusieurs générations, les structures familiales étendues favoriseraient la reconnaissance par familiarité par rapport à un système de reconnaissance allélique (Emlen et Wrege 1994; Emlen 1997). Selon les différents scénarios évolutifs imaginables, l'absence de reconnaissance directe pourrait avoir évoluée (perte récente), être dérivée (absence ancestrale) ou être tout simplement le fait de la répression par un contrôle central. L'évolution conjointe des systèmes de reconnaissance et de la socialité ne peut donc être comprise qu'à l'aide d'études conduites tant dans les espèces coopératrices que non coopératrices. La difficulté majeure de cette approche comparative tient au fait que la reconnaissance dépend du contexte social dans lequel s'exprime le comportement (Sherman et al. 1997; Waldman 1988), donc qu'il est difficile de faire des 'moyennes' par espèce.

Apparement. Agrawal (2001) a étudié l'évolution d'un altruisme discriminant les apparentés avec des erreurs d'acceptation et de refus. L'évolution de l'altruisme discriminant dans une population égoïste est favorisée par une forte proportion d'interactions avec les apparentés et un faible niveau d'erreurs d'acceptation. Ici, l'avantage de l'altruisme dépend essentiellement des bénéfices à favoriser les interactions entre apparentés (Hamilton 1964a). Par contre, l'évolution de la discrimination dans une population altruiste non discriminante est favorisée par une faible proportion d'interactions avec les apparentés et un faible niveau d'erreurs de refus. Dans cette situation, l'avantage de la discrimination tient en effet à sa capacité à rejeter des interactions avec les non apparentés. De plus, Perrin et Lehmann (2001) ont mis en évidence que la discrimination rend possible l'évolution de la coopération malgré les risques accrus de la compétition entre altruistes apparentés

liés à la structure spatiale de la population (Taylor 1992a). La reconnaissance de parentèle constitue en fait un moyen de séparer les voisinages de compétition et d'interaction sociale, en restreignant les interactions sociales entre proches parents (voir sections 4.3 et 5.2). Ces travaux démontrent l'importance d'une aide différentielle entre apparentés, ou *népotisme*, pour l'évolution de la coopération. Ceci nous amène donc à discuter la prévalence et les mécanismes de reconnaissance des apparentés mis en évidence au sein des sociétés coopératives.

Les exemples de népotisme proviennent principalement des oiseaux (Clarke 1984; Curry 1988; Emlen et Wrege 1988; Marzluff et Balda 1990; Mumme 1992) et des mammifères à reproduction coopérative (Sherman 1981; Holmes et Sherman 1982; Owens et Owens 1984). Par exemple, sur la base de données généalogiques récoltées au cours d'une étude à moyen terme (1986-1990) sur la Fauvette des Seychelles, Komdeur (1994) a comparé l'investissement dans la coopération des jeunes individus (2-3 ans) selon qu'ils soient confrontés à des poussins pleins frères ($r = 0.5$), demis frères ($r = 0.25$) ou non apparentés ($r = 0$). Comme attendu, l'investissement dans la coopération augmente avec le niveau d'apparentement au poussin (Fig. 7). Le fait que les auxiliaires distribuent préférentiellement leur aide à des individus apparentés qui les ont nourri, plutôt qu'à des individus apparentés qui ne les ont pas nourri, suggère que le mécanisme impliqué repose sur un apprentissage associatif (Encadré 4). Au cours de la seule étude expérimentale chez les oiseaux à reproduction coopérative, Hatchwell et al. (2001) ont aussi mis en évidence un mécanisme d'apprentissage : les auxiliaires de la Mésange à longue queue recrutent en effet au sein d'une famille indifféremment du statut d'apparentement du couple parental pour peu qu'ils aient été élevés par ce couple. Chez le Rataupe glabre, le népotisme semble peu prononcé malgré l'existence de plusieurs lignées paternelles au sein de la colonie (Lacey et Sherman 1991; Reeve et Sherman 1991). La discrimination des apparentés a été étudiée dans le contexte de l'acceptation d'immigrants au sein de la colonie (O'Riain et al. 1996; O'Riain et Jarvis 1997) et du choix du partenaire (Clarke et Faulkes 1999). Clarke et Faulkes (1999) ont ainsi mis en évidence une discrimination des mâles par les femelles reproductrices reposant sur la familiarité, les mâles non familiers étant préférés par les femelles sexuellement actives. Cette discrimination favoriserait l'intégration des immigrants dans la colonie et limiteraient ainsi les conséquences néfastes de la dépression de consanguinité (O'Riain et Braude 2001). De manière générale, c'est donc la familiarité qui est classiquement invoquée pour expliquer les interactions différentielles chez les vertébrés sociaux (Grafen 1990; Komdeur et Hatchwell 1999). Chez les oiseaux, les indices utilisés sont de nature acoustique (Price 1999; Hatchwell et al. 2001) ou visuelles (Lacy et Sherman 1983), alors que plusieurs travaux suggèrent un rôle des odeurs chez les mammifères, en particulier des marques urinaires (Holmes 1986b). Il n'existe aucun cas de reconnaissance directe chez les vertébrés (Encadré 4), bien que certains auteurs qu'on ne puisse l'exclure en théorie quand le contexte est favorable (faible taille de groupe, forte diversité d'apparentés, forts bénéfices indirects) chez certaines espèces d'oiseaux (Emlen et Wrege 1994; Petrie et al. 1999) ou certains mammifères (Blaustein et al. 1991).

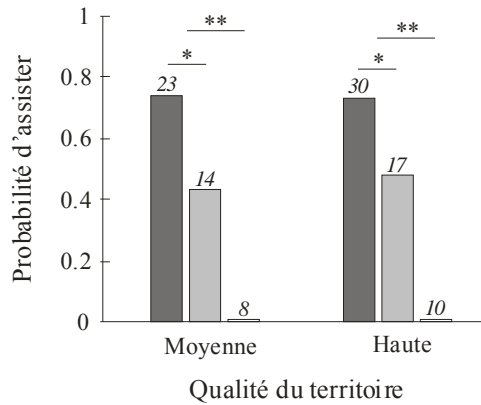


Figure 7. La discrimination des partenaires sociaux chez la Fauvette des Seychelles se traduit par une plus forte coopération envers les jeunes les plus apparentés. La probabilité d'assistance des auxiliaires matures de deux et trois ans des deux sexes de 1986 à 1990 est maximale entre pleins frères (barre sombre), plus faible entre demi frères (barre claire) et nulle entre non apparentés (barre vide) au sein de deux types de territoires (d'après le Tableau 1 dans Komdeur 1994).

Chez les arthropodes eusociaux, le traitement différentiel entre membres de différentes colonies est un comportement fréquent. Les fourmis, les guêpes, les abeilles et les pucerons discriminent des membres appartenant à différentes colonies mais rarement différents apparentés au sein de la même colonie (Pfennig et al. 1983; Gamboa et al. 1986; Getz 1991; Jaisson 1991; Miller 1998). Le mécanisme de la reconnaissance coloniale repose sur une empreinte associée, en général un composant chimique de la cuticule transmis lors des contacts entre membres de la colonie. Au sein d'une colonie, la discrimination des lignées paternelles chez les espèces polyandriques ou des lignées maternelles chez les espèces polygynes serait envisageable si des mécanismes de reconnaissance génétique existent (Keller 1997). Chez l'Abeille mellifère, des expériences ont suggéré l'existence d'un traitement différentiel entre lignées paternelles (Frumhoff et Schneider 1987; Page et Breed 1987; Page et al. 1989). Des travaux plus récents ont cependant relativisé ces résultats du fait (1) du nombre faible de lignées paternelles dans les colonies d'étude et (2) des conditions expérimentales et comportementales artificielles (Carlin et Frumhoff 1990). Dans des conditions plus réalistes, les ouvrières semblent incapables de discriminer les apparentés au sein d'une colonie (Keller 1997).

Les données que nous venons de résumer suggèrent que la reconnaissance des apparentés repose sur des empreintes coloniales ou individuelles dans de nombreux taxons. Les deux seules démonstrations d'une reconnaissance directe concernent la fusion coloniale chez une ascidie marine (Grosberg et Quinn 1986; Grosberg et Hart 2000) et le recrutement des reines au sein des colonies polygynes d'une fourmi (Keller et Ross 1998). A la suite de Grafen (1990), on peut donc dire que la reconnaissance *sensu stricto* des apparentés est très rare, puisque la majorité des mécanismes observés reflètent une reconnaissance de la famille chez les espèces à reproduction coopérative ou de la colonie chez les espèces à reproduction eusociale. Plusieurs facteurs peuvent contribuer à expliquer cet état des lieux paradoxal :

- La mise en évidence empirique d'un mécanisme de reconnaissance par allèle est difficile, ce qui biaiserait les résultats (Grafen 1991). A ce titre, le cas du népotisme chez les Abeilles mellifères démontre toute la difficulté d'une détection expérimentale rigoureuse ;

- Une reconnaissance directe conduit à une augmentation des erreurs de refus si les membres de la même famille partagent des combinaisons différentes d'allèles et peut donc être coûteuse dans certaines situations (Getz 1991) ;
- La discrimination contemporaine résulte d'un compromis entre les reproducteurs et les auxiliaires, ces derniers étant manipulés par le pouvoir central dont l'intérêt est de limiter la discrimination au sein du groupe (Keller 1997, voir section 7).

Image de marque. Il s'agit d'une forme de conditionnement envisagé par Nowak et Sigmund (1998) qui considèrent le cas des populations où il est hautement improbable que le bénéficiaire d'un acte altruiste puisse retourner le geste à son propre bienfaiteur. La réciprocité est néanmoins possible sous une forme indirecte : un individu altruiste, observé par le reste de la population, peut acquérir une « bonne réputation » et se voir aidé, en cas de besoin, sur la base de son « image de marque ». Lors de chaque partie d'un jeu modélisant une telle population, tout joueur voit donc son image de marque affectée par son propre comportement. On peut alors supposer que la coopération s'impose lorsque les individus sont capables d'un jugement discriminatoire : n'aider que les joueurs dont l'image de marque est bonne et s'abstenir vis-à-vis des autres.

Le jeu pose néanmoins un nouveau dilemme non trivial. Supposons qu'un individu discriminateur s'abstienne de coopérer parce qu'il interagit avec un égoïste inconditionnel (dont l'image de marque est forcément mauvaise). Il nuit alors à sa propre image de marque et encourt le risque de se voir refuser ultérieurement l'aide d'un congénère discriminateur qui ne percevra de lui que cette image altérée. En dépit de ce nouveau dilemme, l'analyse mathématique du modèle démontre que la coopération discriminante parvient à supplanter l'égoïsme ambiant. L'image de marque de chaque individu est un score affecté à chaque interaction et la discrimination se fait à hauteur d'une 'barre' sur le score, qui constitue un caractère soumis à mutation et sélection. Ainsi, l'altruiste inconditionnel met la barre au plus bas ; l'égoïste inconditionnel, au plus haut ; et l'altruiste discriminateur, à mi-hauteur. La dynamique adaptative de la population montre alors une alternance d'altruisme inconditionnel, d'égoïsme, et d'altruisme discriminatoire. Une population d'altruistes discriminatoires est alors d'autant plus stable qu'elle est fréquemment agressée par des mutants égoïstes qui purgent la population des altruistes inconditionnels susceptibles de se multiplier par dérive (Nowak et Sigmund 1998).

Dans sa version la plus simple, ce modèle suppose de grandes capacités cognitives individuelles : l'observation et la mémorisation par chaque individu des scores de tous les congénères. La réduction du flux d'information au delà d'un certain seuil met en péril le phénotype discriminatoire, mais la cause même de cette réduction est aussi susceptible de favoriser le développement de nouveaux moyens de communication (Ferrière 1998). Par ailleurs, la pertinence empirique d'un tel modèle reste à démontrer. Alexander (1986) fut sans doute le premier à dégager le concept de réciprocité indirecte dans le cadre de l'évolution des systèmes moraux chez l'homme. Chez

le Cratérope écaillé *Turdoides squamiceps*, les individus semblent se disputer le rôle du donateur pour se forger une bonne réputation, mais l'interprétation de ces comportements demeure toutefois controversée (voir Encadré 3).

7. REGULATION DES CONFLITS

Buss (1987), Maynard Smith et Szathmary (1995) puis Michod (1999) ont introduit et développé la thèse selon laquelle la structuration du vivant en différents niveaux d'organisation (gènes, chromosomes, cellules, organismes pluricellulaires, sociétés) serait le fruit de transitions majeures dans l'histoire de la vie permises par l'évolution de la coopération : coopération des gènes au sein du chromosome, coopération des cellules à l'intérieur de l'organisme pluricellulaire, ou coopération des organismes au sein de leur colonie. Chaque individu du niveau inférieur paye le coût direct de son altruisme et retire le bénéfice indirect que lui garantit le bon fonctionnement de l'unité supérieure à laquelle il appartient. Dans ce contexte, le problème du maintien de la coopération prend une dimension nouvelle dont rend compte la métaphore de la « tragédie des communs » introduite dès la fin des années 1960 par G. Hardin (Hardin 1968) : chacun maximise son bénéfice si tous investissent dans un pool commun, le jeu est miné par la menace de la tricherie mais personne ne peut bénéficier du système si l'égoïsme prédomine. La tragédie des communs est révélatrice d'un conflit essentiel entre niveaux d'organisation : la sélection favorise l'égoïsme entre individus, mais la viabilité de l'unité qui intègre ces individus requiert la coopération. La régulation des conflits entre niveaux d'organisation peut alors émaner du fonctionnement de l'unité supérieure, sous différentes formes :

- Un « coût à l'intégration » imposé à tous les individus du niveau inférieur, indépendamment de leur degré d'altruisme, se traduit par une réduction des bénéfices de l'égoïsme (Michod 1999).
- Un « partage des tâches », où la tâche de reproduction se trouve confinée à une caste particulière, permet une réduction du risque d'apparition d'individus égoïstes et met en jeu la sélection entre unités contre l'égoïsme individuel (Michod 1999).
- L'évolution d'une forme de « contrôle », disposant de moyens coercitifs comme l'éviction du groupe (Johnstone et Cant 1999) ou l'encouragement à l'arrêt des activités égoïstes par des pots de vins (Reeve et Keller 1997), réprime les velléités égoïstes des individus (Ratnieks 1988).

Comprendre les conditions sous lesquelles de tels mécanismes peuvent évoluer nécessite alors de penser l'action de la sélection naturelle à tous les niveaux où elle opère.

7.1. Réduction des bénéfices de l'égoïsme

Le 'jeu des biens collectifs' offre un modèle simple de la dynamique d'un système soumis à la tragédie des communs. Ici, les individus n'interagissent pas directement mais peuvent investir dans une 'mutuelle'. Le capital de la mutuelle augmente et fructifie pour être ensuite redistribué également entre tous les individus, indépendamment de l'investissement de chacun. Comme dans la tragédie des

communs, le gain optimal correspond à l'altruisme de tous, le gain d'un égoïste est toujours supérieur au gain d'un altruiste, et les gains moyens s'amenuisent dès lors que l'égoïsme se répand (Michor et Nowak 2002). Hauert et al. (2002) ont proposé un modèle très simple qui explique alors le maintien de la mutualité, en se fondant sur l'existence d'un 'ticket d'entrée' – la participation à la mutuelle impose un coût à tous les joueurs – et sur l'existence d'un comportement marginal qui décline sa participation au jeu et s'affranchit ainsi du coût du ticket. Les égoïstes s'imposent alors aux altruistes, mais les marginaux dominent les égoïstes, ouvrant la voie à la ré-émergence adaptative de l'altruisme. Dans un tel système où l'altruisme se maintient en coexistant avec les phénotypes égoïstes et marginaux, le succès reproducteur moyen n'est pas supérieur à ce qu'il serait en dehors du jeu, mais le coût de la participation empêche la domination des égoïstes. L'unité intégrant les protagonistes du jeu pourrait être à l'origine de ce coût qui réduit les bénéfices de l'égoïsme.

7.2. Partage des tâches

Chez de nombreuses espèces dont les populations sont structurées en unités sociales, la tâche de reproduction n'est pas distribuée équitablement entre tous les individus. Le degré de confinement de la fonction reproductive, ou 'biais de reproduction', peut être plus ou moins élevé selon l'espèce et selon les conditions environnementales chez une même espèce (Emlen 1982; Vehrencamp 1983; Keller et Reeve 1994; Sherman et al. 1995; Reeve et al. 1998). Un fort biais de reproduction correspond à une structure sociale où un faible nombre d'individus monopolise la reproduction (Fig. 8). Dans le cas extrême de l'Abeille mellifère, les colonies contiennent des milliers d'ouvrières et une seule reine fertile. Un faible biais de reproduction correspond à une division équitable de la reproduction sur l'ensemble des individus (du même sexe), comme chez de nombreuses espèces à reproduction communautaire.

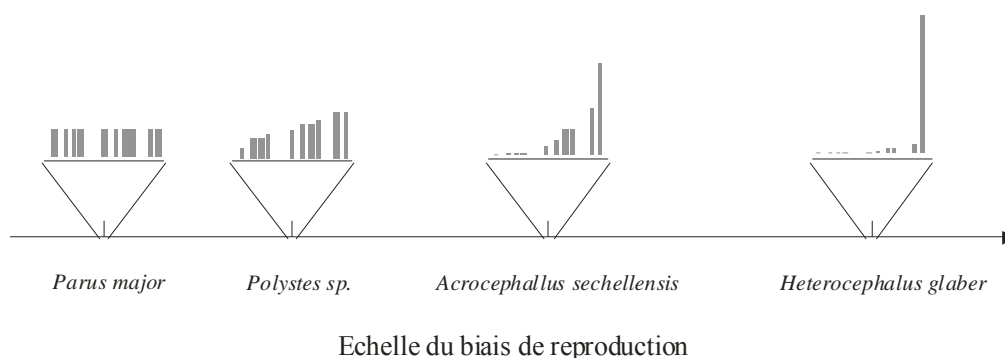


Figure 8. Division de la reproduction au sein des sociétés animales. L'échelle du biais à la reproduction permet de distinguer les espèces le long d'un continuum de la socialité, depuis les types solitaires (e.g., Mésange charbonnière), coloniaux (e.g., guêpe *Polistes*), à reproduction coopérative (e.g., Fauvette des Seychelles) jusqu'aux espèces eusociales (e.g., Rat-taupe). Pour chaque espèce, le succès reproducteur (barre grise) de dix individus du même groupe est représenté dans l'ordre d'un gradient croissant de rang social (de gauche à droite).

Cette distribution permet de calculer le biais de reproduction, qui est un indice de l'asymétrie de la distribution de la reproduction. Chez les espèces solitaires ou coloniales, le succès reproducteur est distribué uniformément. Chez les espèces à reproduction coopérative ou eusociale, les dominants monopolisent la reproduction : il existe un biais élevé du succès reproducteur.

Différenciation germe/soma. Les espèces eusociales offrent un exemple extrême de partage des tâches au sein d'une structure coloniale, la tâche reproductrice étant assurée par un unique individu ou par un groupe de taille très réduite. De nombreux organismes pluricellulaires sont structurés de la même manière : la tâche de reproduction de l'unité coloniale est intégralement déléguée à une classe germinale et son accomplissement est assuré par l'activité coopérative d'une classe somatique. Cette différenciation (qui peut se produire à des stades variés du développement d'un organisme pluricellulaire ou d'une colonie) s'interprète à la lumière du modèle de mutualité exposé précédemment : l'altruisme s'exprime entre individus somatiques qui sacrifient tout ou partie de leur reproduction pour assurer le bien commun que constituent la survie et la fertilité de la classe germinale. Ce service rendu peut prendre des formes variées. Chez des cellules de certains organismes comme les *Volvocales*, la reproduction individuelle au sein de l'unité coloniale est complètement sacrifiée au profit de la motilité, produisant une unité coloniale mobile apte à prospecter l'environnement pour mieux profiter des ressources (Michod 1999). Plus généralement, la reproduction des individus au sein de l'unité coloniale est partiellement sacrifiée chez les organismes différenciés et chez les animaux eusociaux au profit de l'accomplissement du fonctionnement d'un organe ou d'une caste.

Le bénéfice est alors retourné par la classe germinale sous forme de nouvelles unités coloniales fondées par des individus fortement apparentés aux altruistes. Dans un tel système, un tricheur, au sens de Hauert et al. (2002), est un individu somatique qui ne payerait que partiellement le coût de la reproduction collective et conserverait donc une capacité de répllication propre supérieure. L'ordre des *Volvocales* offre un exemple d'organismes chez lesquelles se rencontrent à la fois des formes mutualistes et non-mutualistes. Les résultats expérimentaux de Bell (1985) suggèrent que le succès reproducteur net des premières est effectivement supérieur à celui des secondes, confirmant l'hypothèse du modèle de mutualité relative à la supériorité des altruistes sur les marginaux. Mais comment comprendre le verrouillage adaptatif qui maintient le système dans son état mutualiste en lui évitant le cycle évolutif prédit par ce modèle ?

La sélection à niveaux multiples est probablement essentielle pour comprendre ce verrouillage (Wilson 1997). Le système mutualiste forme une unité supérieure dont les bénéfices de l'altruisme individuel servent à assurer la répllication. Une stricte différenciation germe/soma confère une hérédité à cette unité, car chaque unité est fondée par la copie d'un individu germinal dans les cas les plus simples. Une tendance égoïste peut alors provenir d'une mutation germinale, l'individu mutant fondant une unité dont tous les individus somatiques sont moins altruistes, ou d'une mutation

somatique, l'individu moins altruiste qui apparaît ainsi développant son clan au sein même du soma de l'unité concernée. La différenciation germe/soma et l'hérédité germinale offrent alors les moyens d'une régulation de la tricherie :

- en limitant le risque de mutations germinales et en exposant les unités coloniales qui en seraient issues à l'action de la sélection au niveau supérieur (Michod 1999) ;
- en éliminant le risque de propagation de mutations somatiques : piégées dans leur propre unité, elles disparaissent à la mort de celle-ci ;

Domestication des parasites. Chez de nombreuses espèces dont les populations sont structurées en unités sociales, le partage des tâches peut se révéler plus complexe qu'une simple différenciation germe/soma. Par exemple, la tâche de reproduction n'est pas forcément réservée à un individu ou à une caste germinale exclusive. Ou encore, les individus peuvent se différencier en un plus grand nombre de classes par des processus éventuellement réversibles. Un modèle d'évolution des systèmes métaboliques proposé par Szathmary et Demeter (1987) et Czarán et Szathmary (2000) permet d'analyser la résistance de systèmes sociaux fortement différenciés à la déstabilisation par le parasitisme. Chaque classe d'individus apporte une contribution spécifique à la 'mutuelle' du système en catalysant la synthèse d'un monomère particulier dirigé vers un système métabolique commun. Chaque individu reçoit un bénéfice en retour sous la forme d'enzyme catalytiques synthétisées par le métabolisme à partir des monomères reçus, mais à condition que tous les monomères nécessaires soient parvenus à la mutuelle métabolique.

L'exploration du modèle démontre la capacité de résistance aux parasites que confère la spécialisation du système de coopération par mutualité. Un avantage aux plus rares en est à l'origine : le parasite a peu de chance de prospérer s'il est abondant, car il est alors peu probable que son voisinage soit métaboliquement complet. Alors que l'émergence de structures spatiales auto-organisées apparaît souvent comme un facteur clé de la coexistence d'espèces s'excluant mutuellement, la stabilité de ce jeu métabolique dépend au contraire de son mélange. L'homogénéisation est en effet nécessaire pour que le système métabolique reçoive localement tous les ingrédients nécessaires à la production des bénéfices attendus en retour par les altruistes. Cependant, le système coopératif est généralement incapable d'éliminer complètement ses parasites. Une intéressante éventualité est qu'un parasite soit alors incorporé au système métabolique, ce qui peut s'envisager en deux temps : par une intégration facultative (le parasite contribue au métabolisme là où il est présent), puis obligatoire (le parasite devient indispensable au fonctionnement métabolique). L'intégration accomplie, le système montre généralement une activité métabolique supérieure. Ainsi, la prise en compte du niveau sélectif de la communauté tout entière pourrait expliquer une domestication des parasites par la sélection naturelle. Un tel processus pourrait conduire à l'augmentation évolutive graduelle du degré de coopération d'un système mutualiste (Ferrière et al.

2002) : en favorisant la sélection de génotypes plus altruistes, l'intégration de parasites conduit à un 'marché de la coopération' encore plus actif (Noe et Hammerstein 1995).

7.3. Contrôle

Chez de nombreuses espèces, le partage des tâches dépend d'un contrôle entre classes du comportement altruiste de chaque classe. Chez l'homme, le respect de certaines règles sociales ou morales est imposé par des autorités légales ou religieuses. Chez les espèces sociales où la tâche de reproduction est partagée de façon asymétrique entre une classe dominante et des classes dominées, le contrôle peut être exercé dans trois contextes :

- Le contrôle au bénéfice des dominés, comme chez l'Abeille mellifère (Ratnieks 1988; Ratnieks et Visscher 1989). Les dominés détruisent les œufs produits au sein de leur caste et une faille dans ce type de contrôle peut déclencher un 'cancer', dont un cas est désormais connu chez les abeilles (Martin et al. 2002, voir Encadré 5).
- Le contrôle au bénéfice des dominants, par des *répressions* pour empêcher la reproduction des subordonnés, comme chez les rats-taupes (Bennett et Faulkes 2000), certaines guêpes (Röseler 1991), et certaines fourmis (Heinze et al. 1994), ou par des *concessions* de reproduction aux dominés (Reeve et al. 1998).
- Le contrôle par une coopération entre dominants et dominés, dont certaines fourmis sans reine nous offrent un exemple remarquable.

Contrôle coopératif : l'exemple des fourmis sans reine. Les fourmis Ponérines sans reine ont perdu la caste reine au cours de leur évolution : toutes les femelles sont des ouvrières qui conservent la capacité d'une reproduction sexuée et on appelle *gamergates* les ouvrières fécondées. Chez l'espèce *Dinoponera quadricaps*, une colonie compte en moyenne 80 ouvrières adultes et une seule gamergate qui possède le rang supérieur dans une hiérarchie de dominance entre 3 à 5 ouvrières. Ces femelles de haut rang sont des prétendantes à la reproduction qui travaillent peu et qui remplacent la gamergate à sa mort. La gamergate s'accouple à un seul mâle non apparenté, de sorte que les ouvrières sont des filles ou des sœurs de la gamergate.

Une ouvrière fille de haut rang (la situation la plus typique) peut accroître son aptitude inclusive en éliminant la gamergate plutôt qu'en attendant sa mort et sa substitution par une autre fille ouvrière. En effet, une fille de haut rang est plus apparentée à ses propres rejetons (0.5) qu'à ceux d'une sœur (0.375). Lorsqu'une ouvrière de haut rang entreprend de défier la gamergate, les deux fourmis s'engagent dans une lutte au cours de laquelle la gamergate effleure la prétendante de son dard, la marquant ainsi chimiquement. Le résultat est une immobilisation de la prétendante par des ouvrières de bas rang, immobilisation qui peut durer plusieurs jours et à la suite de laquelle la prétendante se trouve déchu de sa position élevée dans la hiérarchie (Monnin et Peeters 1999; Monnin et al. 2002). Une telle forme de coopération entre la gamergate et les ouvrières de bas rang tire sa valeur adaptative

du fait que les deux parties sont plus apparentées aux rejetons de la gamergate en place qu'à ceux potentiellement produits par la prétendante. De plus, les ouvrières de bas rang ont intérêt à éviter le remplacement pour s'affranchir du 'coût de la succession' induit par une suspension de reproduction sur six semaines environ et de la perte d'une ouvrière (Monnin et Peeters 1999).

Le marquage chimique et l'immobilisation pratiqués par *Dinoponera quadriceps* représente un exemple de régulation mutuelle punitive (Clutton-Brock et Parker 1995). D'autres cas de comportements de régulation punitifs sont connus chez les fourmis sans reine (Monnin et Ratnieks 2001), mais cet exemple est le seul impliquant une coopération entre la gamergate et les ouvrières de basse condition. Chez les autres espèces, une colonie peut compter plusieurs gamergates, et leur nombre semble directement régulé par les ouvrières de bas rang qui paraissent capables de détecter les signaux chimiques émis par l'activation ovarienne d'une prétendante (Liebig et al. 1999).

Encadré 5 – Echapper au contrôle : une forme de 'cancer social' chez les abeilles

Chez les Hyménoptères eusociaux, la caste ouvrière est généralement incapable de reproduction en présence de la reine. Les cas de reproduction par des ouvrières anarchistes ont des conséquences limitées sur la colonie dans la mesure où les œufs produits sont de sexe mâle et parce que les ouvrières exercent un contrôle extrêmement efficace de la reproduction au sein de leur propre caste, en attaquant et détruisant les œufs pondus par les anarchistes (Barron et al. 2001; Ratnieks 1988). En 1990 les apiculteurs d'Afrique du Sud ont transféré une abeille mellifère sauvage, l'Abeille du Cap, *Apis mellifera capensis*, vers le Nord du pays. Dès son transfert l'Abeille du Cap s'est mise à parasiter les colonies de l'Abeille mellifère domestique, *A. m. scutellata*, provoquant une véritable hécatombe chez l'Abeille domestique. Martin et al. (2002) ont montré que les ouvrières de l'Abeille du Cap sont capables :

- de s'introduire dans les colonies de l'Abeille domestique sans provoquer de réaction particulière de rejet par les gardiennes de la ruche (leur niveau de tolérance à l'entrée d'ouvrières extérieures à la ruche étant généralement élevé, Downs et Ratnieks 2000) ;
- d'activer leurs ovaires sans encourir de comportement répressif de la part de la colonie d'accueil ;
- de pondre, sans s'accoupler, des œufs femelles diploïdes, grâce à une parthénogenèse thélytoque (méiose suivie d'une fusion des produits méiotiques qui restaure la diploïdie de l'œuf).

Ces trois propriétés conduisent à la prolifération des ouvrières de l'Abeille du Cap au sein de leurs colonies d'accueil. Deux facteurs de la mort de la colonie ont été identifiés :

- un affaiblissement de la force d'approvisionnement alimentaire de la colonie, à laquelle les Abeilles du Cap participent très peu, qui entraîne la mort de la reine ;
- une forte concurrence pour les ressources disponibles entre la reine et les ouvrières parasites.

Ce phénomène est similaire au cancer qui, par la prolifération de cellules somatiques ne contribuant plus au fonctionnement d'un organe, met en péril l'intégrité collective. Une différence importante, cependant, tient à l'origine du parasite : interne dans le cas du cancer, externe, par voie d'infection horizontale entre colonies, dans le cas des abeilles. *Apis m. capensis* et *A. m. scutellata*, bien qu'appartenant à la même espèce, présentent en effet des différences génétiques substantielles et des distributions géographiques naturelles complémentaires.

Contrôle de la reproduction : répressions, concessions et consanguinité. Chez les espèces à reproduction coopérative, une monopolisation incomplète de la reproduction par la classe dominante peut évoluer dans deux situations : avec un coût de la répression, qui s'exprime lorsque les

dominants n'ont pas l'opportunité, la capacité ou le temps de réprimer la reproduction des dominés (Reeve et al. 1998) ; ou avec des bénéfices tirés de concessions ou d'évitements de consanguinité (Clutton-Brock 1998; Reeve et al. 1998). Les concessions pour la reproduction d'individus dominés sont appelées des 'incitations à la philopatrie' si elles favorisent le maintien des subordonnés dans le groupe, et des 'incitations pacifiques' si elles permettent d'éviter les conflits physiques (Reeve et Ratnieks 1993). On reconnaît trois facteurs pouvant moduler les bénéfices de telles concessions :

- Une moindre différence d'aptitude compétitive entre dominants et subordonnés favoriserait plus de concessions pacifiques (Reeve et Ratnieks 1993).
- Un affaiblissement des contraintes écologiques à la dispersion des subordonnés devrait favoriser les concessions à la philopatrie, car l'option d'un départ et d'une reproduction indépendante étant alors plus attractive pour le subordonné (Vehrencamp 1983).
- Une réduction de l'apparementement entre dominant et subordonnés incite à plus de concessions, car un subordonné peut escompter des bénéfices indirects de la coopération plus faibles (Keller et Reeve 1994) et puisque le risque d'une reproduction consanguine entre un dominant et les subordonnés diminue (Emlen 1996; Faulkes et Bennett 2001).

Des espèces phylogénétiquement proches peuvent avoir des contrôles très contrastés, comme le montre le cas des mangoustes naines et des suricates.

Concessions chez les mangoustes naines. Les mangoustes naines *Helogale parvula* sont des mammifères à reproduction coopérative vivant en groupes de 3 à 18 individus dans les savanes ou les bois ouverts d'Afrique centrale. Les petits groupes sont des unités familiales comprenant un mâle, une femelle et leurs descendants, alors que les groupes plus importants sont formés par l'addition de familles apparentées et d'immigrants. La reproduction des subordonnés est réprimée par le couple dominant (Creel et al. 1992). Les subordonnés peuvent se reproduire directement en accédant au statut de dominant dans leur groupe de naissance ou dans un groupe de dispersion, ou en se reproduisant avec d'autres subordonnés (Creel et Waser 1991). La reproduction des subordonnés n'est pas limitée par des risques d'appariements consanguins (Keane et al. 1990). Les appariements ont lieu indifféremment entre individus plus ou moins apparentés et les appariements consanguins ne sont pas délétères (Fig. 9A). La distribution de la reproduction des subordonnés est bien prédite par un modèle d'optimisation des concessions (Vehrencamp 1983). Les femelles subordonnées plus âgées ont préférentiellement accès à la reproduction, vraisemblablement parce qu'elles ont une aptitude compétitive supérieure dans les conflits avec la dominante (incitations pacifiques). La contribution des subordonnées à la reproduction du groupe est aussi influencée par l'apparementement avec la dominante (Fig. 9A, Keane et al. 1994). Quand une subordonnée est âgée, la reproduction est concédée préférentiellement aux subordonnées les moins apparentées. Chez cette espèce avec une forte dispersion et un contrôle dominant, la répartition de la reproduction est compatible avec un modèle des concessions optimales.

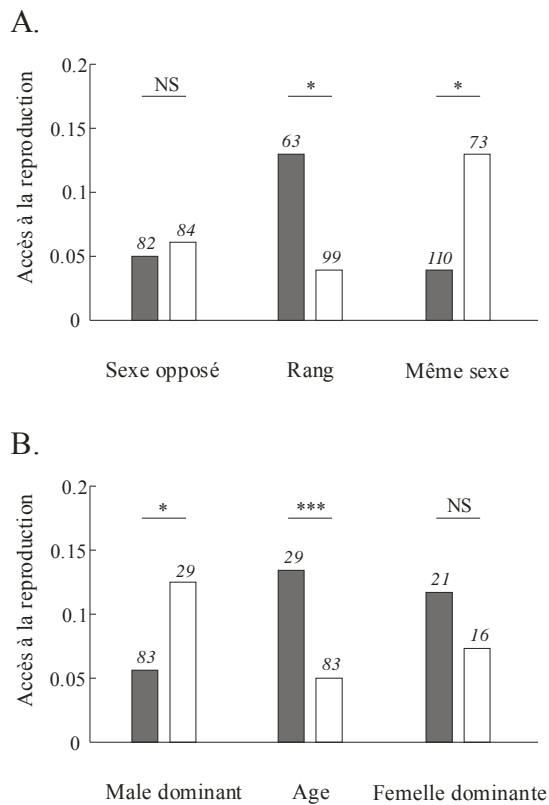


Figure 9. Distribution asymétrique de l'altruisme de reproduction chez deux mangoustes sociales. A. La reproduction des subordonnés chez la Mangouste naine n'est pas affectée par l'apparement avec l'individu dominant du sexe opposé (barre pleine : dominant fortement apparementé ; barre vide : dominant faiblement apparementé), mais est plus fréquente chez les subordonnés de haut rang (barre pleine : second et troisième rang ; barre vide : rang inférieur) et moins apparementées avec l'individu dominant du même sexe (barre pleine : dominant fortement apparementé ; d'après les données aimablement communiquées de Keane et al. 1994). B. La reproduction des femelles subordonnées chez le Suricate est limitée par la présence de mâles apparementés (barre pleine : male apparementé, barre vide : male non apparementé), est favorisée par la compétitivité de la femelle (barre pleine : même génération que la dominante, barre vide : subordonnée plus jeune que la dominante) mais n'est pas affectée par l'apparement avec la dominante (barre pleine : femelle dominante apparementée, d'après Clutton-Brock et al. 2001).

Consanguinité chez les suricates. Les suricates *Suricata suricatta* sont aussi des mangoustes à reproduction coopérative qui vivent en petits groupes de 2 à 30 individus dans des milieux semi-désertiques du sud de l'Afrique. Les groupes sont formés d'un couple parental, d'individus subordonnés et des jeunes. Les membres du groupe coopèrent pour l'élevage des jeunes et la surveillance du groupe, mais la reproduction est monopolisée par un couple dominant (Clutton-Brock et al. 1998; Clutton-Brock et al. 1999a). La reproduction des femelles subordonnées est réprimée par le couple dominant (O'Riain et al. 2001). Les modalités de la reproduction des femelles subordonnées au sein de différents groupes ont pu être analysées à l'aide d'un suivi démographique d'une population du Kalahari (Clutton-Brock et al. 2001). La reproduction des subordonnées est fortement limitée par les risques de reproduction consanguine (Fig. 9B). Au sein des groupes où les mâles sont apparementés aux subordonnées, les femelles subordonnées réalisent moins d'appariements. De même, après la mort d'un mâle dominant, la femelle dominante et les subordonnées ne se reproduisent pas avant l'immigration d'un mâle non apparementé. De plus, les subordonnées se reproduisent préférentiellement lorsqu'elles sont compétitivement supérieures, suggérant un rôle des conflits avec la dominante (Fig. 9B). Par contre, la reproduction des subordonnées n'est influencée ni par l'apparement avec la dominante, ni par sa contribution individuelle au groupe, et ni par sa capacité de dispersion, contrairement aux prédictions du modèle de concessions. Chez cette espèce avec une faible dispersion

et une répression réversible de la reproduction, la reproduction des subordonnées est compatible avec une minimisation des risques de consanguinité et un contrôle limité de la femelle dominante.

8. REVERSION EVOLUTIVE ET PERTE DE LA COOPERATION

Après plus d'un siècle de réflexion sur l'origine évolutive et le maintien de la coopération entre altruistes, les outils de la phylogénie moléculaire ont tout récemment soulevé la question inattendue de sa régression évolutive. Ainsi, de nouvelles données phylogénétiques remettent en cause le principe de l'irréversibilité de la socialité, et en particulier des structures eusociales (Wilson 1975). L'existence de réversions invite à s'interroger sur les causes de la perte de la socialité.

8.1. Données phylogénétiques

La terminologie développée pour décrire les formes de socialité (voir section 1) sous-entend que l'évolution de la coopération conduit irréversiblement vers la complexité sociale. Alors que l'irréversibilité de l'eusocialité semble probable chez certains insectes (Isoptères, Formicidae, Apini, Bombini), et peut-être chez les vertébrés (Bathyergidae), les données phylogénétiques démontrent cependant le caractère labile de la socialité au sein de certains taxons (Crespi 1996; Weislo et Danforth 1997) :

- Chez les abeilles, plusieurs réversions ont jalonné l'histoire évolutive des Halictines (Packer 1991), des Allodapines (Weislo et Danforth 1997) et des Auglochorines (Danforth et Eickwort 1997).
- Chez les Aphidiens, la différenciation de castes de soldats a pu être perdue une ou deux fois (Stern et Foster 1997).
- Chez les thysanoptères eusociaux, on envisage la possibilité d'une ou de deux réversions de l'eusocialité (Crespi 1996).
- Au sein d'un groupe de crevette du genre *Synalpheus*, dont plusieurs représentants sont considérés comme eusociaux, l'analyse comparative met en évidence plusieurs transitions de l'eusocialité vers un système de reproduction coopérative (Duffy 1996; Duffy et al. 2000).

Globalement, ces exemples de réversions, qui demandent à être confirmées par de nouvelles données phylogénétiques, restent limités à quelques groupes. Il semble aussi que ces transitions soient plus rares que les multiples origines indépendantes de l'eusocialité, que l'on a pu mettre en évidence dans le groupe des Hyménoptères (11 occurrences), des Isoptères (2 occurrences), des Aphidiens (7-9 occurrences), des Thysanoptères (2 occurrences), ou des crevettes *Synalpheus* (3 occurrences, Crespi 1996; Stern et Foster 1997; Duffy et al. 2000). Malgré tout, ces nouvelles données incitent à modifier radicalement la vision classique d'une stricte canalisation évolutive de l'eusocialité.

Comparativement, l'évolution des systèmes de reproduction *coopérative* n'a pas encore fait l'objet d'études aussi systématiques. Ces systèmes sociaux sont pourtant représentatifs de nombreuses

espèces d'oiseaux, de mammifères, et de certains ordres d'insectes (Brockmann 1997; Emlen 1997). Chez les oiseaux, la reconstruction phylogénétique au niveau familiale conduite par Arnold et Owens (1999) suggère une perte de la reproduction coopérative dans les familles des oiseaux-lyres et des oiseaux à berceaux. De même, plusieurs réversions ont été décrites dans la superfamille des Corvoidea (Edwards et Naeem 1993). Des phylogénies détaillées de certains genres illustrent aussi plusieurs réversions sociales récentes au niveau spécifique : une réversion chez les Grimpereaux australiens, une chez les Troglodytes du Nouveau Monde, une chez les Geais des buissons et une chez les Geais du Nouveau Monde (Edwards et Naeem 1993). De nombreux travaux d'analyse comparative restent encore à mener concernant le déterminisme de la réversion évolutive de l'eusocialité, et la dynamique évolutive d'une réversion. La modélisation mathématique permet de baliser ce champ de recherche empirique, en identifiant trois mécanismes de l'inversion du bilan des pressions de sélection s'exerçant sur le caractère altruiste :

- Une modification des pressions de sélection suite à un changement des conditions environnementales.
- Le changement d'attracteur écologique du système (Dercole et al. 2002), associé par exemple à un effet de Allee engendré par la coopération.
- L'évolution adaptative conjointe d'autres caractères phénotypiques.

8.2 *Changement environnemental*

Un changement environnemental peut conduire à une diminution des bénéfices directs de la coopération, par exemple par l'intermédiaire des ressources si la coopération procure des avantages pour le nourrissage, et des bénéfices indirects, par exemple en favorisant un plus fort mélange génétique dans la population. Un tel scénario pourrait expliquer la perte de la socialité chez certains insectes dont la structure sociale varie le long de gradients climatiques, suggérant que la dynamique adaptative de leur caractère altruiste puisse répondre à des modifications climatiques globales (Eickwort et al. 1996; Danforth et Eickwort 1997).

Un exemple de perte d'un phénotype social chez la Myxobactérie *Myxococcus xanthus* a ouvert une porte à des investigations expérimentales de ces phénomènes. L'expérience a consisté à maintenir en milieu liquide, homogène et riche plusieurs clones initialement cultivés en milieu solide, hétérogène et appauvri (Velicer et al. 1998). Après 10.000 générations, une comparaison entre les souches dérivées et ancestrales fournit une indication de l'évolution ayant eu lieu dans le milieu de culture. Les comparaisons phénotypiques mettent en évidence une motilité sociale plus faible de la majorité des souches dérivées, une chute de la production de corps de fructification et de la fréquences de sporulation. La caractérisation génotypique des souches dérivées met en parallèle la régression du phénotype social avec la perte d'un système génétique contrôlant la motilité cellulaire. Cette expérience démontre que le maintien génétique d'une fonction sociale complexe est fragile et dépend des conditions écologiques. Dans l'environnement hétérogène et appauvri des souches ancestrales,

l'apparement et des bénéfices directs pourraient favoriser le maintien de la coopération contre la tricherie (Velicer et al. 2000). Dans un environnement homogène et enrichi, les coûts à la coopération dépasseraient ces bénéfices et faciliteraient l'évolution de types asociaux (Velicer et al. 1998).

8.3. *Effet de Allee et conséquences évolutives*

Une population peut se stabiliser dans des états écologiques différents, répondant à la contingence des conditions initiales – par exemple l'état de la population au moment de sa fondation. En particulier, le comportement altruiste induit une bistabilité écologique : pour une valeur fixée de l'investissement individuel dans l'altruisme, la viabilité de la population dépend de l'effectif fondateur. Une population fondée avec un nombre insuffisant d'individus s'éteint par un effet dit de Allee. Les mécanismes d'un tel effet de Allee ont été discutés pour les vertébrés à reproduction coopérative obligatoire où ils impliquent l'insuffisance du nombre de partenaires pour établir un niveau de coopération suffisant ou le manque de partenaires pour la reproduction (Courchamp et al. 1999a, b). Au contraire, si l'effectif initial est suffisant, la population se stabilise dans un état écologique viable. Le Galliard et al. (2003) ont montré que cette bistabilité écologique était perdue chez certains organismes en dessous d'un certain seuil sur le degré individuel d'altruisme ne laissant à la population que la perspective d'une extinction. De plus, les pressions de sélection favorisent une réduction de l'altruisme au dessus de ce seuil ! Une population initialement viable et coopérative se voit donc entraînée par la dynamique adaptative du caractère altruiste vers l'extinction, exemple d'un 'suicide évolutif' (Ferrière 2000) qui implique la perte d'une population sociale.

8.4. *Evolution multidimensionnelle*

L'évolution de la coopération par altruisme s'accompagne de nouvelles conditions génétiques et écologiques (Avilés 1999) qui peuvent se répercuter sur l'évolution de toute la suite des caractères adaptatifs de l'espèce. Ainsi l'état social d'une population peut être soumis à une pression de sélection radicalement différente selon les valeurs des autres caractères adaptatifs représentées dans la population.

Par exemple, le modèle développé par (Hamilton 1964a, b, 1972) pour l'évolution de l'altruisme de reproduction chez les Hyménoptères haplodiploïdes ne tient pas compte des mâles. Trivers et Hare (1976) ont montré que, du fait de l'asymétrie d'apparement, les ouvrières tirent un avantage à l'élevage de sœurs plutôt que de filles (section 5.3), mais qu'en revanche elles tirent un avantage à l'élevage de fils ($r = 0.5$) plutôt que de frères ($r = 0.25$). Ainsi, dans une population à l'équilibre de la sexe ratio et où une ouvrière (appariée) produirait seule le même nombre de descendants qu'une reproductrice, la valeur sélective inclusive de la stratégie de coopération équivaut à celle de la reproduction égoïste (Trivers et Hare 1976; Grafen 1986). Comme Trivers et Hare (1976) l'ont noté, la coopération peut cependant prendre le dessus si les ouvrières sont capables de biaiser la sexe ratio en faveur des sœurs (voir chapitre 12). Dans ces conditions, l'évolution de la coopération

reste possible, et est explorée en détail par Crozier et Pamilo (1996). Dans d'autres situations, comme un contrôle de la sexe ratio par la reine, une limitation du biais femelle de la sexe ratio dans la colonie va défavoriser la coopération entre sœurs.

Encadré 6 – Biologie et altruisme : bref historique

Darwin et les insectes sociaux. La théorie darwinienne classique propose une vision compétitive du monde – la ‘lutte pour la vie’. Les descriptions de comportements coopératifs par des contemporains de Darwin auraient du lever un obstacle majeur à la théorie de la sélection naturelle. Une lecture précise des textes de Darwin indique cependant que le ‘problème de la coopération’ y est effectivement traité, mais avec une forte ambiguïté (Cronin 1991). A de nombreuses reprises, Darwin se montre incapable d'évaluer les coûts associés à un comportement altruiste (Darwin 1859). Par exemple, la stérilité des castes ouvrières des insectes sociaux, qui est un altruisme de reproduction, ne perturbe pas fondamentalement Darwin (Darwin 1859, p.234-263). Darwin est plus fondamentalement gêné par un problème d'hérédité : comment une différenciation morphologique entre castes stériles et castes fertiles peut-elle évoluer en l'absence de transmission des caractères acquis chez la caste stérile ? Il assimile parfois la stérilité des ouvrières à une difficulté préliminaire : « L'explication de la stérilité des ouvrières est une difficulté, mais pas plus que tout autre modification frappante de structure (...). Si de tels insectes ont été sociaux et qu'il ait été profitable à la *communauté* qu'une proportion de la descendance soit capable de travailler, mais incapable de procréer, cela ne pose pas de problème sérieux à la sélection naturelle. » (Darwin 1859, emphase personnelle). L'explication de l'altruisme des ouvrières chez Darwin fait appel à de la sélection naturelle au niveau d'un groupe : « Nous pouvons voir l'intérêt à produire des castes stériles pour la *communauté* sociale d'insectes, de la même façon que la division du travail est utile à l'homme civilisé » (Darwin 1859, emphase personnelle). On trouvera les séquelles de cette explication dans les courants néodarwiniens et chez les premiers éthologues.

Dans son ouvrage sur la sélection sexuelle et les comportement humains, Darwin identifie clairement des comportements altruistes, et évoque les problèmes d'interprétation qu'ils posent pour un mécanisme de sélection naturelle agissant au niveau individuel (Darwin 1871, Première partie, Sur la descendance de l'homme, chapitres 3 et 5). Pour autant, il n'en fournit pas d'explication convaincante ou s'en remet à nouveau à des explications par la sélection au niveau de la communauté ou du groupe (Hamilton 1972). Parfois, Darwin suggère aussi la possibilité d'une sélection de l'altruisme au niveau de la famille : « La sélection peut être appliquée à la *famille*, de même qu'à l'individu (...). Par la sélection continue et prolongée des parents fertiles qui produisent le plus de descendants stériles avec la modification favorable, tous les individus stériles ont fini par porter cette modification. » (Darwin 1859, emphase personnelle). Cette explication ressemble à l'argumentation embryonnaire d'une théorie de l'altruisme entre apparentés qui sera développée un siècle plus tard (Hamilton 1964a).

Néodarwinisme, bien de l'espèce ou égoïsme des gènes ? L'étude de l'altruisme dans le cadre de la théorie néodarwinienne de l'évolution est plus complexe, parce que ce mouvement du début du vingtième siècle inclut de nombreuses écoles de pensée. Pour la majorité des écologistes de cette époque, la coopération s'érige en standard du monde vivant, et s'explique parce qu'elle favorise le groupe ou l'espèce. Cette vision opposée au modèle compétitif darwinien trouve son origine dans l'écologie des communautés et la biologie des populations. Ainsi, pour l'écologiste Clements (1916), l'écosystème fonctionne comme un individu, les espèces étant assimilées à des organes qui coopèrent, se développent et meurent avec l'écosystème. Le démographe Allee (1949) décrit les populations comme des organismes, avec des propriétés de régulation et d'organisation. Au contraire, l'éthologie s'intéresse peu aux comportements altruistes, comme en témoignent les écrits de deux de ses pères fondateurs (Lorenz 1966; Tinbergen 1951, 1964). Tinbergen (1951) distingue les instincts bénéfiques à l'individu, ‘éléments individuels’, des instincts bénéfiques au groupe mais non à l'individu, ‘éléments sociaux’, dont il propose une classification. Et de conclure alors : « Pour résumer cette investigation des comportements sociaux, et bien que leurs mécanismes aient été démontrés expérimentalement dans un faible nombre de situations, il est aisé de conclure que ce sont des adaptations servant à promouvoir la coopération entre individus de la même espèce pour le bénéfice du groupe »

(Tinbergen 1951, chapitre VII). Au travers de ses multiples avatars, ce consensus, fondé sur un bénéfice de la coopération pour le groupe ou l'espèce, ne trouve pas d'opposition jusqu'à la publication de l'ouvrage de (Wynne-Edwards 1962). Ces explications au niveau du groupe provoquent alors de vifs débats qui les remettent en cause aux profits d'explications par la sélection individuelle (Fisher 1930; Williams 1966; Trivers 1971; Dawkins 1976; Axelrod et Hamilton 1981), la sélection de parentèle (Haldane 1955; Hamilton 1964a, 1964b, 1972) et la sélection à niveaux multiples (Michod 1999). Ainsi, des travaux mettent en lumière la difficulté pour un caractère désavantageant l'individu de se fixer dans une population par l'intermédiaire d'un seul bénéfice pour le groupe ou pour l'espèce (Dawkins 1976). L'explication tient au fait que la sélection est beaucoup plus rapide entre individus à l'intérieur d'une population qu'entre populations (Williams 1966; Gouyon et al. 1997).

9. CONCLUSIONS

Près de 150 ans après les premières notes de Darwin, 40 ans après qu'Hamilton eut jeté les bases d'une théorie de l'évolution de l'altruisme, et plus de 30 ans après que Wilson eut donné ses lettres de noblesse à la sociobiologie (voir Encadré 6), force est de reconnaître que l'identification même des comportements altruistes demeure problématique (Clutton-Brock 2002). Non pas que la théorie ne nous ait pas permis de progresser grandement dans notre approche analytique de ces comportements. Précisément, mettant en lumière les pressions de sélection susceptibles de les affecter, la modélisation nous a forcé de dresser des bilans plus fins des coûts et bénéfices impliqués, qui sous-tendent la définition même de l'altruisme. On s'accorde aujourd'hui pour reconnaître que les bénéfices directs et les coûts indirects des comportements altruistes ont été sous-estimés (Cockburn 1998; West et al. 2002), et que l'ensemble des coûts et bénéfices dépendent d'un contexte écologique et génétique qui ne peut être ignoré. Le phénomène de la reproduction coopérative chez les oiseaux offre sans doute le meilleur matériel d'une telle étude économique de l'altruisme, qui se voit aujourd'hui replacée dans le cadre plus général de l'analyse comparative de suites de caractères comportementaux et démographiques (Arnold et Owens 1998, 1999).

La fragilité d'un programme adaptationniste de la biologie des comportements sociaux, tel qu'il fut conçu par Wilson (1975), a longtemps tenu à la méconnaissance des bases génétiques des caractères considérés, et l'appréhension insuffisante qui était faite de leur plasticité. La génétique moléculaire des insectes sociaux et de certains microorganismes, et l'étude expérimentale de leur comportement en interaction avec leur environnement, ont permis de franchir des pas décisifs en la matière (Keller et Chapuisat 1999; Crespi 2001). Seuls, quelques commentateurs de bas étage, prétendument philosophes et guère scientifiques, ignorant du mouvement de la biologie, continuent de décrier aujourd'hui ce qu'est devenu la sociobiologie de Wilson – une écologie comportementale de la socialité dotées de bases mathématiques et expérimentales solides, dont les avancées sont parmi les plus marquantes et les plus spectaculaires de la recherche sur l'évolution du vivant.

L'écologie comportementale de la socialité a désormais dépassé les limites de la biologie animale pour trouver les avatars de son objet d'étude à tous les niveaux d'organisation du vivant – du niveau moléculaire de l'information génétique, jusqu'au niveau sociétal de la communication humaine

– et fournir les clés ultimes de l'existence même de ces niveaux (Maynard Smith et Szathmary 1995). La coopération permet l'émergence d'unités intégrées capables de réplication, au niveau desquelles sont transférés les conflits que le fonctionnement coopératif excite entre individus (Dawkins 1976). Reconnaître l'action de la sélection naturelle sur une hiérarchie de niveaux biotiques est ainsi devenu fondamental pour aborder la régulation des conflits qui mine tout système vivant. Cette notion de régulation n'est probablement pas, d'ailleurs, le concept le plus approprié pour décrire le maintien précaire d'une activité coopérative soumise au perpétuel assaut d'éléments égoïstes, sans cesse renouvelés et gérés dans les limites qu'autorisent les mécanismes de reconnaissance, de répression, et de domestication.

Si Darwin posa le problème la spéciation évolutive, Buss (1987), Maynard Smith et Szathmary (1995) et Michod (1999) ont fait de l'évolution de la coopération la question centrale d'une biologie de la complexification. Deux problèmes pas forcément séparés si l'on suit Margulis et Dorion (2002) dans leur interprétation de la spéciation comme résultat d'une coopération entre génomes...

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QUESTIONS

Question 1. Construisez la valeur sélective inclusive complète du comportement décrit à l'aide de la Figure 3, et déduisez en une règle économique simple pour l'évolution de l'altruisme envisagée dans la section 4.

Question 2. Déduisez des paramètres de la matrice du jeu décrit dans l'Encadré 3 les règles pour la stabilité évolutive des deux stratégies et la dynamique en temps discret de la population de coopérateurs dans un milieu homogène ?

Réponse 2. La stabilité décrit la résistance d'une stratégie établie à l'invasion de la stratégie alternative. Lorsque $R > T$ ou $R = T$ et $P < S$ la coopération est évolutivement stable et lorsque $P > S$ ou $P = S$ et $R < T$ l'égoïsme est évolutivement stable. Lorsque $R = T$ et $P = S$ la coopération et l'égoïsme sont évolutivement neutres. Lorsque $R < T$ la coopération est évolutivement instable et lorsque $P < S$ l'égoïsme est évolutivement instable. Par ailleurs, si on désigne par $p_{C,t}$ la fréquence relative des individus coopérateurs dans une population bien mélangée des stratégies C et D, l'équation des réplicateurs décrit la dynamique de la population des coopérateurs comme :

$$p_{C,t+1} = \frac{R p_{C,t} + S(1 - p_{C,t})}{W_c p_{C,t} + W_D (1 - p_{C,t})} p_{C,t}, W_c = R p_{C,t} + S(1 - p_{C,t}), W_D = T p_{C,t} + P(1 - p_{C,t})$$

Question 3. Considérez une extension du jeu de l'Encadré 3 à une population structurée dans l'espace. Quelles sont les prédictions évolutives dans ce contexte ?

Question 4. Discuter de la différence entre reconnaissance et discrimination des partenaires. Quelles sont les conséquences pour l'interprétation des résultats expérimentaux ?

Question 5. L'article de Zahavi (1995) donne une description très atypique du problème de la coopération. A l'aide de cet article, soulevez les contradictions de l'argumentation de Zahavi quand il présente la théorie de la sélection de parentèle et sa propre théorie du handicap. Plus généralement, jugez de la pertinence scientifique de la structure du texte de Zahavi et de la neutralité de l'auteur dans son texte.

Réponse 5. Les réponses critiques de Pomiankowski et Iwasa (1998) et de Wright (1999) peuvent servir de correction à ce problème.

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ANNEXE 2 – CARACTERISTIQUES DU MODELE BIOLOGIQUE

THEY WERE BORN ALIVE



“**Baby lizards and Their Mother.** Most lizards produced eggs from which their young are hatched, but the Common Lizard of Europe (*Lacerta vivipara*) bears living young, producing up to a dozen miniature lizards at a birth. While we have often exhibited the Common Lizard, the birth of young specimens on the Zoological Park is rare. The six inch-long babies shown above, with the female, were born in July. This particular lizard has the further distinction of being the only reptile in Ireland.” dans *Animal Kingdom*. 1950.

UNE PETITE HISTOIRE NATURELLE DU LEZARD VIVIPARE

Jean-François Le Galliard

RESUME

Le lézard vivipare *Lacerta vivipara* (Jacquin) est une petite espèce terrestre de vertébré de la famille des Lacertidae, un groupe de squamates répandu en Eurasie, Afrique et Océanie du nord-ouest et rassemblant environ 215 espèces. L'espèce est de petite taille, sombre sur le dos et avec un ventre coloré allant du blanc à l'orange, plus coloré chez les mâles. Elle est présente sur une grande partie de l'Eurasie où elle affectionne divers milieux humides et froids. Elle se nourrit de façon opportuniste de proies de petites tailles rencontrées lors de déplacements actifs. Les individus vivent sur des territoires chevauchant et toutes les lézards rentrent en compétition pour les ressources et l'espace

L'espèce a la particularité d'avoir un mode de reproduction vivipare sur la plupart de son aire de répartition. La maturité sexuelle peut-être atteinte dès l'âge de un an en fonction de la taille de l'individu. Les mâles matures émergent de l'hibernation en premier et préparent ainsi les appariements. Ceux-ci ont lieu à l'émergence des femelles et sont ensuite suivies par plusieurs mois de gestation. Les appariements sont multiples et le régime de reproduction est polygynandrique avec des taux de multipaternité élevés. A la fin de la gestation, la portée est pondue en une seule occasion. Les jeunes sont autonomes dès la naissance et peuvent disperser dès l'âge de quelques jours.

Le fonctionnement démographique de la population implique trois classes d'âges : les juvéniles nés dans l'année, les sub-adultes d'un an et généralement immatures, et les adultes de plus de deux ans et généralement matures. Les mâles adultes seraient soumis à une compétition sexuelle intense lors de la sortie de l'hiver pour la défense d'un domaine vital et l'accès aux femelles. Les femelles, qui réalisent l'essentiel de l'investissement dans la reproduction, seraient plutôt soumises à une compétition pour les ressources locales. Finalement, les sub-adultes et les juvéniles seraient soumis à de fortes pressions de croissance corporelle pour atteindre le statut de reproducteur. La compétition est asymétrique avec une dominance des mâles adultes sur les femelles, et des adultes sur les sub-adultes et les juvéniles.

SYSTEMATIQUE

L'espèce *Lacerta vivipara* (Jacquin 1787), ex *Zootoca vivipara*, est un lézard terrestre de la famille des Lacertidae, famille qui comprend 29 genres et 215 espèces de lézards dans l'Eurasie, l'Afrique et l'Océanie du nord-ouest (Pough et al., 2001). La famille des Lacertidae appartient à un vaste ensemble monophylétique de lézards et de serpents, les Squamata, et forme un groupe monophylétique avec d'autres familles de lézards dans ce sous-ensemble (dont les Teiidae et les Scincidae). Les caractéristiques morphologiques typiques de la famille reposent sur l'ontogénie et la structure de l'ossification, en particulier au niveau de la structure céphalique. La systématique intra-familiale provisoire est basée sur des données morphologiques (Arnold, 1989) ou immunologiques (Mayer et Benyr, 1994). Dans l'hypothèse morphologique, l'espèce forme un clade avec *Acanthodactylus erythrurus* et le genre *Tackydomus*. Dans l'hypothèse immunologique, l'espèce forme un clade avec d'autres espèces du genre *Lacerta*.

MORPHOLOGIE

La queue est relativement courte et épaisse par rapport au tronc, la tête est petite et les pattes sont courtes. Les individus atteignent à l'âge adulte la longueur du museau à l'anus de 40 à 60 mm chez les mâles et de 45 à 75 mm chez les femelles (Pilorge, 1987; Pilorge et Castanet, 1981). Les juvéniles ont une taille de 15 à 25 mm à la naissance. La taille totale varie entre 120 et 170 mm pour les mâles adultes, et entre 120 et 180 mm pour les femelles adultes. Le poids moyen d'un individu adulte est de l'ordre de 3 à 4 grammes, en dehors de la gestation.

Les caractéristiques des écailles de l'espèce sont les suivantes (Fretey, 1975): « Dorsales hexagonales, parfois imbriquées et carénées. Ventrales sub-rectangulaires et lisses, dont 1 ventrale externe. Collerette denticulée postérieurement et formée de 7 à 12 plaques séparées des pré-ventrales par 4 à 5 séries d'écailles minuscules. Supra-caudales fortement carénées. Anale bordée de deux rangs d'écailles (14 à 16). Pileus variable. Frontale en écusson. Une loréale subrectangulaire en contact avec l'internasale. Rostrale peu visible de dessus et sans contact avec la narine. Deux à quatre temporales touchant les pariétales, tempes recouvertes d'écailles irrégulières dont toujours une tympanique et souvent une massétérine circulaire. Occipitale plus petite que la précoccipitale ; parfois de petits granules (1 à 4) entre les supraoculaires et les supraciliaires. Présence de 5 à 15 pores fémoraux à chaque cuisse ».

Les adultes ont le dos et les flancs bruns, parfois de façon uniforme, mais des taches claires et sombres forment souvent des bandes longitudinales à ce niveau, en particulier une bande continue sagittale large. Le ventre est coloré et plus ou moins ponctué de noir. Chez les mâles, les couleurs ventrales sont vives (orange à rouge) et la ponctuation est intense. Chez les femelles, le ventre est de couleur crème à jaune et la ponctuation est plus faible.

HABITAT ET REPARTITION

D'un point de vue biogéographique, le lézard vivipare est l'espèce de Lacertidae la plus septentrionale (70° de latitude Nord). Elle habite toute l'Eurasie depuis le Nord-Ouest de l'Espagne et la Yougoslavie jusqu'à l'Asie septentrionale à l'Est et la Scandinavie au Nord, dans des secteurs qui ont été recolonisés depuis des refuges glaciaires situés dans le sud de l'Europe. On la trouve depuis le niveau de la mer jusqu'à 3000 mètres d'altitude dans les Alpes, 2670 m dans les Pyrénées et 1790 m dans le Massif Central (Fretey, 1975). En France, l'espèce existe dans le Bassin Parisien, la Bretagne, les plaines du Nord, de l'Est, les massifs des Vosges, du Jura et des Alpes, le Massif Central, les Landes, les Pyrénées et le Massif de l'Espinousse et du Caroux (Heulin et Guillaume, 1989).

A l'échelle locale, le lézard vivipare habite les milieux humides et frais. On le trouve par exemple dans les tourbières, les bords d'étangs et de ruisseaux riches en végétation, les landes humides (*Erica ciliaris* et *Erica tetralix*), les clairières et les lisières de forêts humides ou bien encore dans des prairies humides (*Jungus sylvaticus* et *Molinia coerulea*). Dans le nord de l'Europe, on le trouve aussi sur les falaises à proximité de la côte et dans les près salés littoraux.

Le site d'étude de Massot et al. (1992) au Mas de la Barque dans les Cévennes consiste en une lande à Callune, à Nard riche et à Pins à crochets. Ces auteurs y notent (i) que les populations sont plus denses dans les habitats humides et les zones où la strate herbacée est fortement représentée et (ii) que les lézards tendent à se concentrer sur les zones rocheuses et les arbres. Plus ouverts, mais situés au même niveau altitudinal, les sites de T. Pilorge dans le Massif Central (Pilorge, 1982a; Pilorge, 1982b; Pilorge et Xavier, 1981) sont des landes à Callune, à Genêts pileux et à chamaephytes dans le stade terminal de l'évolution vers une tourbière. B. Heulin (198, 1985b) a quant à lui étudié trois populations naturelles dans la forêt de Paimpont en Bretagne : une lande méso-hygrophile (*Pinus sylvestris*, *Molinia coerulea*, *Calluna vulgaris*, *Ulex nanus*), une lande tourbeuse sur *Sphagnum sp.* et un écotone en bordure d'étang (passage d'une prairie humide à *Agrostis canina*, puis *Molinia coerulea* à la lande). Les populations les plus denses se rencontrent dans ce dernier milieu qui est plus humide, plus diversifié et plus riche en insectes (Heulin, 1985b). Le même auteur a étudié la répartition spatiale des lézards le long de plusieurs transects en bordure d'étangs : les densités les plus fortes se retrouvent au bord de l'eau, ce qui témoigne des besoins hydriques élevés de cette espèce (Heulin, 1985b). Après des prospections intenses dans ce secteur, Heulin (1981) conclut que le « lézard est bien représenté dans les séries hydrarches », mais il note qu'il l'a aussi observé en bordure de chemin, sur les talus et dans des friches déboisées après coupes. Ces espaces servent probablement de corridors entre populations pour la dispersion.

H. Strijbosch (1988) a mené une étude semblable en Hollande mais en réalisant des transects à travers des habitats plus variés, depuis des milieux humides à secs, et depuis des milieux ouverts à des bois denses. Le lézard vivipare est présent dans tous ces habitats, mais il existe des contrastes

importants entre des habitats de forte densité séparés par des barrières de zones non habitées ou à très faible densité (forêt dense, terres arables et prairie sèche). Les secteurs dans lesquels la densité populationnelle atteinte est maximale sont les habitats oligotrophes à molinie et bruyère en bordure d'un lac et des zones de type dunaires, qui sont sèches et caractérisées par des buissons et des jeunes arbres (Strijbosch, 1988). Le paysage apparaît donc structuré le long de gradients de densités, mais on ne connaît pas la dynamique d'extinction et de colonisation de ce système.

Tableau 1. Alimentation du lézard vivipare. Données comparatives (% des proies observées). Le régime varie entre populations mais aussi au sein d'une population entre classes d'âge et entre années (Avery, 1962).

	Somerset (Grande Bretagne) (Avery, 1962)	Lac Pavin (Puy de Dôme) (Pilorge, 1982a)	Paimpont (Bretagne) (Heulin, 1981)	
			Adultes	Juveniles
Homoptères	3	59	1	40
Araignées	28	17	60	34
Gastéropodes	1,5	7	1	0,5
Coléoptères	0,5	6	9	0,5
Lépidoptères	2	4	5	1
Diptères	4,5	4	17	11
Hétéroptères	36	1	0	0
Hyménoptères	5,5	1	1	2
Orthoptères	3	0,5	0	0
Autres	16	0,5	6	11

ALIMENTATION

Le régime alimentaire de ce lézard se compose essentiellement de petits animaux d'une taille moyenne de 3-4 mm (Avery, 1971; Pilorge 1982a), en particulier des Homoptères et des araignées mais aussi des Gastéropodes, des Coléoptères et des Diptères (Avery, 1966; Heulin, 1981; Pilorge, 1982a). Les Hyménoptères et les Orthoptères seraient plus rarement consommés (Pilorge, 1982a). Le Tableau 1 résume les résultats des analyses des contenus stomacaux dans différentes populations d'étude. Heulin (1981, 1984a) conclue de ses nombreuses analyses et observations de terrain que l'espèce est opportuniste au plan alimentaire et que les adultes sélectionnent des proies plus grosses, mais peu d'observations comportementales directes sont réellement disponibles. Les régimes alimentaires et les tailles des proies se chevauchent entre adultes et juvéniles, impliquant une compétition alimentaire significative entre toutes les classes d'âges de la population (Heulin, 1981).

COMPETITION ET PREDATION

La grenouille rousse (*Rana temporaria*) et le lézard agile (*Lacerta agilis*) sont des compétiteurs cités dans la littérature. Pourtant, Pilorge (1982b) a montré que *R. temporaria* n'exploitait pas le même spectre de proies que *L. vivipara* dans des populations sympatriques du Massif Central, et donc que le recouvrement de niches entre les deux espèces était faible. De la même façon, Strijbosch (1986) a trouvé une différenciation de niches entre le lézard vivipare et le lézard des souches en sympatrie en Hollande.

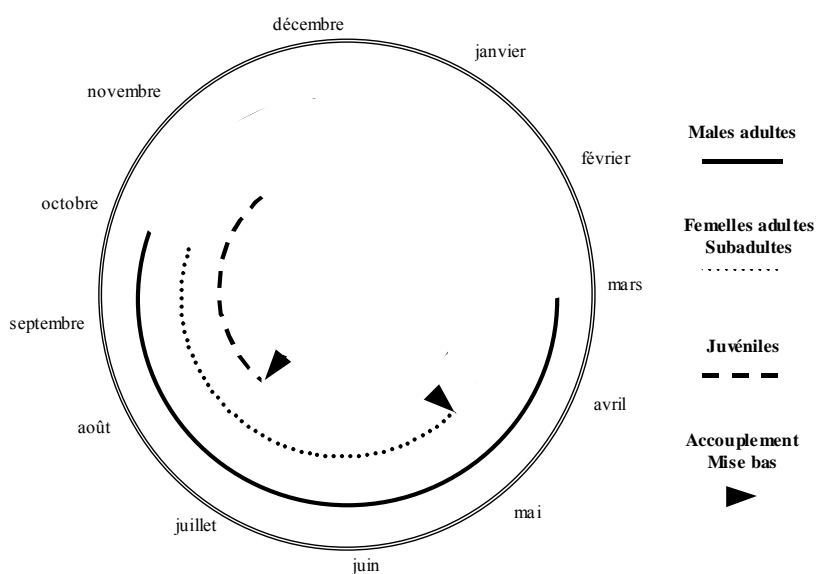
L'espèce serait la proie de jeunes *Vipera berus* et de *Coronella austriaca*, ces dernières fréquentant cependant rarement les mêmes habitats que le lézard vivipare (Heulin, 1984a). Heulin (1984a) indique aussi que les musaraignes, les Mustelidae et certaines espèces d'oiseaux (busard, circaète, faucon crécerelle, corneille, pics) sont des prédateurs potentiels. Dans une revue des différents prédateurs des lézards indigènes des Pays-Bas, Strijbosch (1981) recense de nombreuses espèces se nourrissant sur le lézard vivipare : 10 espèces d'oiseaux (Cigogne blanche, Bondrée apivore, Buse variable, Aigle pomarin, Busard pâle, Chouette hulotte, Faucon crécerelle, Sterne hansel, Pie-grièche grise, Rouge-gorge, Merle noir), 1 espèce de mammifère (Renard, mais d'autres observations recensent aussi 8 espèces de petits mammifères dont des musaraignes), et 4 espèces de reptiles (Lézard des souches, Vipère péliade, Coronelle, Couleuvre à collier).

CYCLE ANNUEL D'ACTIVITE ET DE REPRODUCTION

Le cycle annuel de l'espèce dépend fortement des conditions climatiques locales qui sont très variables au sein de l'aire de répartition. Dans les Cévennes, les mâles émergent de l'hibernation pendant les mois de mars et d'avril alors que les femelles et les sub-adultes sortent vers les mois d'avril à mai (Massot et al., 1992). Les mâles adultes font preuve d'un comportement territorial, agressif et d'une plus forte mobilité à l'émergence : ces comportements seraient responsables d'un coût en reproduction (Pilorge et al., 1987). L'essentiel de l'activité spermiogénétique s'effectue à l'émergence, où l'on observe une augmentation du volume testiculaire (Bauwens et al., 1989). Le cycle de spermatogenèse est réactivé directement après la reproduction (juin à juillet) et la spermatocytogenèse serait complète avant l'hibernation. Les femelles adultes réalisent la vitellogenèse, la gestation et la parturition pendant les quelques mois du printemps. L'activation du cycle reproducteur chez les femelles serait contrôlée par l'action conjointe du froid et un stimulus lié à l'accouplement. La vitellogenèse serait activée à l'émergence par l'accouplement (Dauphin-Villemant et Xavier, 1987), et il a été montré qu'elle n'est possible qu'après une exposition aux températures froides de l'hiver (Gavaud, 1983). L'accouplement dure parfois plusieurs heures. Le mâle est réceptif après une mue de reproduction (Bauwens et al., 1989), et il repère la femelle en à l'aide de signaux visuels typiques des femelles de l'espèce (Bauwens et al., 1987). Il s'agrippe le long des flancs de la femelle, s'arc-boute et introduit un de ses hémipénis dans le cloaque de la femelle (Heulin, 1984b). Le

système de reproduction est polygynandrique et impliquerait à la fois un contrôle mâle et un contrôle femelle de l'accouplement (Boudjemadi et al., 1999; Heulin, 1984b, de Fraipont et Fitze, com. pers.). La multipaternité résultant de ces processus comportementaux est très élevée, avec en moyenne la moitié des pontes résultant d'appariements multiples ainsi que deux pères par portée dans les populations naturelles et dans le site expérimental de la thèse (Laloi et al. soumis). La multipaternité peut varier en fonction de l'âge de l'individu, mais pas entre les populations étudiées.

L'ovulation débute après l'accouplement (vers mai à juin) et la fécondation a lieu dans la partie supérieure de l'utérus (Dauphin-Villemant et Xavier, 1987). Le cycle sexuel printanier se poursuivrait par la vitellogenèse de certains follicules dominants parmi les follicules ayant passé l'hiver sous une forme quiescente (Dauphin-Villemant et Xavier, 1987). La gestation dure environ 45 à 60 jours. Le développement embryonnaire a lieu dans les utérus de la femelle, où se met en place un placenta très rudimentaire, sauf dans les populations ovipares situées au Sud-Ouest de la France, en Espagne et aussi en Europe centrale. Les échanges, essentiellement hydriques et minéraux, ont lieu à travers la très fine membrane coquillière qui recouvre l'œuf. La parturition s'effectue entre la fin du mois de juillet et le début du mois d'août (Heulin, 1984a; van Nuland et Strijbosch, 1981). Les pontes sont composées de 1 à 12 œufs avec une moyenne de 5 œufs (Massot et al., 1992). Les œufs sont pondus en grappe en quelques minutes et sont enfoncés dans le sol. Le temps séparant la ponte de l'émergence du premier jeune peut atteindre plusieurs heures. Il n'y a pas de soins parentaux. Les juvéniles sont autonomes et dispersent à partir de l'âge de dix à quinze jours. La saison d'activité se termine en général vers la fin septembre pour les adultes et les sub-adultes, et vers la fin du mois d'octobre pour les juvéniles



CYCLE DIURNE D'ACTIVITE

Le lézard vivipare a des exigences thermiques moins importantes que la majeure partie des espèces sympatriques de la famille des Lacertidae. La préférence thermique corporelle se situe autour de 30 à 32°C, mais la température corporelle sélectionnée (TCS) en conditions expérimentales varie avec la taille de l'individu et son statut reproducteur (van Damme et al., 1990). Le profil comportemental classique d'une journée d'activité est caractérisé par des thermorégulations longues en début de matinée (émergence vers des températures de 15 à 16°C), suivies d'alternance de mouvements et de périodes de thermorégulation, puis de déplacements plus intenses, associés à la recherche de nourriture, aux heures les plus chaudes de la journée. Le cycle s'inverse en fin d'après-midi, la disparition des lézards étant observée pour des températures de 16 à 18°C (Avery, 1982; Avery et McArdle, 1973 ; House et al., 1980).

On observe des différences du profil de thermorégulation aux mêmes saisons entre individus de classes d'âge et de sexe différentes, et aussi entre saisons au sein d'une même classe (House et al., 1980). Les mâles adultes ont des TCS supérieures aux autres individus (32 à 33°C), avec des pics à l'émergence et en été lors des périodes les plus intenses de la spermiogenèse et de la spermatocytogenèse (Bauwens et al., 1989). La TCS des femelles est plus faible (30 à 32 °C) avec un pic au printemps lors de la vitellogenèse et de l'ovogenèse (32°C) et une chute significative lors de la gestation (30°C). Cette diminution s'expliquerait par la température optimale de développement des embryons, qui se situerait autour de 27°C (Lecomte et al., 1993). La température corporelle sélectionnée par les juvéniles et les sub-adultes est plus faible que chez les adultes. Des contraintes physiologiques s'exercent donc selon le statut reproducteur d'un individu pour l'accès à des températures optimales. Ces contraintes peuvent contribuer aux différences de comportement, d'utilisation de l'habitat et de dispersion, notamment chez les femelles gestantes (Lecomte et al., 1993).

DEMOGRAPHIE

Les populations naturelles du lézard vivipare sont composées de juvéniles après la saison de reproduction (individus nés dans l'année), de sub-adultes (individus nés l'année précédente) et d'individus adultes (individus de deux ans et plus, voir Pilorge et Castanet (1981) pour une description des différences de taille et de morphologie entre les différentes classes d'âge). L'âge de la maturité sexuelle est de deux ans en général dans les Cévennes mais la proportion de reproducteur dans cette classe peut varier d'une année à l'autre (Pilorge, 1987). Le même mécanisme se retrouve en Bretagne et en Belgique où, respectivement, une proportion des sub-adultes (Heulin, 1985c) et une proportion des adultes de deux ans (Bauwens et Verheyen, 1987) peut atteindre le statut reproducteur certaines années.

La densité et la structure d'âge et de sexe des populations naturelles sont très variables dans l'espace mais régulées dans le temps (Bauwens et al., 1986; Pilorge, 1987). On dispose de données pour des populations de montagne dans les Cévennes (Pilorge, 1987) et pour des populations de plaine en Bretagne (Heulin, 1985b) et en Belgique (Bauwens et Verheyen, 1985; Tableau 2).

Tableau 2. Données démographiques comparatives dans trois populations de *Lacerta vivipara*. (d'après Sorci et al., 1996a).

	Bretagne (Heulin, 1985a)	Belgique (Bauwens et al., 1986)	Cévennes (Pilorge, 1987)
Habitat	Prairie humide	Lande humide	Lande humide
Densité	200-300	700-800	700-1300
Fécondité	6-7	4-5	5-6
Survie juvénile	0.1 à 0.15	-	0.25 à 0.3
Survie adulte	0.4-0.5	-	0.5 à 0.7
Taille femelle adulte (mm)	55-65	53-55	60-65

Dans un habitat favorable au Mont Lozère, la densité totale peut atteindre plus de 1000 individus à l'hectare (densité maximale observée pour l'espèce) et la structure d'âge stable avant reproduction est environ de 50% d'adultes (biaisée en faveur des femelles : 60% de femelles et 40% de mâles) et de 50% de sub-adultes (Pilorge, 1987). La densité varie fortement entre populations, même à une échelle très locale, et cette variance spatiale est supérieure à la variance temporelle au sein de chaque population (Bauwens et al., 1986). Il semblerait que la densité de la population reflète une qualité physique de l'habitat local, bien que celle-ci soit difficile à définir et à mesurer (Khodadoost et al., 1987; Strijbosch, 1988). On trouverait les lézards en abondance dans des habitats hétérogènes offrant des surfaces de thermorégulation, des abris et des zones de nourrissage favorables. Par contre, il n'existe pas de relation entre l'humidité du milieu ou la quantité de nourriture et la densité de la population, en tout cas dans les habitats des Cévennes (Khodadoost et al., 1987). Les densités atteintes sont comparables dans un habitat de plaine en Belgique (Bauwens et al., 1986). Dans les montagnes du Puy de Dôme, les densités sont par contre plus faibles (200 à 300 individus par hectare ; Pilorge et Xavier, 1981), ce qui correspond aussi aux densités moyennes observées en Bretagne (Heulin, 1981).

Des études comparatives, basées sur une description des histoires de vie individuelles, montrent que les différences entre classes de sexe et d'âge sont importantes. Ces différences seraient l'expression de réponses stratégiques démographiques alternatives. Dans cette hypothèse Pilorge et al. (1987) proposent en particulier que :

(i) les mâles sont soumis à une compétition sexuelle intense lors de la sortie de l'hiver pour le maintien d'un territoire et l'accès aux femelles, période où ils paieraient donc un fort coût à la

reproduction. Au contraire, les femelles sont plutôt soumises à une compétition pour les ressources locales, ce qui rendrait leur survie plus sensible à des différences de disponibilité des proies au printemps (investissement dans la ponte) et après la mise bas (récupération du coût à la reproduction) ;

(ii) les sub-adultes et les juvéniles seraient soumis à une compétition pour l'accès aux ressources et pour la croissance corporelle, afin d'atteindre le statut de reproducteur ;

(iii) la compétition serait asymétrique chez cette espèce avec une dominance des mâles adultes sur les femelles, et des adultes sur les sub-adultes et les juvéniles (Lecomte et al., 1994).

Les mâles adulte ont une survie et une durée de vie plus faible que les femelles dans les populations naturelles (Pilorge et al., 1987). La survie des mâles est corrélée négativement avec la température en avril, ce qui suggère un coût associé à une sortie précoce de l'hibernation (Pilorge et al., 1987). La survie des femelles est corrélée négativement à une augmentation de l'effort reproducteur, suggérant des coûts en reproduction (Pilorge et al., 1987; Sorci et al., 1996b). La survie juvénile est influencée négativement par une augmentation de la densité, contrairement à celle des sub-adultes et des adultes qui n'est pas sensible à la manipulation de densité, ce qui est en accord avec l'hypothèse d'une compétition asymétrique (Massot et al., 1992). Bauwens (1981) note par ailleurs que la survie juvénile hivernale est diminuée par une perte des réserves de graisse stockées dans la queue. De manière générale, les survies juvéniles ou sub-adultes sont plus faibles que les survies adultes, et sont plus sensibles à des variations environnementales (Massot et al., 1992; Pilorge et al., 1987). Finalement, il a été aussi récemment mis en évidence un phénomène de sénescence en survie chez les femelles adultes (Ronce et al., 1998) qui pourrait s'expliquer par l'accumulation de coûts successifs à la reproduction (Sorci et al., 1996b).

Selon Pilorge (1988), une grande partie de la variation spatiale et temporelle est expliquée par des différences de longueur du museau à anus, donc en particulier des taux de croissance corporelle. Par exemple, les variations temporelles des traits reproducteurs dans une population de Belgique sont expliquées par des différences de la taille des femelles entre années (Bauwens et Verheyen, 1987). Par ailleurs, des transferts croisés entre des populations de Lozère et de Bretagne ont démontré que ces différences géographiques de taille corporelle sont l'expression de phénomènes de plasticité phénotypique (Sorci et al., 1996a). Les lézards de plaine sont actifs plus longtemps dans l'année et réalisent une croissance plus importante pendant leur première année.

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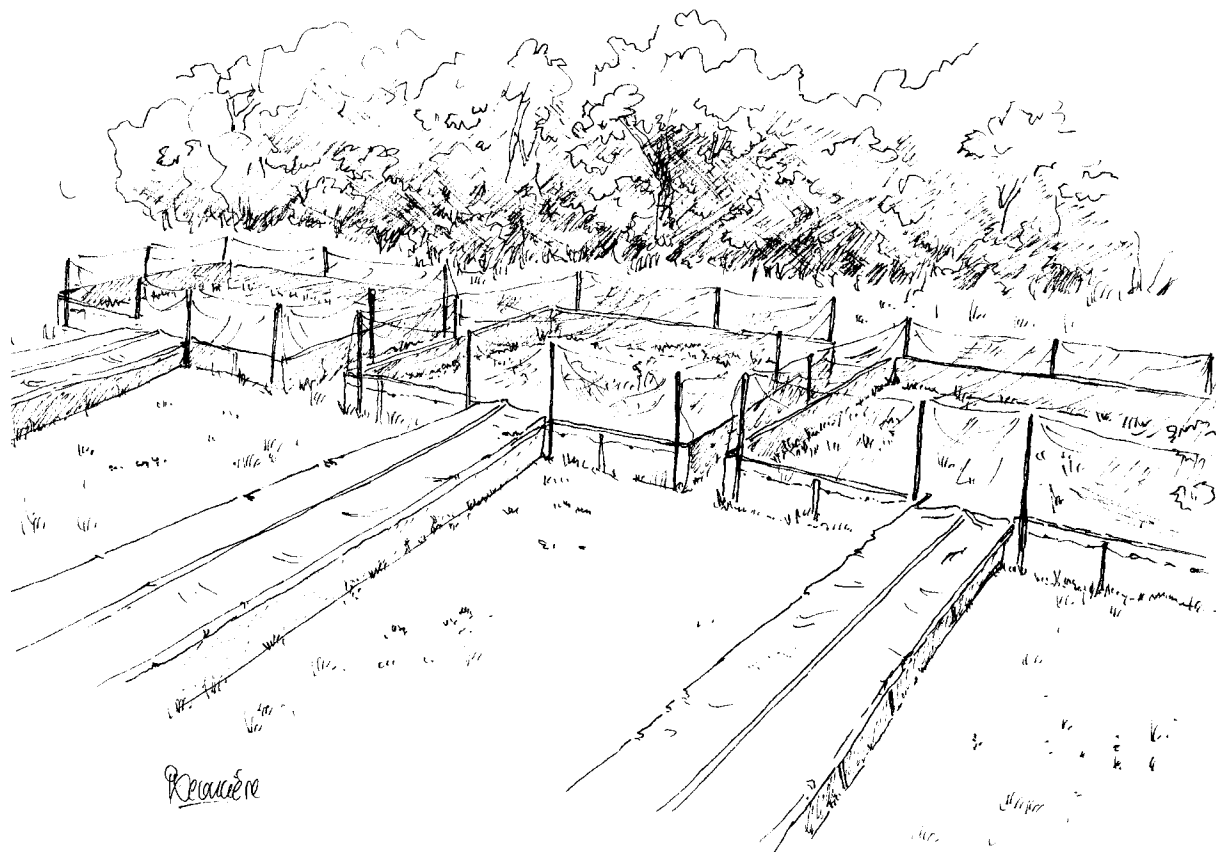
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ANNEXE 3 – INTERACTIONS SOCIALES DANS UN HABITAT FRAGMENTE



CONSEQUENCES DEMOGRAPHIQUES DES INTERACTIONS SOCIALES DANS UN HABITAT FRAGMENTE DU LEZARD VIVIPARE

Jean-François Le Galliard, Régis Ferrière & Jean Clobert

RESUME

Les interactions sociales dépendantes de la densité et de l'apparement peuvent influencer la dynamique de la population par la modification des processus démographiques locaux et régionaux. Nous avons récemment étudié les effets de la compétition entre congénères et des interactions mère à enfants sur la dispersion. Ici, nous analysons l'effet de ces interactions sociales sur la démographie locale du lézard vivipare (*Lacerta vivipara*) dans des système expérimentaux de deux populations connectées. Au début de l'étude, nous avons relâché des densités faibles et fortes de lézards dans des populations connectées au sein du même système. Conjointement, nous avons relâché les jeunes de différentes populations en présence ou en absence de leur mère. Nous avons mesuré les traits d'histoire de vie des résidents (survie, reproduction, croissance en masse et en taille) et la dynamique de la population pendant deux années successives.

La présence de la mère a induit une diminution de survie des jeunes, mais n'a pas affecté leur croissance et leur reproduction. Les taux de survie ont été indépendants de la densité, sauf pour le cas d'une augmentation de survie des femelles adultes à haute densité. L'âge à la première reproduction et la taille de ponte totale à l'âge de deux ans ont été diminuées par la densité de la population. La croissance en taille des sub-adultes et la reprise de masse des femelles adultes après la parturition ont aussi été plus faibles à haute densité, mais pas la croissance juvénile. Ces résultats suggèrent une rétroaction faible de la densité sur les traits d'histoire de vie qui ont un impact rapide sur la taille de la population, et un effet négatif de la présence de la mère sur la valeur sélective des jeunes.

Aucun effet de la présence de la mère sur la dynamique de la population n'a été détecté. Aucune régulation densité dépendante de la taille de population n'a eu lieu. Les contrastes de taille entre les traitement de densité ont persisté pendant les deux années de l'étude. Nous concluons que l'indépendance de la survie et de la dispersion à la densité de la population a induit une forte stabilité de la distribution d'abondance des populations récemment introduites.

Référence : Ces données n'ont pas été publiées, soumises à publication ou révisées par mes collaborateurs.

Mots-clés: compétition, interactions mère à enfants, survie, reproduction, croissance, démographie.

DEMOGRAPHIC CONSEQUENCES OF SOCIAL INTERACTIONS IN A PATCHY HABITAT OF THE COMMON LIZARD

Jean-François Le Galliard, Régis Ferrière & Jean Clobert

SUMMARY

Density-dependent and kinship-dependent interactions can influence population dynamics through local and regional demographic processes. We recently analysed the effects of conspecific density and mother-offspring interactions on dispersal behaviour. Here, we investigate the impacts of the same treatments on local population dynamics of the common lizard (*Lacerta vivipara*) in experimental two-patch systems. At the start of the study, we released low and high density of lizards in coupled patches of the same two-patch systems. Jointly, we released the offspring of different patches either in the absence or in the presence of the mother. We measured residents life-history traits (survival, reproduction, growth in size and mass) and population demography during two years.

We found that mother presence decreased offspring survival, but had no effect on growth or reproduction. Survival probabilities were density-independent in most age classes, except that adult females survived better at high density. Age at first reproduction and total clutch size of two years old females were negatively affected by population density. Yearlings growth in size and adult females mass recovery after parturition were also lower at high density, but not juveniles growth. These results suggest a poor feedback of population density on life history traits with short-term impacts on population size, and a negative effect of mother presence on offspring fitness.

No effect of the mother presence on population demography was detected. No density-dependent population growth occurred: population size contrasts between high- and low-density patches persisted during the two years of the study. We conclude that density-independent survival and dispersal patterns can induce resilience in the abundance pattern of recently introduced populations.

[Reference](#) : These data have not been published, submitted for publication nor reviewed by my collaborators.

Keywords: competition, mother-offspring interactions, survival, reproduction, growth, demography, common lizard

INTRODUCTION

The effects of social interactions on population dynamics can be strong (Christian 1970, Krebs 1978, Sinervo et al. 2000). In particular, competitive interactions among conspecifics and cooperative interactions between relatives are thought to drive the fluctuating population dynamics of some rodents and the build up of complex social systems in some vertebrates (e.g., Lambin and Krebs 1991a, Emlen 1997). Yet, interactions between density-dependent and kinship-dependent regulation of population size and their mechanistic basis are still poorly known.

Competition among conspecifics generates negative density dependence on population size, which has the potential to stabilise population dynamics if regulation occurs rapidly (Bjørnstad and Grenfell 2001). Negative density dependence has been detected in several species through long-term observations of population dynamics (e.g., Woiwod and Hanski 1992, Lande et al. 2002). Furthermore, studies conducted at appropriate temporal and spatial scales suggest that density-dependent regulation is an ubiquitous feature of most natural populations (Ray and Hastings 1996). However, time series analyses rarely give informations on the underlying mechanisms of population regulation. In particular, even appropriate population monitoring can hardly conclude about the type of individuals affected by density dependence, the effects of density on the different demographic parameters, and the basis of the delay in demographic responses. Mark-recapture studies have also been used to investigate density-dependent variation on survival and maturation probabilities in some populations (e.g., Leirs et al. 1997, Renault et al. 2003). Although such life-history models are more mechanistic, false density-dependent regulation can be demonstrated when population density correlates with some environmental factors. In turn, this leads to strong difficulties in distinguishing between environmental and density-dependent sources of population regulation (Bjørnstad and Grenfell 2001). Alternatively, manipulative studies of population size offer valuable and causal informations on density dependence (Krebs 1988). However, several field experimental using removal and translocation procedures have been unable to control for population structure, or have lacked true replication (e.g., Rodd and Boonstra 1984, Massot et al. 1992, Both 1998). Here, we used translocation experiments to establish several local populations of the common lizard (*Lacerta vivipara*) at low and high density in enclosed, fragmented habitats (see also Aars and Ims 1999, 2000). We then monitored the regional and local regulation factors affecting the dynamics of population abundance during two years.

Interactions between relatives have the potential to induce changes in life-history traits and in population demography (e.g., Mappes et al. 1995). Mother-offspring interactions are promoted by the higher investment of females in reproduction and parental cares, and by the strong philopatry of adult females. Several studies have reported that mother-offspring interactions can be involved in habitat choice, resources sharing, and reproductive strategies (e.g., Kawata 1987, Cockburn 1998, Lambin et

al. 2001). Interactions between mother and offspring can be arranged along a gradient from competitive interactions, through tolerance to actively altruistic relationships. In some species, the mother shares space and resources with their offspring, leading to familial clusters within the population (e.g., Andreassen and Ims 1998, Bjørnstad et al. 1998). In microtine rodents, such mother-daughters overlap has been suggested to enhance daughter reproductive success, through increased tolerance and reduced infanticide among relatives (Pusenius et al. 1998). However, the contribution of these social interactions within clusters of relatives to the overall population dynamics has been controversial, with some studies finding positive effects of kinship and familiarity on population growth (Ylönen et al. 1988, Lambin and Yoccoz 1998) and other studies not (Dalton 2000). While the consequences of mother-offspring interactions have been deeply investigated in the context of space sharing in small rodents, relatively few studies have searched for kinship-dependent demography in other taxa. In the common lizard, viviparity and breeding site fidelity in mature females facilitate mother-offspring interactions, and have promoted the evolution of mother-offspring recognition and habitat choice strategies based on maternal characteristics (Clobert et al. 1994). Offspring are able to discriminate their mother from unrelated females using olfactory cues, and make use of these cues during habitat choice (Léna and de Fraipont 1998, Léna et al. 2000). Furthermore, natal dispersal has been found to be influenced by the risks of potential mother-offspring competition, as shown by the effects of maternal age, parasitism, hormonal status and condition during gestation on offspring movements (Sorci et al. 1994, Massot and Clobert 1995, Léna et al. 1998, de Fraipont et al. 2000, Ronce et al. 2000, Meylan et al. 2002). Here, we manipulated the presence of the mother in several populations of the common lizard to investigate the effects of mother-offspring interactions on individual life-history traits and on population dynamics during two years. We crossed this effect with the density manipulation to analyse the interplay between density-dependent and kinship-dependent social interactions.

We recently showed that (i) mother-offspring interactions increased the natal dispersal of daughters, but decreased sons movements, (ii) that a high population density decreased natal dispersal during the first study year and had no effect on breeding dispersal, and (iii) that density-dependent and kinship-dependent effects on dispersal were independent from each other (Le Galliard et al. 2003b). In this study, we analysed the effects of the experimental treatments on individual growth trajectories, reproductive outputs, survival probabilities, and population demography.

METHODS

The species

The common lizard *Lacerta vivipara* (Jacquin 1787) is a small, viviparous lizard inhabiting humid habitats such as peatbogs, heathlands, or meadows. It is widespread across Eurasia with

populations ranging from the polar circle to the south of Europe and from the coast to 3,000 m elevation (Avery 1975). Three age classes can be distinguished according to size and secondary sexual characters: juveniles (year born individuals), yearlings (one year old), and adults. In the experimental populations, the activity season spreads from March to October. Adults and yearlings hibernate first (October) whereas juveniles delay hibernation up to mid-October. Winter emergence begins in mid-February or early March, where mostly adult males are active, whereas adult females and yearlings emerge from hibernation during the end of March and April (Le Galliard *pers. obs.*). Matings last two to three weeks. Gravid females complete gestation within two to three months. Parturition spreads from June to July. Females lay on average 5 shell-less eggs (range 1-12). Hatchlings are autonomous at birth and parents do not provide care. Additional informations with regard to the life-history, mating system, and population biology of the species can be found in Avery (1975), Pilorge (1982, 1987) and Heulin (1985b).

Experimental system

The experimental system consists of enclosed populations located in a natural meadow at the Ecological Research Station of Foljuif (Saint-Pierre-lès-Nemours, Seine et Marne). During this study, we used eight experimental two-patch systems (10 × 10 m) connected by two 20 m length one-way corridors (Fig. 1). Corridors allow movements of lizards between patches within the same two-patch system. The distance between the two patches is also used to define dispersal in natural populations (Massot 1992), and has been found to be efficient to produce similar dispersal patterns as in nature (Lecomte and Clobert 1996, Boudjemadi et al. 1999, Le Galliard et al. 2003b). Enclosures were mowed one time per month during the activity season, but food was never provided. From the onset of the experiment, all enclosures were protected from avian predators by nylon nets and from intrusive mammals by daily trapping (2 Sherman traps per enclosure). However, we could not avoid short-term intrusions of shrews (*Crocidura russula*) in five patches in 1999 (Fig. 1). From 2000 to 2001, the external and internal area was trapped with Ugglan traps (GrahnbTM, Sweden) and predation was virtually prevented, except in one enclosure at the fall of the last hibernation (Fig. 1).

Experimental protocol

Our experiment was conducted from June 1999 to June 2001. We introduced lizards from a mountain area in four different types of patches using a factorial manipulation of patch density (low or high density) and of kinship (presence or absence of the mother). Lizards behaved freely during their lifetime, up to their removal from the experimental system in June 2001. Reproductive characteristics were measured during the first year of the experiment by keeping all females in the laboratory until laying, and at the end of the experiment by capturing all individuals.

Sampling. We sampled lizards in three high density areas located close to the Chalet du Mont Lozère (Cévennes, 1500-1600 m a.s.l.) during two weeks of June 1999. These populations are distributed along a 3 km length transect, and are called Population 1 (Panches, 44°25'N, 3°46'E), Population 2 (Banassac, 44°25'N, 3°45'E), and Population 3 (Chalet du Mont Lozère, 44°27' N, 3°44'E). We applied similar capture effort in each population (i.e., 15h. per population) and collected 146 gravid females, 95 adult males, and 257 yearlings. Lizards were marked by toe clipping and measured for length (to the nearest mm, SVL) and weight (to the nearest 0.05g). Until introduction, lizards were kept in terraria littered with heath ground and provided with food and water *ad libitum* (Lorenzon et al. 1999). A heat source generated an optimal thermal gradient (van Damme et al. 1991). For logistic reasons, yearlings and adults were kept in groups of 6 males or 15 yearlings within large terraria (130 × 47 × 35 cm), while gravid females were isolated in small terraria (17 × 11 × 12 cm). After laying, hatchlings were kept during two days with their siblings and mother to allow familiarisation (Léna and de Fraipont 1998). Post-laying female body mass was measured. Siblings were measured for length and body mass (to the nearest μg), and their sex was determined by counting ventral scales (Lecomte et al. 1992). Each offspring was marked by toe clipping.

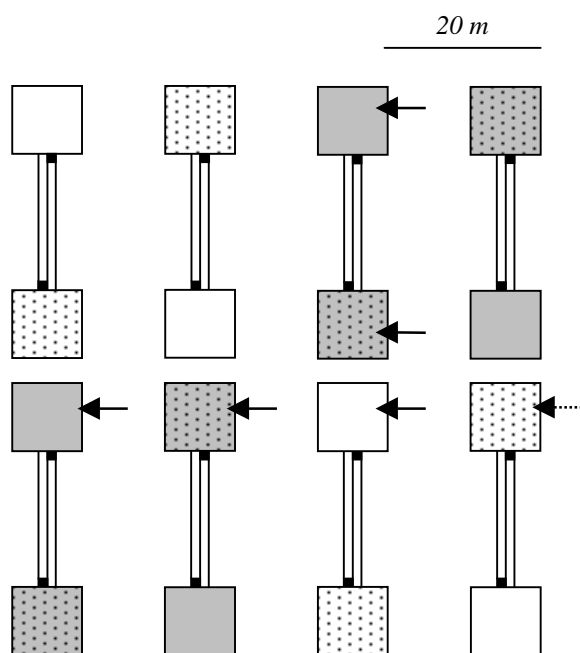


Figure 1. Experimental design. Gray indicates two-patch systems where offspring were released with an unfamiliar adult female, while offspring were released with their mother in the other two-patch systems. Dotted indicates high-density patches. Plain arrows indicate patches affected by predation during 1999 and the dashed arrow indicate one patch predated during spring 2001.

Experimental design. We used a factorial design to address the effects of patch density and of the presence of the mother. We manipulated initial density in July 1999 (each enclosure being a replicate), and crossed this effect with the kinship treatment (each two-patch system being a replicate, Fig. 1). We manipulated patch density by coupling a low-density ($56.5 \text{ individuals} \pm 2.4 \text{ SE}$) and a high-density patch ($111.2 \text{ individuals} \pm 3.9 \text{ SE}$) within each two-patch system. The population structure was matched to the natural structure, and comprised yearlings (10 or 20 individuals, balanced

sex-ratio), adults males (4 or 8 individuals), and adult females (6 or 12 individuals), plus the corresponding offspring. In four two-patch systems, we introduced all siblings with their mother. In the four other two-patch systems, we replaced the mother of all siblings with a randomly chosen unfamiliar adult female. Populations were not manipulated in the following.

Introduction. Yearlings and adult males were introduced at the start of the parturitions on the 14 of July 1999. Corridors were closed before the first clutch was introduced to avoid prospective movements and maintain homogeneous densities before the introduction of offspring. Siblings and mothers were introduced three days after parturition. Geographical origin, clutch size, sex-ratio, body size, and body condition were similar between treatments (ANOVAs on differences between treatments, all $P > 0.4$).

Census. We monitored populations by recapture methods. At each capture, body length and body mass were recorded. Dispersers were captured in pitfall traps located at the end of corridors and checked daily during the activity season (August to October 1999, March to October 2000, March to June 2001). Furthermore, we captured lizards in each enclosure by hand recaptures during seven main sessions spaced by at least one month. Within some main sessions, we also captured and released individuals during several independent daily sessions (Table 1). Main sessions can be used to estimate growth and survival using open population models (Pollock et al. 1990). Daily sessions can be used to estimate population size during each main session using closed population models (Otis et al. 1978). Due to the large number of lizards introduced at the start of the experiment, it was not possible to do daily sessions in 1999. However, the unique census of August 1999 was long enough (2-3 days per enclosure) to allow exhaustive captures (capture probability > 0.9), so that we estimate population size as the total number of individuals captured. Females were also captured a few weeks before parturition in June 2000, and randomly distributed in individual terraria until laying. After laying, hatchlings were marked by toe-clipping, measured, and released in the natal patch the following day. All lizards were captured at the end of the experiment and kept in individual terraria.

Table 1. Design of the demographic monitoring from 1999 to 2001. The total duration of the main sessions (days), the number of daily sessions, the duration of each daily session per patch (days), and the total number of captures are indicated.

	August 1999	September 1999	April 2000	August 2000	September 2000	April 2001	June 2001
Total duration	13	9	12	15	4	8	12
Number daily session	1	1	3-4	3	1	2	-
Duration daily session	2-3	1	1	1	1	1	-
Total number of captures	842	438	954	977	236	403	242

Data analysis

Analyses were done using the eleven non predated enclosures (Fig. 1). The sample was divided in four groups (juveniles, yearlings, and adults from the 1999 cohort; juveniles from the 2000 cohort), and only resident individuals were studied.

Individual covariates. Our models include the following individual covariates: sex, geographical origin (population 1 to 3), snout-vent length (SVL), body condition, density treatment, kinship treatment, and all first-order interactions. Body condition was measured as the residual from a linear regression of body mass on SVL for lizards that had not lost their tail (Massot et al. 1992). All analyses were conducted with the software SAS. Results are presented as means \pm SE unless otherwise stated.

Initial characteristics, growth and reproduction. Initial characteristics of lizards were compared among origin populations within each age class. Analyses were conducted using ANOVA testing for origin effects with the procedure GLM. Changes in body length and body condition during the experiment were studied from 1999 to 2001. Since lizards were not active during the winter season, we excluded hibernation months (November to March) from the growth rates calculations. The effect of treatments was examined within each class during each study year. Because growth rates depend on the initial morphological state, initial length or initial body condition were included in the model (Schoener and Schoener 1978). Reproductive characteristics were studied on females kept in the laboratory. Each year, females were classified as gravid / non gravid based on the palpation of vitellogenic eggs and egg production in the laboratory, and the proportion of gravid females was compared among treatments. Hatching success was measured as the proportion of neonates among the total clutch, and compared between treatments, as well as hatchling size, condition, and sex.

All analyses were conducted by backward selection from a model including the experimental effects, first-order interactions with individual covariates and patch as a random, nested effect (Bennington and Thayne 1994). The mixed-effect models were implemented with the procedure MIXED (Littell et al. 1996). Assumptions of normality and homoscedasticity of residuals were tested by Shapiro-Wilk tests and Bartlett tests. When heteroscedasticity was detected without departure from normality, we weighted each observation by the reciprocal of the residual variance.

Survival. Survival analyses were conducted on life history data using the software MARK with a Cormack-Jolly-Seber model (White and Burnham 1999, Cooch and White 2001). These models allowed us to estimate survival probabilities independently from capture probabilities (Lebreton et al. 1992). Individual life histories of residents were constructed with the most exhaustive censuses of the first study year (Introduction, August 1999, April 2000, August 2000). The last census was not

accounted for in this model, because these results correspond to preliminary analyses started before the end of the experiment.

A full model was first fitted to the data. This model included the effects of (i) treatments, time, sex, and origin, (ii) patches nested within treatments, (iii) interactions between treatments and time, and (iv) interactions between patches and time. The goodness-of-fit of this model was assessed with a parametric bootstrap of 1,000 simulations (Pollock et al. 1990, Anderson and Burnham 1994, White and Burnham 1999). When lack-of-fit of the initial model was detected, an overdispersion factor was included in the analysis (Anderson and Burnham 1994). This overdispersion parameter was calculated as the deviance of the model divided by the average deviance of the resampling (Cooch and White 2001). Model selection was then conducted in two steps in order to keep the number of comparisons tractable. We first simplify the model describing variation among patches on survival and capture probabilities using likelihood ratio tests (Lebreton et al. 1992). Then, we used the selected model as a starting point to study main effects with likelihood ratio tests and analyses of deviance (Skalski et al. 1993). Only the selected models are reported here.

Population size. The population size of more than one year old individuals was estimated for each patch in August 1999, April 2000, August 2000, and June 2001. In April and August 2000, population sizes were obtained from a Jolly-Seber model (Seber 1965, Otis et al. 1978). The “closed population” assumption was justified by the short duration of our censuses (Table 1). Estimations were conducted with the software CAPTURE (Otis et al. 1978, White and Burnham 1999). A model describing heterogeneity in capture probabilities in each age class was selected from several possibilities (see Otis et al. (1978) for more details). We do not report the results of this model selection here. Population demography was studied with repeated measurements analyses. Patch was included as a random effect. Temporal variation was modelled with a variance-covariance structure minimising the Aikake Index Criterion of the model (Littell et al. 1996).

RESULTS

Initial characteristics

We compared lizards among origins (Table 2). Juveniles SVL and body condition at birth did not differ among origins, but were affected by the offspring sex. Males were smaller and more corpulent than females at birth (Males: 22.9 ± 0.09 mm, 0.183 ± 0.002 g, $n = 438$; Females: 23.8 ± 0.09 mm, 0.178 ± 0.002 g, $n = 401$). Yearlings had higher SVL and higher body condition in population 3 (contrasts between Population 1-2 and Population 3, $P < 0.001$ for body size and body condition). Also, the sexual size dimorphism was significant in population 3 (Tukey’s contrast, $P = 0.05$), with males being smaller than females (Males: 45.3 ± 0.37 mm, Females: 46.9 ± 0.41 mm), but not in populations 1 and 2 ($P > 0.80$, Table 2). The SVL of adult males was not affected by origin, but

their body condition was lower in population 1 (contrast between Population 1 and Populations 2-3: $P = 0.002$, Table 2). Adult females had significantly longer body size in population 3, as well as earlier laying dates and higher clutch sizes independently from size (contrast between Population 3 and Populations 1-2: $P < 0.001$, Table 2). Because of a higher reproductive investment in population 3, gravid females had similar post-parturition body condition among origins (Table 2).

Table 2. Morphological and reproductive differences among origins. Laying date, clutch size, and body mass were analysed using body size as a covariate. Laying dates are given as the number of days from July 1. Body size is given in *mm* and body mass is given as *g* after correction for body size differences. Body condition of adult females is measured after laying. Data are least-square means (\pm SE).

Predictors of	Juveniles <i>n</i> = 839		Yearlings <i>n</i> = 257			
	SVL	Mass	SVL	Mass		
Sex	$F_{1,692} = 172.8$ ***	$F_{1,691} = 35.9$ ***	$F_{1,251} = 0.75$	$F_{1,250} = 43.1$ ***		
Origin	$F_{2,141} = 0.80$	$F_{2,141} = 2.05$	$F_{2,251} = 161.2$ ***	$F_{2,250} = 10.1$ ***		
Sex \times Origin	$F_{2,692} = 1.25$	$F_{2,691} = 0.40$	$F_{2,251} = 3.27$ *	$F_{2,250} = 2.12$		
Population 1	23.2 ± 0.17 <i>n</i> = 142	0.183 ± 0.003 <i>n</i> = 142	40.5 ± 0.43 <i>n</i> = 88	1.24 ± 0.02 <i>n</i> = 88		
Population 2	23.4 ± 0.14 <i>n</i> = 219	0.182 ± 0.002 <i>n</i> = 219	41.1 ± 0.47 <i>n</i> = 57	1.22 ± 0.03 <i>n</i> = 57		
Population 3	23.4 ± 0.11 <i>n</i> = 478	0.177 ± 0.002 <i>n</i> = 478	46.0 ± 0.28 <i>n</i> = 112	1.37 ± 0.02 <i>n</i> = 112		
	Adult males <i>n</i> = 95		Adult females <i>n</i> = 146			
Predictors of	SVL	Mass	SVL	Laying date	Litter size	Mass
Origin	$F_{2,92} = 0.76$	$F_{2,91} = 5.56$ ***	$F_{2,143} = 7.45$ ***	$F_{2,142} = 12.2$ ***	$F_{2,142} = 10.8$ ***	$F_{1,142} = 0.81$
Population 1	55.9 ± 0.45 <i>n</i> = 40	3.27 ± 0.06 <i>n</i> = 40	61.6 ± 0.70 <i>n</i> = 29	21.5 ± 0.62 <i>n</i> = 29	5.77 ± 0.36 <i>n</i> = 29	3.01 ± 0.06 <i>n</i> = 29
Population 2	55.8 ± 0.51 <i>n</i> = 31	3.48 ± 0.07 <i>n</i> = 31	62.2 ± 0.64 <i>n</i> = 46	20.8 ± 0.37 <i>n</i> = 46	5.40 ± 0.22 <i>n</i> = 46	3.11 ± 0.05 <i>n</i> = 46
Population 3	56.7 ± 0.58 <i>n</i> = 24	3.58 ± 0.08 <i>n</i> = 24	64.1 ± 0.34 <i>n</i> = 71	18.9 ± 0.26 <i>n</i> = 71	6.62 ± 0.15 <i>n</i> = 71	3.06 ± 0.04 <i>n</i> = 71

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

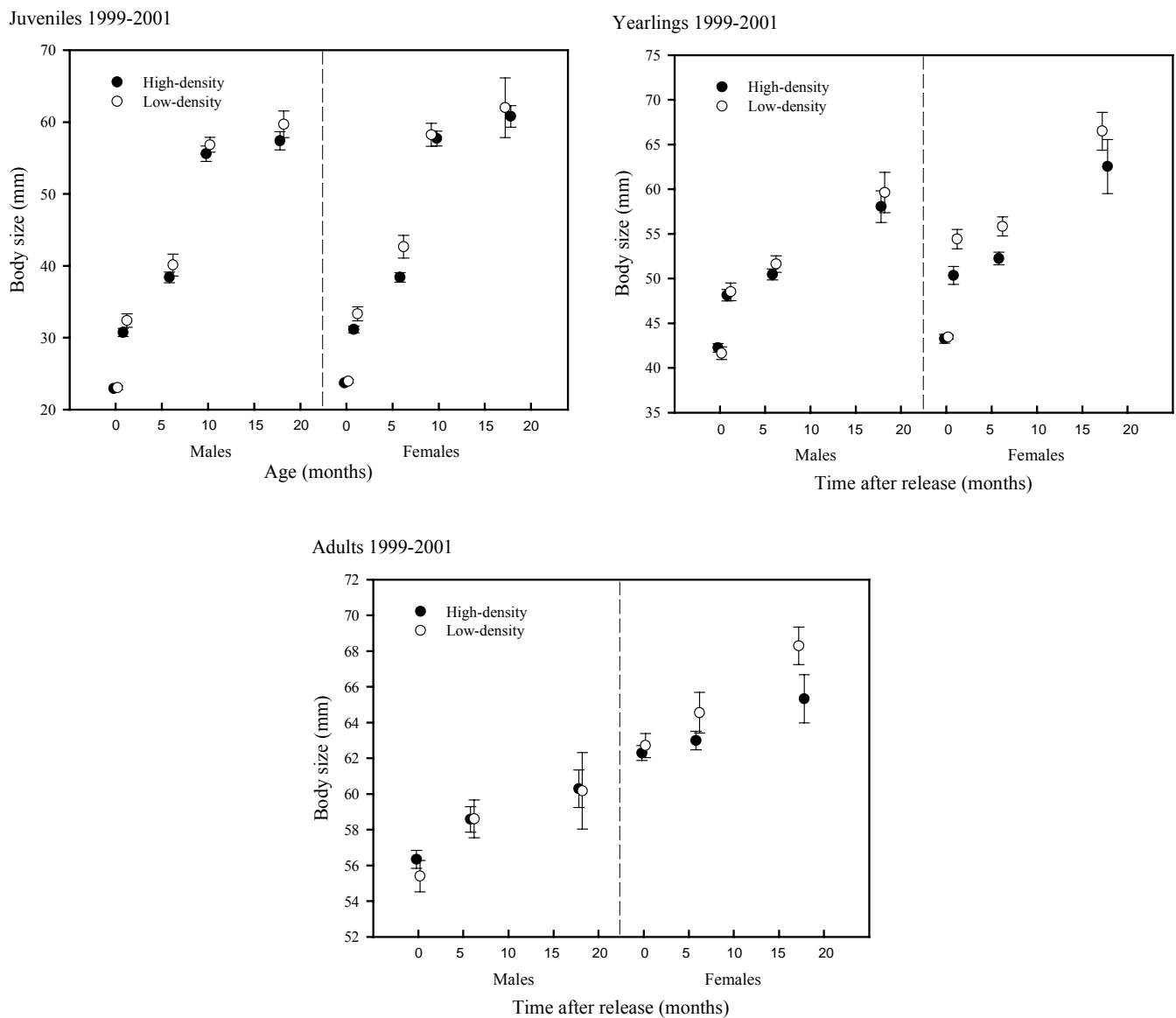


Figure 2. Body size for males and females from 1999 to 2001 in low- and high-density patches. Values are least-square means \pm SE for the SVL of resident individuals, derived from a linear mixed-effect model including origin as a covariate and patch as a random effect. Data are illustrated separately for juveniles, yearlings, and adults. Time axis excludes wintering months.

Changes in size and condition

Juveniles 1999-2001. This cohort was examined using four censuses (August 1999, April 2000, August 2000, June 2001). Body condition variation was similar between treatments ($P > 0.32$), and was higher for males than for females ($P < 0.001$). During the first year, body size growth was affected by origin, but not by kinship or density treatments (Table 3). During the summer, juveniles originating from populations 2 and 3 grew more than juveniles from population 1 (contrast between Population 1 and Populations 2-3 = -0.05 ± 0.01 mm.day⁻¹, $P < 0.001$). During the next autumn and spring,

juveniles from population 3 grew more than juveniles from populations 1 and 2 (contrast = $-0.02 \pm 0.005 \text{ mm.day}^{-1}$, $P < 0.001$). The effect of the density manipulation tended to be significant from August 1999 to April 2000, with reduced growth rates at high-density (High-density: $0.07 \pm 0.01 \text{ mm.day}^{-1}$, $n = 125$; Low-density: $0.11 \pm 0.01 \text{ mm.day}^{-1}$, $n = 42$). Therefore, body size at the age of one year was only affected by origin (Density effect: $F_{1,9} = 3.96$, $P = 0.08$; Origin effect: $F_{2,61} = 15.88$, $P < 0.0001$, $n = 180$). Body size was lower in lizards from population 1 compared to the two other populations (Population 1: $36.23 \pm 1.03 \text{ mm}$, $n = 22$; Population 2: $39.10 \pm 0.96 \text{ mm}$, $n = 40$; Population 3: $40.41 \pm 0.87 \text{ mm}$, $n = 118$; Tukey's contrasts, $P < 0.01$), but not between low- and high-density patches (High-density: $36.9 \pm 1.1 \text{ mm}$, $n = 135$; Low-density: $40.3 \pm 1.3 \text{ mm}$, $n = 45$, Fig. 2).

From spring to summer 2000, density manipulation, kinship treatment, and origin did not influence growth, but sexual size dimorphism initiated (Table 3). Body growth was higher for females than for males (Females: $0.16 \pm 0.006 \text{ mm.day}^{-1}$, $n = 48$; Males: $0.14 \pm 0.006 \text{ mm.day}^{-1}$, $n = 56$). From August 2000 to June 2001, growth was not affected by sex, neither by origin or experimental treatments (Table 3). At the end of the experiment, body size was only influenced by sex (Density effect: $F_{1,7} = 2.00$, $P = 0.20$; Origin effect: $F_{2,24} = 0.95$, $P = 0.40$; Sex effect: $F_{1,24} = 14.36$, $P < 0.001$, $n = 68$, Fig. 2). Size reached similar values in high- and low-density patches (Low-density: $61.4 \pm 1.3 \text{ mm}$, $n = 18$; High-density: 59.1 ± 1.0 , $n = 50$) and females were longer than males (Females: $61.8 \pm 1.0 \text{ mm}$, $n = 24$; Males: $58.7 \pm 0.9 \text{ mm}$, $n = 44$).

Table 3. Effects of sex, origin, and density manipulation on growth in body size for juveniles. Analyses were conducted from introduction to August 1999, from August 1999 to April 2000, and from April 2000 to August 2000, and from August 2000 to June 2001. F tests are from mixed-effect models where patch and family are included as a random effects. Estimates are given in italic.

Predictors of body growth	First period	Second period	Third period	Fourth period
Initial body size	$F_{1,276} = 14.32$ ***	$F_{1,96} = 31.21$ ***	$F_{1,45} = 9.83$ ***	$F_{1,23} = 1.01$
<i>Slope</i>	-0.017 ± 0.005	-0.005 ± 0.0009	-0.003 ± 0.0009	-0.0004 ± 0.0004
Sex	$F_{1,276} = 2.92$ †	$F_{1,96} = 0.38$	$F_{1,45} = 9.53$ ***	$F_{1,23} = 1.99$
<i>Female</i>	0.015 ± 0.009	-0.002 ± 0.004	0.014 ± 0.004	0.004 ± 0.003
Origin	$F_{2,90} = 7.54$ ***	$F_{2,55} = 6.64$ **	$F_{2,45} = 2.22$	$F_{2,32} = 0.25$
<i>Population 1</i>	-0.058 ± 0.01	-0.024 ± 0.007	0.02 ± 0.01	0.001 ± 0.004
<i>Population 2</i>	-0.006 ± 0.01	-0.016 ± 0.006	0.0004 ± 0.006	-0.002 ± 0.004
Density treatment	$F_{1,7} = 1.71$	$F_{1,7} = 4.58$ †	$F_{1,6} = 0.02$	$F_{1,5} = 3.54$
<i>Low density</i>	0.116 ± 0.081	0.038 ± 0.022	0.006 ± 0.01	0.011 ± 0.008
Kinship treatment	$F_{1,7} = 0.07$	$F_{1,7} = 0.20$	$F_{1,6} = 1.71$	$F_{1,5} = 1.53$
<i>Absence</i>	0.05 ± 0.09	-0.005 ± 0.02	-0.006 ± 0.01	-0.003 ± 0.004
Density × Kinship	$F_{1,7} = 0.19$	$F_{1,7} = 0.02$	$F_{1,6} = 0.54$	$F_{1,5} = 0.35$
<i>Low density and Absence</i>	-0.06 ± 0.13	-0.004 ± 0.03	-0.01 ± 0.02	-0.005 ± 0.009

† $0.05 < P < 0.10$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

Yearlings 1999-2001. Changes in body size and body condition were analysed from introduction to August 1999, from August 1999 to April 2000, and from April 2000 to June 2001. Kinship treatment had no detectable effect on growth ($P > 0.25$). Body condition variation was not affected by density manipulation ($P > 0.07$). During the first month of the experiment, growth in body size was not affected by density, but was higher for females than for males (Females: 0.16 ± 0.01 mm.day⁻¹, $n = 53$; Males: 0.13 ± 0.01 mm.day⁻¹, $n = 69$, Table 4). Density manipulation influenced body growth from August 1999 to April 2000 (Table 4): body growth was lower in high-density patches (High-density: 0.018 ± 0.003 mm.day⁻¹, $n = 62$; Low-density: 0.033 ± 0.005 mm.day⁻¹, $n = 22$). From April 2000 to June 2001, the effect of density was no more significant (Table 4). Females had higher growth rates than males (Females: 0.05 ± 0.003 mm.day⁻¹, $n = 10$; Males: 0.03 ± 0.002 mm.day⁻¹, $n = 27$, Fig. 2). An analysis of body size at the end of the experiment indicated that initial differences between origins disappeared, that females reached a higher body size than males, and that the effect of density was marginal (Density effect: $F_{1,8} = 4.53$, $P = 0.06$; Sex effect: $F_{1,30} = 47.5$, $P < 0.001$; Origin effect: $F_{2,30} = 2.49$, $P = 0.10$, $n=43$). Therefore, a growth's catch up did not fully compensate the early growth impediment detected at high density (High-density: 60.4 ± 0.5 mm, $n = 33$; Low-density: 62.4 ± 0.8 mm, $n = 10$, Fig. 2).

Table 4. Effects of sex, origin, and density manipulation on growth in body size for yearlings from introduction to August 1999, from August 1999 to April 2000, and from April 2000 to June 2001. F tests are from mixed-effect linear models where patch is included as a random effect. Estimates are given in italic.

Predictors of body growth	First period	Second period	Third period
Initial body size	$F_{1,107} = 2.23$ <i>Slope: - 0.002 ± 0.001</i>	$F_{1,69} = 19.91$ *** <i>Slope: - 0.003 ± 0.0007</i>	$F_{1,23} = 40.4$ *** <i>Slope: - 0.003 ± 0.0005</i>
Sex	$F_{1,107} = 9.49$ ** <i>Female: 0.032 ± 0.01</i>	$F_{1,69} = 0.11$ <i>Female: 0.002 ± 0.005</i>	$F_{1,23} = 30.0$ *** <i>Female: 0.02 ± 0.003</i>
Origin	$F_{2,107} = 2.39$ † <i>Pop. 1: 0.015 ± 0.014</i> <i>Pop. 2: 0.035 ± 0.016</i>	$F_{2,69} = 1.85$ <i>Pop. 1: - 0.011 ± 0.006</i> <i>Pop. 2: - 0.009 ± 0.007</i>	$F_{2,23} = 0.50$ <i>Pop. 1: - 0.003 ± 0.004</i> <i>Pop. 2: 0.002 ± 0.004</i>
Density treatment	$F_{1,9} = 1.58$ <i>Low: 0.021 ± 0.017</i>	$F_{1,9} = 7.38$ * <i>Low: 0.016 ± 0.006</i>	$F_{1,8} = 2.44$ <i>Low: 0.006 ± 0.004</i>

† $0.05 < P < 0.10$, * $P < 0.05$, ** $P < 0.01$, P < 0.001 ***

Adults 1999-2001. Body size growth was only significant during the first year of the experiment, and growth was therefore analysed from introduction to April 2000. Kinship manipulation had no detectable effect on growth ($P > 0.37$). Furthermore, the density manipulation, sex, and origin did not affect growth (Table 5, Fig. 2). Body condition was analysed separately between males and females due to the burdening and release of mass associated with gravidity and parturition in females.

Males body condition was not affected by population density during the first study year (Table 5). Change in body mass was influenced by density in females (Table 5): body mass recovery after parturition doubled in low-density compared to high-density patches (High-density: 0.01 ± 0.001 g.day⁻¹, $n = 45$; Low-density: 0.004 ± 0.001 g.day⁻¹, $n = 8$). A similar trend occurred in 2000 (summer recovery, treatment level, Density effect: $F_{1,30} = 3.03$, $P = 0.09$, $n = 33$).

Table 5. Effects of sex, origin, and density manipulation on change in body size and body condition in adults during the first study year. F tests are from mixed-effect linear models where patch is included as a random effect. Estimates are given in italic.

Predictors of change in	Body size	Body condition	Body condition
		Males	Females
Initial value	$F_{1,67} = 17.5$ *** <i>Slope: - 0.002 ± 0.0004</i>	$F_{1,36} = 31.79$ *** <i>Slope: - 0.013 ± 0.002</i>	$F_{1,31} = 0.14$ <i>Slope: - 0.0004 ± 0.002</i>
Sex	$F_{1,67} = 0.78$ <i>Female: - 0.003 ± 0.004</i>	-	-
Origin	$F_{2,67} = 0.11$ <i>Pop. 1: 0.0 ± 0.004</i> <i>Pop. 2: 0.001 ± 0.003</i>	$F_{2,36} = 0.25$ <i>Pop. 1: 0.002 ± 0.002</i> <i>Pop. 2: 0.001 ± 0.002</i>	$F_{2,31} = 0.58$ <i>Pop. 1: 0.0005 ± 0.002</i> <i>Pop. 2: - 0.001 ± 0.001</i>
Density treatment	$F_{1,8} = 4.01$ † <i>Low: 0.007 ± 0.004</i>	$F_{1,8} = 1.43$ <i>Low: 0.002 ± 0.002</i>	$F_{1,7} = 12.01$ * <i>Low: 0.005 ± 0.002</i>

† $0.05 < P < 0.10$, * $P < 0.05$, ** $P < 0.01$, $P < 0.001$ ***

Juveniles 2000-2001. The number of offspring in this cohort was low ($n = 123$ individuals belonging to 50 families). Density manipulation did not affect growth from introduction to the first month, and from the first month to the next year (all $P > 0.26$).

Female reproduction

Kinship manipulation and origin had no effect on reproduction across all age classes during the two study years (all $P > 0.11$). In 2000, unusual mortality was observed in the laboratory during late gestation (survival = 0.69 ± 0.07 , $n = 87$), irrespective to treatments, age, body size and body condition at the start of the rearing (all $P > 0.15$). Mortality was associated with moulting problems, difficulties in breathing, and lost of appetite, and comes with external and internal fungal infections, suggesting a severe immunodepression. Female gravidity and clutch size were determined for all females in the laboratory by visual inspection or by dissection of dead animals. Brood characteristics (hatching success, offspring size, offspring condition, and clutch sex-ratio) were only analysed on gravid females which survived until parturition. Female maturation probability before the age of one year was affected by density manipulation ($\chi = 12.83$, $P < 0.001$, $n = 106$): females reached maturity before the age of one year more frequently in low-density than in high-density patches (odds Low-

density : odds High-density = 19.38). The probability that a female was gravid after the age of one year was not affected by density manipulation ($F_{1,8} = 0.55$, $P = 0.48$, $n = 81$). The effect of population density treatment on total clutch size differed among age classes (Density effect: $F_{1,9} = 1.70$, $P = 0.22$; Age effect: $F_{2,45} = 0.62$, $P = 0.54$; Age \times Density effect: $F_{2,45} = 6.34$, $P = 0.004$, $n = 60$): two-years old females produced smaller clutches in high-density patches (contrast between Low-density and High-density = 2.35 ± 0.61 eggs, $P < 0.001$), while no difference was observed in younger and older females ($P = 0.95$). Density had no other effects on hatching success, offspring size, condition, and clutch sex ratio (all $P > 0.20$).

In 2001, no females reached maturity before the age of one year, while most females were gravid after the age of one year (56 over 61 individuals). Density did not affect total clutch size, hatching success, offspring size, offspring condition or offspring sex at birth (all $P > 0.29$). Mother age influenced hatching success, offspring condition, and offspring sex at birth (all $P < 0.03$). Compared to two years old females, three years old females had higher hatching success (odds Three years : odds Two years = 2.61), heavier offspring (contrast = 0.02 ± 0.006), and produced more females in their clutches (odds being a daughter of a Three years old female : odds being a daughter of a Two years old female = 5.10).

Survival

Our modelling of individual life histories allowed us to estimate capture and survival probabilities independently from introduction to August 1999 (summer survival and capture), and from August 1999 to April 2000 (winter survival and spring capture). Model selection was conducted in two steps leading to a first series of models describing heterogeneity among patches within treatments and to a second series of models describing heterogeneity among treatments, sexes, and origins (Table 6). No heterogeneity among patches was detected on survival and capture probabilities for adults, and on survival for yearlings. In juveniles, capture and survival probabilities varied significantly among patches, and this variation differed between the censuses in the case of survival. Kinship and density treatments had no effect on capture probabilities in any age class. Capture probabilities were affected by age at all ages, and were lower during spring than during summer. Furthermore, adult males were captured more frequently than adult females irrespective of the season.

In adults, survival was affected by an interaction between sex and density treatment. Females survived better in high-density than in low-density patches (patch level comparison, $P = 0.05$, Table 6), while males tended to survive better in low-density patches (treatment level comparison, $P = 0.36$, Table 6). In addition, survival decreased from summer to winter. In yearlings, survival was similar in summer and winter, and was not affected by treatments (Table 6). In juveniles, density manipulation had no effect on summer or winter survival, but survival decreased strongly during the winter. In addition, the kinship manipulation influenced both summer and winter survival: survival was higher

when the mother was absent in the introduction patch than when the mother was present, even when heterogeneity among patches on survival and kinship effects on capture were accounted for (Table 6).

Table 6. Survival and capture probabilities in juvenile, yearling, and adult residents obtained by a Cormack-Jolly-Seber modelling of individual life histories from introduction to August 2000. A weak lack of fit was detected for adults, where an overdispersion correction factor was used (GOF test, $P = 0.03$, $c = 1.60$).

Age class	Selected model	Statistical tests	Estimates [CI]
Juveniles Survival	<i>Time</i>	$\chi = 38.08$ ***	<i>Summer survival</i>
	<i>Kinship treatment</i>	$F_{1,7} = 12.00$ **	Mother presence: 0.74 [0.68, 0.79], Absence: 0.91 [0.86, 0.93]
	<i>Density treatment</i>	$F_{1,7} = 1.19$	<i>Winter survival</i>
	<i>Patch(Density \times Kinship)</i>	$\chi = 15.8$ *	Mother presence: 0.44 [0.37, 0.51], Absence: 0.72 [0.65, 0.79]
Juveniles Capture	<i>Time</i>	$\chi = 7.59$ **	<i>Summer capture</i> : 0.91 [0.86, 0.94]
	<i>Kinship treatment</i>	$F_{1,7} = 0.31$	<i>Spring capture</i> : 0.78 [0.71, 0.84]
	<i>Density treatment</i>	$F_{1,7} = 0.56$	
	<i>Patch(Density \times Kinship)</i>	$\chi = 8.78$	
Yearlings Survival	<i>Time</i>	$\chi = 2.81$ †	<i>Summer survival</i> : 0.85 [0.78, 0.90] <i>Winter survival</i> : 0.79 [0.69, 0.86]
	<i>Time</i>	$\chi = 4.73$ *	<i>Summer capture</i> : 0.87
	<i>Density treatment</i>	$F_{1,9} = 1.57$	<i>Spring capture</i> : 0.82
	<i>Patch(density)</i>	$\chi = 22.58$ **	
Adults Survival	<i>Time</i>	$F_{1,16} = 44.8$ ***	<i>Summer survival</i>
	<i>Sex</i>	$F_{1,16} = 2.11$	Males, Low density 0.98 [0.67, 0.99]; High: 0.97 [0.55, 0.99]
	<i>Density treatment</i>	$F_{1,16} = 5.14$ *	Females, Low density: 0.95 [0.46, 0.99]; High: 0.99 [0.73, 0.99]
	<i>Sex \times Density treatment</i>	$F_{1,16} = 5.19$ *	<i>Winter survival</i> Males, Low density: 0.66 [0.68, 0.99]; High: 0.48 [0.30, 0.67] Females, Low density: 0.40 [0.18, 0.65]; High: 0.69 [0.53, 0.82]
Adults Capture	<i>Time</i>	$F_{1,16} = 12.9$ ***	<i>Summer capture</i>
	<i>Sex</i>	$F_{1,16} = 4.27$ *	Males: 0.99 [0.84, 0.99]; Females: 0.97 [0.72, 0.99] <i>Spring capture</i> Males: 0.89 [0.76, 0.96]; Females: 0.79 [0.65, 0.89]

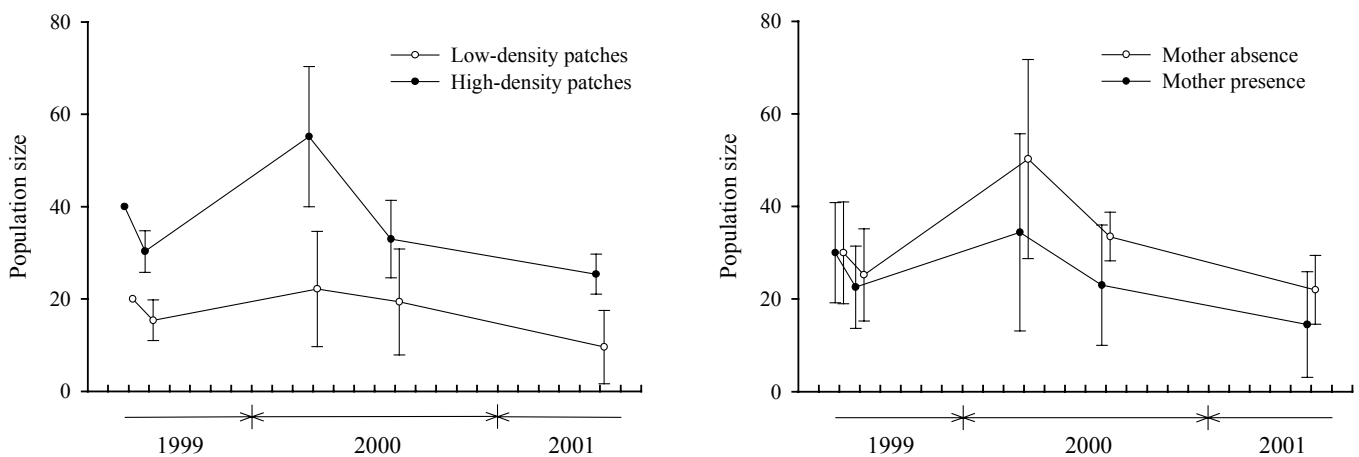
† $0.05 < P < 0.10$, * $P < 0.05$, ** $P < 0.01$, $P < 0.001$ ***

Population size

The number of yearling and adult individuals in a patch varied significantly during the time scale of the study (repeated measures ANOVA on log-transformed population size, unstructured covariance matrix, Time effect: $F_{4,7} = 8.19$, $P = 0.009$, $n = 10$ patches). Population size decreased from late spring 2000 to June 2001, as expected from the mortality of gravid females in the laboratory and

the low, associated reproductive recruitment (Fig. 3). Kinship manipulation had no effect on population demography (Kinship effect: $F_{1,7} = 3.58$, $P = 0.10$; Kinship \times Time effect: $F_{4,7} = 1.04$, $P = 0.45$). Density manipulation affected population demography (Density effect: $F_{1,7} = 16.72$, $P = 0.005$; Density \times Time effect: $F_{4,7} = 7.76$, $P = 0.01$), but this effect did not result from density-dependent regulation (Fig. 3). First, population size differences between high and low density treatments remained significant during all censuses (contrast within each census, all $P < 0.05$). Second, the significant effect of the density manipulation on population demography came from (i) a higher local recruitment during the first winter of the study in high-density patches (exponential growth rate in high-density patches: 0.67 ± 0.28 , low-density patches: 0.18 ± 0.28), and from (ii) a population decrease during late spring and summer of the second year in high-density patches (exponential growth rate in high-density patches: -0.59 ± 0.18 , low-density patches: -0.05 ± 0.18 , Fig. 3). Third, population growth rates up to the end of the experiment did not differ between low- and high-density patches (high-density patches: -0.49 ± 0.09 , low-density patches: -1.19 ± 0.48 , Wilcoxon two-sample test, $P = 0.29$).

Figure 3. Population demography. Data are mean population size of individuals older than one year old \pm SD. Left panel: density treatment. Right panel: kinship treatment.



DISCUSSION

We analysed the effects of mother presence and population density on the demography of common lizard populations in a patchy habitat. Our results are weakened by the fact that we lost some patches due to uncontrolled predation and by unusual mortality of gravid females after the first year of the experiment. This last result could reveal a severe cost of translocation in adult females, as documented in earlier studies on the same system (Boudjemadi 1999). Our analysis was restricted to

resident individuals, but the effects of treatment on dispersal have been reported elsewhere (Le Galliard et al. (2003b), see chapter 4 of the thesis).

Experimental design

Our design was chosen to investigate the effects of population density and mother presence on life-history traits and demography. We coupled a low-density with a high-density patch in each two-patch system to analyse the effect of density-dependent dispersal on local population regulation within a metapopulation (see also Aars et al., 1999). Then, we manipulated kinship at the metapopulation level since a two-patch system was not large enough to accommodate the four treatments. However, this design was not powerful because (i) kinship is manipulated at the metapopulation level, leading to only four replicates for this effect, and (ii) each patch affected by a perturbation in the experimental system (Hurlbert 1984), such as the predation observed during this study, causes the loss of one metapopulation replicate. Typically, our analysis should have been realised at the metapopulation level, with each metapopulation nested within the kinship treatment and blocking the density manipulation. However, due to predation, we decided to conduct our tests at the patch level and to ignore the non-independence of patches connected within the same metapopulation. As an alternative, we could have manipulated mother presence/absence within each patch, leading to eight metapopulation replicates with all combinations of kinship and density treatments. Moreover, the presence of both types of offspring in the same patch softens the possible social perturbation induced by the removal of many mothers in the same patch. Currently, an experiment is running on the same system to test this possibility. However, remark that a definite proof of the involvement of mother-offspring interactions can only be obtained by independent manipulations of single families within the same habitat (Léna et al. 1998).

Origin effects

Spatial variation in life history traits of lizards among upland populations was detected prior to introduction, as in other studies conducted at larger or similar spatial scales in the same species (Pilorge et al. 1983, Heulin 1985a, Bauwens et al. 1986, Sorci et al. 1996, Lorenzon et al. 2001). In population 3 (a large heath area), yearlings had larger body size and higher body condition, and adult females had larger body size and higher reproductive investment than in populations 1 and 2 (small peatbogs areas). Such contrasts could originate from genetic differences, long-term maternal effects, and/or environmental effects on growth and selection gradients. By releasing individuals from all age classes in similar environmental conditions within a lowland habitat (a common garden experiment), we disentangled whether these differences result from short-term environmental effects, or from long-term environmental, maternal or genetic effects. In yearlings and adults, growth, reproduction, and survival did not differ among origins during our study. In particular, a growth catch up was observed during the first study year, leading to body size convergence. This suggests that differences among

populations in adults and yearlings originated from short-term environmental effects, and were rapidly compensated for by phenotypic plasticity. However, patterns of natal growth in juveniles somehow paralleled the differences expected to result in the body size contrasts observed in natural populations. During their first year, offspring from population 2 and 3 grew more than offspring from population 1, and were larger at the age of one year. After the age of one year, growth was not influenced by origin, and a growth catch up was observed. This suggests that maternal or genetics effects influenced natal growth contrasts between these populations.

Density dependence in the common lizard

Our study found distinct density dependence effects on different demographic parameters after introduction into unfamiliar enclosures, a result paralleling on several points the density-dependent regulation observed in natural populations of the same species (Pillorge 1987, Massot et al. 1992, 1994). First, density manipulation had similar effects on growth and reproduction of adults and yearlings than in the non replicated experiment by Massot et al. (1992). The growth in size of adults was not affected by the doubling of the initial density of the population, while yearlings growth decreased at high density during the first year. However, no such effects were detected in juveniles, contrasting with the observations of density-dependent natal growth (Boudjemadi 1999) and of increased natal growth during colonization (Le Galliard et al. 2003a). Furthermore, at high density, a decrease in reserve recovery after parturition was observed in adult females during the two study years, the total clutch size of two years old females was depressed, and fewer females matured before the age of one year. In natural populations, density has been found to delay the age at first reproduction, to reduce total clutch size, and to increase hatchling failures (Massot et al. 1992). These results are concordant with most of our observations. Second, survivorship of juveniles and yearlings was not affected by the density manipulation, and adult females survived better at high density during the first study year. In their study, Massot et al. (1992) found that survival of adults and yearlings was density-independent, and that local recruitment was lower at high density, but they were unable to measure natal survival. Third, we have recently found that (i) emigration and immigration movements of yearlings and adults were not affected by density, that (ii) emigration movements decreased at low population density in juveniles, and that (iii) immigration movements of juveniles were not affected by density (Le Galliard et al. (2003b), see chapter 4). In continuous habitats, immigration from surrounding habitats has been found to be critically enhanced at low population density (Massot et al. 1992), suggesting that habitat saturation limits transience and settlement opportunities (Hestbeck 1982). Therefore, our results differ from the one of Massot et al. (1992) on two distinct points. First, we did not find reduced recruitment and growth in juveniles at high density, but observed a higher survival of adult females. Second, immigration was not affected by population density and emigration movements decreased at high density, suggesting that dispersal in our patchy habitat was not as effective to regulate population size as dispersal in a continuous habitat.

Effects of mother presence manipulation

Mother presence induced a change in survival patterns. A marked increase in residents natal survival was observed in patches where the mother was absent. This result runs counters to the mother-offspring facilitation process involved in territory establishment of resident offsprings in some cooperatively breeding or semi-social birds and mammals (Lambin and Yoccoz 1998, Lambin et al. 2001). For example, experiments and observations in several small rodents have shown that matrilineal kin clusters involving mothers and sisters can have positive effects on breeding success or nestling survival (e.g., Kawata 1987, Lambin and Krebs 1991b, Mappes et al. 1995, Pusenius et al. 1998). The negative effect of mother presence on resident offspring survival in the common lizard can not be explained by this higher tolerance among relatives (Hamilton 1964a, 1964b). A first hypothesis is that mother harassed or tried to expel their offspring in the context of our study. If this hypothesis would be true, then these ‘aggressive’ interactions between mother and offspring may underlie the relationship between natal dispersal and mother-offspring competition observed in several past studies on the common lizard (review in Clobert et al. 1994, Lambin et al. 2001). A second hypothesis would be that our experimental design revealed some maladaptive consequences of some (otherwise adaptative) mother-offspring interactions. In particular, if resident offspring use maternal olfactory or visual cues to select their habitat and avoid deleterious social interactions with their conspecifics (Léna and de Fraipont 1998, Léna et al. 2000), then the non familiarity of the mother with the introduction patch could have induced maladaptive behavioural choices of their offspring (Stamps 2001). Underlying this hypothesis is the idea that the disruption of the prior familiarity of the mother with the natal home range increases the value of the information obtained by juveniles from the private exploration of the habitat rather than from the information provided by the mother. Disentangling these two scenarios would require experiments where both the presence of the mother and the context (familiarity of the mother with the natal patch) are manipulated simultaneously.

Resilience in population demography

Contrary to the rapid density-dependent regulation observed in natural populations (Massot et al. 1992), our experiment did not detect any negative feedback between population density and population growth during two consecutive years. In turn, contrasts persisted between high- and low-density populations, with population size differences at the end of the study paralleling the initial levels. Our methodological problems could have contributed to this scenario. Unusual female mortality in the laboratory reduced the influence of density dependence through local reproduction. However, this effect would only have been detected after local recruitment, hence at the end of our study. Also, predation altered the coupling between high- and low- density patches, and therefore the impact of rescue effects through dispersal from high-density to low-density populations (Brown and Kodric-Brown 1977, Aars and Ims 2000). However, in three instances of predation affecting only one

population of a two-patch system at the start of the study, two cases occur in low-density patches, hence increasing the difference between our initial treatments (see Fig. 1). Furthermore, we found no evidence of short-term adjustment in population size. Natal emigration movements were less frequent at low-density and adults tended also to emigrate more from low-density patches (Le Galliard et al. (2003b), see chapter 4). This generated balanced dispersal between the two populations during the first study year (Doncaster et al. 1997), which preserved density contrasts more than purely random dispersal. Second, survival was most often unaffected by population density, and adult females survived better in high-density populations. Differences between the results of this study and the one of Massot et al. (1992) could be due to the spatial structure of the habitat (continuous versus fragmented in our case) and to the manipulation of population density (partial translocation versus complete translocation in our case). The fragmented structure of the experimental habitat could induce time-lags in density dependence through dispersal compared to a more continuous habitat, where vacancies can be rapidly occupied through local dispersal (e.g., Komdeur 1992). Also, translocation of animals from upland areas to an unfamiliar, lowland site could reduce survival and mask the critical determinants of population demography in natural habitats. Strictly, translocation experiments only test demographic characteristics of recently introduced populations.

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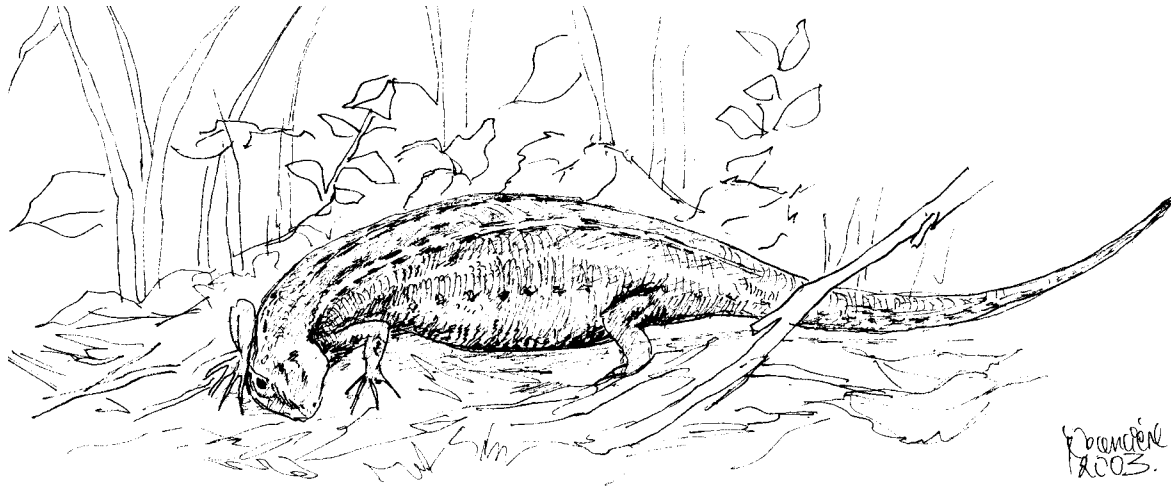
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ANNEXE 4 – LOCOMOTION ET THERMOREGULATION



CHRONOLOGIE DES COÛTS LOCOMOTEURS ET DES PREFERENCES THERMIQUES CHEZ UNE ESPECE VIVIPARE DE LEZARD

Jean-François Le Galliard, Marion Le Bris & Jean Clobert

RESUME

1. Une dégradation des performances locomotrices et un changement des préférences thermiques ont été observés chez certains lézards, mais la chronologie de ces modifications est relativement mal connue. Dans cette étude, la capacité d'endurance, la vitesse de sprint et la température corporelle de femelles gravides du lézard vivipare *Lacerta vivipara* ont été mesurées toutes les semaines avant et après la parturition.

2. Une variation temporelle significative des capacités d'endurance et de sprint a été mise en évidence. Une décroissance marquée des capacités locomotrices a eu lieu dans les deux dernières semaines de la gestation (approximativement, 35 % pour l'endurance et 25 % pour la vitesse de sprint). Une récupération a été observée quelques jours après la parturition pour l'endurance, et lentement pour la vitesse de sprint.

3. Un affaiblissement physique provoquée par la prise de masse a été détectée pour la capacité d'endurance, mais pas pour la vitesse de sprint. La récupération des capacités locomotrices a été indépendante de l'intensité de l'investissement dans la reproduction. Les variations de performances locomotrices non liées à la masse corporelle sont probablement expliquées par des conséquences physiologiques de la reproduction indépendantes de la charge physique.

4. Les femelles maintenues en conditions optimales ont sélectionné des températures corporelles faibles lors du dernier mois de la gestation ($29.8^{\circ}\text{C} \pm 0.12 \text{ SE}$) et une augmentation drastique a eu lieu dans les jours suivant la parturition ($33.4^{\circ}\text{C} \pm 0.13 \text{ SE}$).

5. Ces résultats appellent à une étude plus détaillée des mécanismes sous-tendant les liens compensatoires entre la reproduction, la locomotion et la thermorégulation chez les lézards.

Référence : Le Galliard, J.-F., Le Bris, M. et J. Clobert. 2003. Timing of locomotor impairment and shift in thermal preferences during gravidity in a viviparous lizard. Soumis avec révisions à *Functional Ecology*.

Mots-clés: locomotion, thermorégulation, charge physique, coûts de la reproduction.

TIMING OF LOCOMOTOR IMPAIRMENT AND SHIFT IN THERMAL PREFERENCES DURING GRAVIDITY IN A VIVIPAROUS LIZARD

Jean-François Le Galliard, Marion Le Bris & Jean Clobert

SUMMARY

1. Locomotor impairment and shift in thermal preferences during gestation have been documented in some lizards, but few studies have investigated their timing. Here, endurance capacity, sprint speed and selected body temperature of gravid females of the viviparous lizard *Lacerta vivipara* were measured weekly before and after parturition.

2. Significant temporal variation of endurance and sprint speed was detected. A marked decrease in locomotor abilities occurred two weeks before parturition (c.a., 35 % for endurance and 25 % for sprint speed). A rapid recovery was observed a few days after parturition for endurance, while sprint speed recovered more slowly.

3. A physical impairment due to body mass was detected for endurance capacity, but not for sprint speed. The recovery of locomotor abilities after parturition was independent of the intensity of reproductive investment. Mass independent variation in locomotor performances might be explained by physiological consequences of reproduction independent from the physical burden.

4. Females basking under laboratory conditions selected low body temperatures during the final month of gestation ($29.8^{\circ}\text{C} \pm 0.12 \text{ SE}$) and a drastic increase occurred in the few days following parturition ($33.4^{\circ}\text{C} \pm 0.13 \text{ SE}$).

5. These results call for a more detailed investigation of the mechanisms underlying trade-offs between reproduction, locomotion and thermoregulation in lizards.

Reference : [Le Galliard, J.-F., Le Bris, M. and J. Clobert. 2003. Timing of locomotor impairment and shift in thermal preferences during gravidity in a viviparous lizard. Revised version submitted to Functional Ecology.](#)

Key-words: locomotion, thermoregulation, reproductive burden, costs of reproduction.

INTRODUCTION

A reduction in the reproductive value associated with current reproduction has been observed in many species and has been called costs of reproduction (Reznick, 1985). In squamates, reproductive costs in females might result from a reduction in sprint speed, jumping distance or endurance capacity (among other locomotor abilities) associated with gravidity (Shine, 1980). The role of locomotor performances has been emphasised because locomotion can act as an intermediate between the physiology, morphology and behaviour of an individual and the components of its lifetime reproductive success (Arnold, 1983; Bennett & Huey, 1990; Garland & Losos, 1994; Irschick & Garland, 2001). Locomotor performances depend on metabolic capacities, musculature strength and body shape of individuals (e.g., Bauwens et al., 1995; Garland, 1993). Locomotor performances set physiological limits on ecologically relevant tasks, such as foraging, predator avoidance or mate searching abilities (Bennett & Huey, 1990), although the empirical evidences of this link are still scant (Garland & Losos, 1994; Irschick & Garland, 2001). Therefore, a reduction in locomotor performances could impact the future reproductive value of gravid females (e.g., Miles et al., 2000).

Reproductive trade-offs involve several physiological components, such as hormones with pleiotropic effects, resource allocations or the physical mass burdening (Schwarzkopf, 1994; Shine, 1980; Sinervo, 1999). For example, both physical and physiological modifications associated with gestation can decrease locomotor performances. Increased body mass raises the energetic costs of transport, reduces body manoeuvrability and diminishes ventilation abilities in many lizards (Miles et al., 2000; Schwarzkopf, 1994). These effects are likely to result in a ‘physical burden’ on locomotor capacities during gestation (Shine, 1980). Physiological modifications associated with reproduction, such as changes in steroid hormones profiles, can also influence locomotor performances on the short term, for example through direct effects on metabolic pathways, and on the long term, for example through a muscle attrition process (review in Olsson et al., 2000). These effects are likely to result in a ‘physiological burden’ on locomotor capacities during and after gestation.

Locomotor costs of reproduction can also be influenced by the thermoregulation behaviour of gravid females. In most lizards, locomotor performances reach maximum values over a species-specific optimal thermal breadth (Huey & Kingsolver, 1989). Typically, lizards basking freely achieve body temperatures within this range, provided thermoregulation is not constrained by the environment (e.g., van Damme et al., 1987). However, body temperature is also strongly linked with embryonic development, implying possible conflicts between multiple thermal optima during gravidity (Huey & Kingsolver, 1989). It has been found that female lizards usually exhibit different body temperatures during pregnancy through behavioural preferences or through constraints on basking activities (e.g., Brana, 1993; Mathies & Andrews, 1997). Such shifts in thermoregulation could affect locomotor

abilities in the wild, reducing or enhancing the locomotor costs of reproduction depending on whether body temperature increases or decreases during gestation.

Although some studies have identified changes in locomotion and thermoregulation associated with reproduction in reptiles, the timing and proximate determinants of these variations have been more rarely examined. Comparisons between gravid and post-parturient females have indicated that performances are smaller before than after parturition (review in Schwarzkopf, 1994). However, such changes may have less ecological consequences if they occur only during a short time period. To overcome this problem, we collected weekly repeated measurements of locomotor performances and thermal preferences on gravid females of the common lizard *Lacerta vivipara* (Jacquin), a viviparous ground-dwelling species. We addressed three problems successively. First, we analysed temporal changes in sprint speed and endurance capacity from one month before parturition to two weeks after parturition, a time scale much larger than previous studies. This allowed us to observe both the impairment of locomotor capacities during gestation, and the recovery process after parturition. Second, we studied the effects on locomotor changes of variations in body mass during gestation and parturition. If changes in locomotor performances during reproduction are driven by a 'physical burden', most temporal variations in locomotion could be explained by body mass changes (Olsson et al., 2000). On the contrary, a 'physiological burden' on locomotion during reproduction would imply that locomotor performances varied independently from changes in body mass. Third, we also observed shifts in thermal preferences under laboratory conditions, therefore excluding most environmental constraints on thermoregulation (Huey, 1974).

MATERIALS AND METHODS

Collection and maintenance of females

A sample of 19 gravid females was collected in the Cévennes (South France) between 25 and 28 of May 2001 in one local population (44°25'N, 3°46'E). Individuals were measured for length and body mass to the nearest mm and μg respectively. Animals were transferred to the Ecological Research Station of Foljuif (Seine et Marne) on the 29 of May. We then maintained females under standard conditions in individual terraria ($25 \times 15 \times 15 \text{ cm}^3$). Terraria were heated on one side with an incandescent bulb (25W) from 09.00 to 12.00 hours and from 14.00 to 17.00 hours local time providing a gradient from room temperature (19-24°C night-day) to 33-35°C. This gradient encompasses the thermal breadth of the common lizard (van Damme et al., 1986). Animals were fed every fourth day with a moth larvae (*Pyralis sp.*) or with a large cricket (*Acheta domestica*). After parturition, postpartum females were isolated from offsprings, measured for body mass, fed once with one moth larvae, and then maintained under the standard conditions. Relative clutch mass (ratio of clutch mass to post-parturition body mass) and clutch size were measured. Photoperiod was naturally

imposed and one fluorescent UV-light bulb was added each four days (Iguana Light 5.0 UV-B, ZooMed, 40W).

Measurement of locomotor performances

Locomotor performances (endurance, sprint speed) and selected body temperature were characterised along seven 8 days intervals from the 18 June to the 8 August. Data were collected in the following daily order: endurance (3 days after feeding), thermoregulation (with food provided *ad libitum*) and sprint speed. Endurance and sprint speed were measured by the same person. All measurements were completed on lizards heated during 30 min at 32°C ($\pm 1^\circ\text{C}$).

Endurance was measured by running each lizard on an horizontal, circular treadmill covered with cork to ensure traction (external diameter 61 cm, internal diameter 41 cm). The treadmill was maintained between 30-31°C with two heat lamps (120W). The lizard was stimulated to run at a constant speed (c.a. 0.66 km.h⁻¹ in both trials), and motivated after each stop with soft brush taps behind the tail. The running was stimulated until exhaustion of the animal, as estimated from the loss of a righting response after strong stimulations on the tail. Endurance was measured during the morning (9.00 to 12.00 hours local time) in a random order, and calculated as the time elapsed during the trial (to the closest s). The number of stimulations given per unit distance was recorded to index the motivation of each lizard, as advised by some authors (Bennett & Huey, 1990; Sorci et al., 1995; Tsuji et al., 1989). Body mass was measured at completion of running. These measurements of endurance capacity have been found to be repeatable (repeated measurements on yearlings in 2000, $r = 0.87$, $F_{44,45} = 10.42$, $P < 0.001$, $n = 45$ individuals, $N = 90$ observations; Lessels & Boags, 1987).

A sprint speed value was obtained on a 1-m length linear racetrack covered with cork from four repeated trials spaced by 30 min. This length was preferred to shorter intervals advocated by (Bennett & Huey, 1990), because we wanted to measure sprint speed along a realistic flight distance (see Bauwens & Thoen, 1981; Lecomte et al., 1993). The lizard was run on 30 cm to avoid the initial acceleration phase (Huey & Hertz, 1984), and then chased along the racetrack with a soft brush. Taps were given with the brush when the lizard stopped, and the total number of taps was recorded. The maximal sprint speed and the corresponding number of stimulations were retained for analysis. Body mass was measured at the end of the running. The four sprint speed measurements obtained during the seven measurements all indicated significant repeatability ($r > 0.23$, $P < 0.006$).

Measurement of selected body temperature

Selected body temperature was measured on pairs of females housed in large terraria (130 × 47 × 35 cm³) heated on one side with an incandescent bulb (40W) from 09.00 to 17.00 hours local time. The thermal gradient ranged from room temperature (19-20°C) at the end of the terrarium to 40°C under the bulb. We thought that pooling two individuals did not bias our measurements because Patterson & Davies (1978) observed that common lizards tested alone or in groups had similar body

temperatures. Furthermore, we found no resemblance in daily averages of body temperatures among individuals within terraria ($F_{9,44} = 0.45$, $P = 0.90$). We reduced costs of thermoregulation by providing food and water *ad libitum*, and by arranging under the heat lamp a substrate used for basking and hiding (15 cm length, 5 cm large). Lizards were placed in the terraria the evening before measurements to permit acclimation, and observations were obtained from repeated sampling every 45 min from 9.30 to 12.30, and from 14.15 to 16.30 hours local time. Cloacal temperature was measured with a K-thermocouple thermometer (Hanna Instruments, K-thermocouple 1.5 mm, $\pm 0.2^\circ\text{C}$ accuracy). The repeatability of this protocol between two successive days has been established on adults ($r = 0.66$, $P = 0.002$, $n = 20$, $N = 40$ observations).

Statistical analyses

All analyses were performed with the SAS statistical software, and repeated measurements were analysed with covariance models using PROC MIXED (Littell et al., 1996). We used Shapiro-Wilk tests of the normality of residuals and Bartlett tests of variance homogeneity. Endurance data were log-transformed to meet these assumptions. A covariance model was selected from the suite provided by the statistical procedure using Aikake Criterion Index (Littell et al., 1996). To test differences between pairs of repeated observations, we used adjusted Tukey's multiple comparison for differences of least-square means.

The effect of time varying covariates on locomotor performances was not analysed with a standard regression, because this method assumes independence among observations from the same individual (Diggle et al., 1994). Rather, we conducted a regression accounting for the repeated-measure design using a covariance model in PROC MIXED. To disentangle the between- and within-subject effects of body mass and motivation on locomotor changes, we calculated for each covariate the mean per individual over the trials (between-subject component) and the difference from the mean for each trial (within-subject component, Neuhaus & Kalbfleisch, 1998). We then used locomotor performance as a response variable in a regression including the mean and deviation of all predictor variables as factors.

RESULTS

Timing of the reproductive burden

Body length did not change during measurements, and body mass was used to index reproductive burden. Body mass varied significantly during gestation ($F_{6,108} = 26.98$, $P < 0.001$, $N = 133$ observations, Fig. 1A). Body mass increased from the start of the measurements (adjusted Tukey's multiple comparison, all $P < 0.001$), and reached a plateau the last week before parturition (sessions 3 and 4 in Fig. 1A). Mass decreased strongly at parturition, resulting in the loss of 53 % (± 3

SE) extra-mass relative to post-parturition levels (average date: 21 July \pm 3 days SD; clutch size: 5.7 ± 0.4 SE).

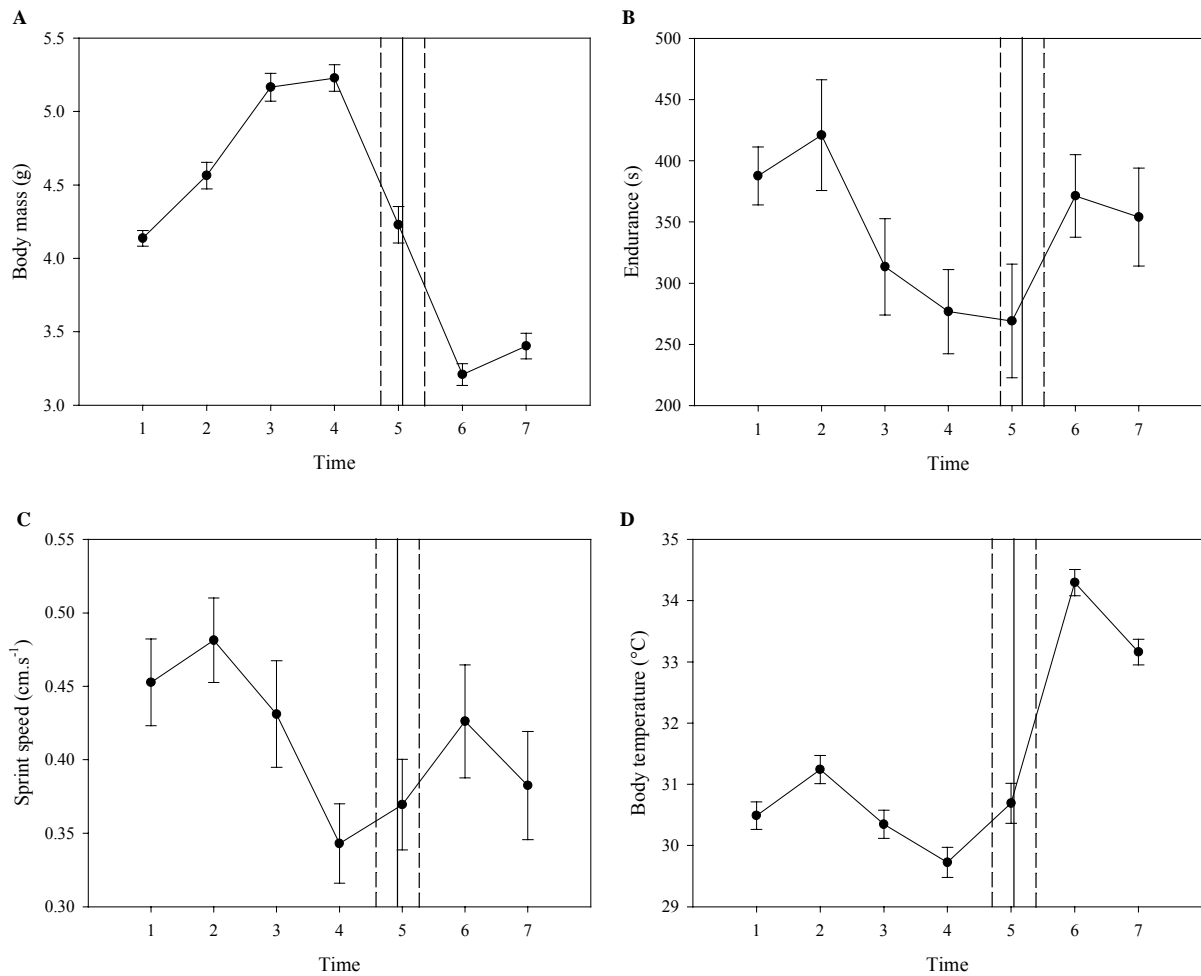


Figure 1. Timing of reproductive burden, locomotor impairment and shift in thermal preferences in the common lizard. A. Individual body mass (g, \pm SE) of gravid females measured. B, C and D. Females endurance capacity (time (s) spent on the racetrack, \pm SE), sprint speed ($\text{cm}\cdot\text{s}^{-1}$, \pm SE) and average daily temperature ($^{\circ}\text{C}$, \pm SE). A eight day time lag separated each trial. The average parturition date (\pm SD) is indicated as a line in each frame.

Timing of the locomotor impairment

A significant temporal variation for both endurance and sprint speed was detected (log-transformed endurance, $F_{6,108} = 5.38$, $P < 0.001$, $N = 133$ observations; sprint speed, $F_{6,108} = 5.65$, $P < 0.001$, Fig. 1B, 1C). Endurance capacity decreased from the first two measurements to the fifth measurement, and then quickly returned close to its initial state (Tukey's tests, $P < 0.05$ between sessions 1-2 and 5 and between session 5 and sessions 6-7, Fig. 1B). Endurance capacity reached a minimum level during the last week of gestation ($250 \text{ s} \pm 46.4 \text{ SE}$). This reduction equalled approximately 35 % of the values observed at the start of gestation and following parturition (initial

value: $387 \text{ s} \pm 23.6 \text{ SE}$, post-parturition value: $371 \text{ s} \pm 33.7 \text{ SE}$). Sprint speed decreased from the first three measurements to the fourth measurement (Tukey's test, $P < 0.05$ between session 1-3 and 4, between session 2 and sessions 4-5, Fig. 1C). Sprint speed reached minimum values during the last week of gestation ($0.34 \text{ m.s}^{-1} \pm 0.03 \text{ SE}$), a relative reduction corresponding to 25 % of the initial value ($0.45 \text{ m.s}^{-1} \pm 0.03 \text{ SE}$).

We found a significant repeatability of individual differences in locomotor performances over the seven trials (log-transformed endurance, intraclass correlation coefficient: $r = 0.30$, $F_{18,114} = 3.98$, $P < 0.0001$; sprint speed, $r = 0.55$, $F_{18,114} = 9.69$, $P < 0.0001$). Therefore, individual differences in locomotor performances were consistent despite variability within each individual during gestation. This would not have been expected if the directions and intensities of locomotor changes were different among individuals.

Table 1. Effects of body mass, motivation (stops per unit distance) and time on repeated measures of locomotor performances during impairment (five first measurements). Slope (\pm SE) terms are given in italics. Similar results were obtained when body size was controlled for in the analysis.

	Endurance	Sprint speed
Between-subject effects		
Body mass	$F_{1,16}=3.95 \dagger (-0.09 \pm 0.04)$	$F_{1,16}=0.44 (-0.01 \pm 0.02)$
Motivation	$F_{1,16}=6.68 * (-0.52 \pm 0.20)$	$F_{1,16}=3.12 (-0.14 \pm 0.08)$
Within-subject effects		
Body mass	$F_{1,70}=11.6 *** (-0.31 \pm 0.09)$	$F_{1,70}=0.83 (-0.01 \pm 0.02)$
Motivation	$F_{1,70}=9.31 *** (-0.33 \pm 0.11)$	$F_{1,70}=4.55 * (-0.03 \pm 0.01)$
Time	$F_{4,70}=3.08 *$	$F_{4,70}=5.59 ***$

$\dagger 0.05 < P < 0.10$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

Proximate determinants of locomotor impairment

The motivation to run of a lizard (number of stops per unit distance) varied significantly among trials for endurance ($F_{6,108} = 2.54$, $P = 0.02$), but not for sprint speed ($F_{6,108} = 1.62$, $P = 0.15$). In the case of endurance, motivation was lower during late gestation compared to other trials (sessions 1-3: $0.46 \text{ stops.round}^{-1} \pm 0.04 \text{ SE}$, session 4: $0.65 \text{ stops.round}^{-1} \pm 0.09 \text{ SE}$, session 5: $0.83 \text{ stops.round}^{-1} \pm 0.15 \text{ SE}$, sessions 6-7: $0.49 \text{ stops.round}^{-1} \pm 0.05 \text{ SE}$).

We estimated the proximate determinants of locomotor impairment using the five first trials (see Table 1). Regression of endurance with time, body mass and motivation showed that both body mass and motivation contributed to the temporal variation. Endurance was negatively correlated with body mass, indicating that an increase in body mass was associated with a decrease in endurance capacity. Also, the number of time the lizard stops per unit distance was negatively correlated with endurance capacity. The residual endurance obtained from the joint regression of endurance on body mass and

motivation was still varying between trials: residual endurance decreased progressively from the first to the fifth measurement, although only the comparison between session 2 and 5 was significant (Tukey's test, $P = 0.04$).

The analysis of sprint speed was dissimilar to endurance capacity on two points (Table 1). First, body mass had no significant effect on sprint speed. However, as for endurance data, motivation correlated with sprint speed, and the correlation between sprint speed and the number of stops was negative. Second, most temporal variation of sprint speed remained unexplained by motivational changes or mass increase. Residual sprint speed from the model incorporating motivation and body mass decreased after the second trial and reached a minimum during the fourth trial (Tukey's tests between session 2 and sessions 3-4, $P < 0.02$). Therefore, locomotor impairment for sprint speed was concomitant with, but apparently not driven by the mass burden.

Locomotor recovery

An analysis of locomotor recovery was conducted using the closest pre-parturition and post-parturition measurements. We found an increase of endurance and sprint speed after parturition, although it was only marginally significant for sprint speed (endurance, $F_{1,18} = 16.69$, $P = 0.0007$; sprint speed, $F_{1,18} = 4.30$, $P = 0.053$). Endurance increased from $196.7 \text{ s} \pm 21.4 \text{ SE}$ before parturition to $365.7 \text{ s} \pm 42.6 \text{ SE}$, a proportional 46 % recovery. Sprint speed increased from $0.35 \text{ m}\cdot\text{s}^{-1} \pm 0.03 \text{ SE}$ before parturition to $0.39 \text{ m}\cdot\text{s}^{-1} \pm 0.03 \text{ SE}$, only a 10 % proportional recovery. Motivation to run was not significantly different before and after parturition neither for endurance ($F_{1,18} = 0.49$, $P = 0.49$) nor for sprint speed ($F_{1,18} = 1.66$, $P = 0.21$).

If the locomotor recovery is due to the physical relaxation associated with parturition, we should find a correlation between locomotor changes and mass loss. Differences between locomotor performances after and before parturition were therefore regressed against the individual mass loss. There was no correlation between the change in endurance and sprint speed on one side and the change in body mass during parturition on the other side (endurance: $r = -0.13$, $F_{1,17} = 0.30$, $P = 0.59$; sprint speed: $r = 0.06$, $P = 0.81$). Relative clutch mass (RCM) and total clutch size were also not correlated with endurance recovery (endurance, RCM: $r = -0.31$, $P = 0.20$; clutch size: $r = 0.11$, $P = 0.66$), or sprint speed recovery (RCM: $r = -0.22$, $P = 0.36$; clutch size: $r = -0.16$, $P = 0.52$).

Selected body temperature

Body temperature was affected by the hour of the day (ANOVA, $F_{8,1116} = 25.02$, $P < 0.0001$, lizard identity as a random effect, $n = 19$ individuals, $N = 1197$ observations). Both gravid and post-parturient females had lower body temperatures at the start of the day (Fig. 2A). Because we were interested in body temperatures of active lizards, we excluded data from the first observation, which could be confounded with emergence time. We then used the daily average body temperature to measure the selected body temperature. A repeated measurement analysis on this variable detected

highly significant temporal variation ($F_{6,108} = 43.31, P < 0.0001$). The temporal change followed a two step pattern (Fig. 1D): gravid females selected lower temperatures before parturition (average: $30.5^{\circ}\text{C} \pm 0.15$ SE for sessions 1-4) than after parturition (average: $33.7^{\circ}\text{C} \pm 0.13$ SE for sessions 6-7; Tukey’s contrasts between first and second period, all $P < 0.001$).

Table 2. Thermal preferences before (sessions 3-4) and after parturition (sessions 6-7) following on the conventions of Bauwens et al. (1995). The preferred body temperature (PBT) was estimated as the median of the thermal distribution. The temperature breadth was estimated as the central 80 % of body temperature observations (TB). Minimum and maximum body temperatures observed are also indicated. $N=342$ observations.

	Average temperature ($^{\circ}\text{C} \pm \text{SE}$)	PBT ($^{\circ}\text{C}$)	TB ($^{\circ}\text{C}$)	T_{\min} ($^{\circ}\text{C}$)	T_{\max} ($^{\circ}\text{C}$)
Before parturition	29.8 ± 0.12	29.5	5.3 (27.0, 32.3)	21.6	34.8
After parturition	33.4 ± 0.13	34.1	4.8 (30.7, 35.5)	22.5	38.4

The daily variance in body temperature, a measure of the stability of thermoregulation, was not different among trials (Bartlett’s test, $\chi^2 = 6.47, \text{df} = 6, P = 0.37$). This homogeneity of variance was explained by the fact that both maximum and minimum daily temperatures shifted during pregnancy (maximum, $F_{6,108} = 25.22, P < 0.0001$; minimum, $F_{6,108} = 19.44, P < 0.0001$). The minimum and maximum daily temperatures increased following parturition (pre-parturition minimum: $27.9^{\circ}\text{C} \pm 0.28$ SE, post-parturition: $31.8^{\circ}\text{C} \pm 0.34$ SE; maximum: $32^{\circ}\text{C} \pm 0.19$, and $35.4^{\circ}\text{C} \pm 0.15$ SE respectively). To summarise, gravidity was associated with a downward shift in thermal preferences affecting the whole thermal distribution, and a drastic upward shift occurred after parturition (Fig. 2B, Table 2).

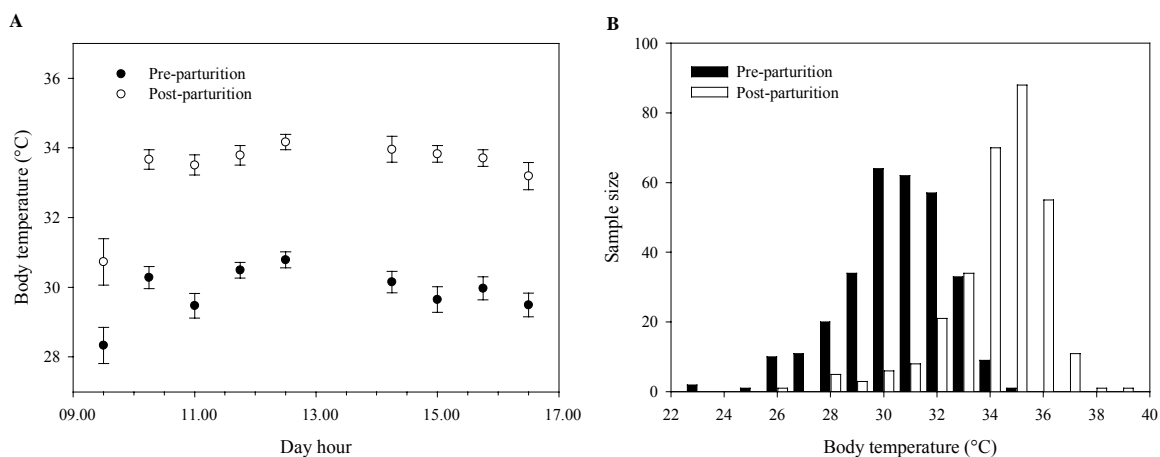


Figure 2. Thermoregulation before and after parturition in the common lizard. A. Mean selected body temperature ($^{\circ}\text{C}, \pm \text{SE}$) of females before (sessions 3-4) and after parturition (sessions 6-7) during the day ($N=38$ observations per day hour). B. Distribution probability of body temperatures before and after parturition after excluding the first daily measurement.

DISCUSSION

We observed a significant reduction in locomotor performances during mass burdening. Relative to post-parturition values, the reduction was on the same order of magnitude than for sprint speed (c.a., 10-40%) and endurance data (c.a., 40-60%) of other lizards (review in Schwarzkopf, 1994). Also, as in most studies (Bauwens & Thoen, 1981; Cooper, 1990; Garland, 1985; Qualls & Shine, 1997; Schwarzkopf & Shine, 1992; Shine, 1980; Sinervo & Licht, 1991), parturition was associated with an increase in performance abilities. However, sprint speed performances recovered more slowly. Concomitant with these locomotor changes, we observed a shift in selected body temperatures: females selected lower average body temperature during gestation than after parturition.

Significance of locomotor changes

Temporal variations in locomotor performances during gestation could originate from (1) gestation effects, (2) seasonal variations in locomotor performances independently of gestation, (3) acclimation to laboratory conditions, or (4) training and fatigue effects (Garland et al., 1987). Training and acclimation effects on locomotion have little supports in lizards (Garland et al., 1987; Gleeson, 1979; Snell et al., 1988). Also, it is unlikely that our experimental trials have been deleterious, because measurements were obtained at sufficiently spaced intervals, and we observed a significant increase in performances at some places. The second alternative is more difficult to reject because locomotor performance could vary independently from reproductive burden. However, the matching between mass burdening, timing of parturition and temporal variations of locomotor abilities has very little chance to be accidental. A more rigorous proof could be obtained by comparing gravid females with non gravid females from the same populations, or by manipulating reproductive effort of females.

Locomotor impairment and recovery

Our results show that gravid females suffered from a reduction in locomotor performances during late gestation, recovered quickly their endurance capacities after parturition, but recovered more slowly their sprint speed abilities. There was a significant individual effect on locomotor performances, suggesting parallelism in locomotor changes among individuals. To our knowledge, similar investigations on the timing of locomotor costs of reproduction in squamates have **only** been incidental. Indeed, most studies have compared pre- and post-parturition locomotion to measure recovery (defined as the increase in locomotor performances during parturition), while the impairment phase (defined as the decrease in locomotor performances during gravidity) has been generally disregarded. Seigel et al. (1987) found a decreasing pattern of locomotor performances during gravidity in one snake species, with a minimum for endurance during late gestation and for sprint speed during mid-gestation. On the contrary, Olsson et al. (2000) observed a reduction in sprint speed performance of female skinks only after parturition. In one oviparous lizard, endurance capacity

decreased continuously during gestation, as estimated from covariation with the size of the follicle (Miles et al., 2000). Also, Sinervo et al. (1991) observed that sprint speed increased significantly with time after oviposition, suggesting long-lasting recovery of sprint speed ability. Such variations of locomotor performances before and after parturition may occur in many species, and may be one reason for inconsistencies across studies in the ability to detect locomotor costs of reproduction (review in Schwarzkopf, 1994). For example, sprint speed could decrease during gestation and recover extremely slowly after parturition, if investment in reproduction reduces condition and musculature (Sinervo et al., 1991). In this scenario, the recovery of locomotor performances observed at parturition would be low and we may conclude that the costs of reproduction are small, while the situation corresponds to the case of a long-lasting locomotor impairment.

Proximate determinants of locomotor changes

Studies on impairment and recovery are likely to yield similar results if change in locomotor ability is explained only by the physical mass burdening of gravid females. In our study, we were able to investigate the effects of body mass, motivation and independent time-varying factors on locomotion. First, we observed a decrease in motivation during gestation, and found a negative correlation between motivation and locomotor performances. Such an effect illustrates the covariation between locomotor capacities and behavioural factors (Garland & Losos, 1994), and shows that behavioural shifts mediated by reproduction contribute to the locomotor costs of reproduction (Schwarzkopf & Shine, 1992). Second, locomotor recovery was independent of reproductive effort, but body mass affected endurance capacity during impairment. This suggests that the endurance impairment could be driven by the physical burden of reproduction. Higher body mass can increase the energetic costs of transport and decrease body manoeuvrability or ventilation capacity, all of which are important for sustained aerobic efforts during endurance trials (Garland & Losos, 1994). The fact that sprint speed, an anaerobic performance, does not decrease for similar reasons is not completely surprising. Indeed, comparative studies within and among species have found that sprint speed relates mostly to muscular structure and body shape, while endurance capacity depends upon body mass and aerobic metabolism (Bennett & Huey, 1990). Finally, time-varying factors independent from body mass or motivation affected sprint speed and endurance, especially during recovery. This suggests some important physiological effects of gestation not associated directly to the physical burden, such as modifications due to hormones or musculature shape (e.g., Dauphin-Villemant et al., 1990; Olsson et al., 2000). These patterns call for a more detailed investigation of the physiological mechanisms underlying trade-offs between reproduction and locomotion.

Selected body temperature

Females selected lower average body temperature during gestation than after parturition, and body temperatures after parturition were similar to values reported in other populations (Bauwens et

al., 1995; Patterson & Davies, 1978; van Damme et al., 1986, 1987, 1990). Similar modifications associated with reproduction have been observed in other lizards (Beuchat, 1986; Daut & Andrews, 1993; Shine, 1980), with body temperature being higher during gestation in some cases (Brana, 1993; Stewart, 1984).

The lower body temperature during gestation was achieved by a downward shift in the thermal distribution rather than by a change in extreme thermal choices (Beuchat, 1986; Stewart, 1984). Field data on this species also indicated a decrease in body temperature during gravidity (Heulin, 1987; van Damme et al., 1987). Our results show that this modification partly results from an active selection. The stringent association between thermal preferences and the timing of parturition also suggests that both are linked (Patterson & Davies, 1978; van Damme et al., 1987), and that thermal requirements are independent from the physical burden. This contradicts the hypotheses that body temperature is lower during gestation because of a reduction in warming speed due to mass burdening (Claussen & Art, 1981), or because of an hypoxia due to impairment of ventilation ability (Beuchat, 1986). In fact, this pattern might be explained by endocrinological modifications. For example, progesterone levels are affected by gestation and change the selected body temperature (Garrick, 1974). Also, abrupt modifications in corticosterone profiles at parturition could induce the rapid thermal shift observed in our study (Belluire et al. submitted).

A shift in selected temperatures during gravidity can be adaptative if thermoregulation affects mothers and offspring fitness differently. Body temperatures higher than 31-32°C optimise energy acquisition and fat storage (van Damme et al., 1991), ability to escape predators (van Damme et al., 1990), and speed of gestation (Mathies & Andrews, 1997). Therefore, gravid females should select body temperatures similar to post-parturient females. However, in lizards, thermal environment can also modify embryonic success and life-history traits of neonates (e.g., Anguilletta et al., 2000; Mathies & Andrews, 1997). In cell cultures of the common lizard, embryos developed optimally around 27°C *in vitro*, which is lower than the preferred adults body temperature during summer (Maderson & Bellairs, 1962). Therefore, the body temperature of mothers during embryological development (c.a., 30°C) was intermediate between *in vitro* and maternal optima. This might indicate that maternal behaviour helps to resolve a parent-offspring conflict on thermoregulation.

Thermoregulation and locomotion

According to our thermal measurements, gravid females should spend less time basking during the day, should be less active during warmer periods and should be more cryptic. These behavioural modifications associated with gestation have indeed been observed in the common lizard (Bauwens & Thoen, 1981; Heulin, 1984; Lecomte et al., 1993). Usually, however, such changes from flight to cryptic strategies have been attributed to predation (Bauwens & Thoen, 1981; Brodie III, 1989; Cooper, 1990; Schwarzkopf & Shine, 1992). Our data indicate that thermal requirements might be another reason, although the distinction between thermal and anti-predation strategies warrants further

studies. The two strategies are complementary here because a cryptic behaviour decreases both visibility toward predators (Bauwens & Thoen, 1981) and basking (Lecomte et al., 1993).

Locomotor costs of reproduction will depend on performances realised under natural conditions rather than on locomotor abilities measured under laboratory conditions (Hertz et al., 1988; Irschick & Garland, 2001). This means that shifts in body temperature have to be accounted for. Because gravid females selected lower body temperatures during late gestation, locomotor costs of reproduction are likely to be higher than predicted by our laboratory study. For example, sprint speed increases with body temperature up to an optimal thermal range located at 32-35°C in this species (van Damme et al., 1990), which is higher than the thermal preferences displayed during gestation. Therefore, measurements of locomotor abilities should be obtained under a larger range of body temperatures in the future. Of particular interest is the problem of whether differences between gravid and post-parturient females are consistent across a thermal range.

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ANNEXE 5 – VARIATION DES CAPACITES D'ENDURANCE



Photo: M. Massot

“More studies of natural selection on individual differences within populations should be done. The available data base for reptilian locomotor performance is exceedingly small. We need to know whether selection on performance is pervasive or rare, strong or weak, directional or stabilizing. [...]. We might also test whether selection ever acts directly on morphology.” T. Garland Jr. & J. B. Losos in *Ecological morphology of locomotor performance in squamate reptiles*. 1994.

EVALUATION DU SCHEMA MORPHOLOGIE-PERFORMANCE-FITNESS: VARIATION DE LA CAPACITE D'ENDURANCE CHEZ UN LEZARD

Jean-François Le Galliard, Marie-Laure Jarzat, Jean Clobert & Régis Ferrière

RESUME

La morphologie influence les performances locomotrices qui influencent la valeur sélective. Nous évaluons ce schéma morphologie-performance-fitness pour la capacité d'endurance à la naissance (le temps de fatigue à faible vitesse) chez les jeunes lézards vivipares *Lacerta vivipara*. Nous avons combiné des approches corrélatives et expérimentales pour étudier trois problèmes : (i) le *gradient de performance* depuis la morphologie vers la performance, (ii) la *consistance ontogénique* des différences de performance entre individus, et (iii) le *gradient de fitness* depuis la morphologie et la performance vers la survie natale.

Nous avons trouvé des résultats en accord avec le schéma morphologie-performance-fitness. Premièrement, le gradient de performance indique une relation du type 'le plus large est le meilleur' : les jeunes de grande taille et de forte condition ont des performances plus élevées. Deuxièmement, la capacité d'endurance varie fortement entre familles, malgré l'absence d'effets maternels, suggérant une héritabilité significative du trait locomoteur. Troisièmement, les différences entre individus sont globalement consistantes sur le premier mois de vie. Quatrièmement, une sélection directionnelle favorise des capacités d'endurance à la naissance plus élevées, et la sélection naturelle affecte parallèlement la morphologie.

Cependant, la variation interindividuelle d'endurance est seulement consistante dans un environnement pauvre pour la disponibilité en ressources. Ceci pose une limite forte sur la prédictibilité de la sélection naturelle et l'héritabilité des variations entre individus dans un environnement riche. De plus, le gradient de fitness tire essentiellement son origine d'une sélection contre les individus très faiblement performants rapidement après la naissance, alors que la sélection sur les performances élevées est faible et inconsistante. Ceci suggère que les avantages associés à une endurance élevée sont compensés par le comportement, des liens compensatoires ou des changements ontogéniques, ou bien que ces capacités ne sont pas utilisées au cours des activités naturelles.

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Mots-clés additionnels: *Lacerta vivipara* – ontogénie – ressources nutritives – survie.

EVALUATION OF THE MORPHOLOGY-PERFORMANCE-FITNESS PARADIGM: INTERINDIVIDUAL VARIATION ON ENDURANCE CAPACITY AT BIRTH IN A LIZARD

Jean-François Le Galliard, Marie-Laure Jarzat, Jean Clobert & Régis Ferrière

SUMMARY

Morphology can influence locomotor performances which themselves can influence fitness. We evaluate this morphology-performance-fitness paradigm for endurance capacity at birth (the time to exhaustion on a treadmill) in offspring common lizards *Lacerta vivipara*. We combined observational and experimental approaches to address three related issues: (i) the *performance gradient* from morphology to performance, (ii) the *ontogenic consistency* of individual differences on locomotor performance, and (iii) the *fitness gradient* from morphology and performance to fitness.

We found some results agreeing with the morphology-performance-fitness paradigm. First, the performance gradient supports the 'bigger is better' hypothesis: longer and heavier offspring have higher performance capacities. Second, endurance capacity varies strongly among families, despite no evidence of maternal effects, suggesting significant heritability of the locomotor trait. Third, individual differences at birth are overall consistent over one month of life. Fourth, directional selection on annual survival favours larger endurance capacities at birth, and natural selection occurs jointly on morphology.

However, interindividual variation on endurance capacity are only consistent across ontogeny when food availability is low. This places a strong limit over time on the predictability of natural selection and the heritability of interindividual variation in good environments. Also, the fitness gradient originates from selection against low-performance individuals quickly after birth, while natural selection on high-performance individuals is weak and inconsistent. This suggests that the advantages of strong performance levels are bypassed by behavioural shifts, trade-offs or ontogenic changes, or that high performance are not used during field activities.

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Additional key words: *Lacerta vivipara* – ontogeny – food availability – survival.

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INTRODUCTION

Locomotor abilities have been studied extensively in squamate reptiles (Bennett & Huey, 1990; Garland & Losos, 1994; Shine, 1980). They have been used to assess performances at ecologically relevant tasks such as escape of predators (Christian & Tracy, 1981), foraging success (Huey, Bennett, John-Alder & Nagy, 1984), or mate search ability (Cuthill & Houston, 1997). Quantitative variation in locomotor performances has been described among species, among populations within a single species, between individuals within a population and also within individuals (Garland & Losos, 1994). Combining physiological and mechanical hypotheses on the functional determinism of these traits (Farley & Ko, 1997; Losos, 1990) with explanations of the adaptive basis of locomotion (Bennett & Huey, 1990), natural variation on locomotor performances has been analysed at two successive stages: the path from “morphology” (in a broad sense, including also physiological properties) to performance, and the path from performance to fitness (Arnold, 1983; Huey & Stevenson, 1979; Pough, 1989).

Performance gradient

The path from morphology to performance can be elucidated by comparing morphological, biochemical and physiological attributes of individuals with quantitative measures of locomotor performances (Bennett & Huey, 1990). In this way, variability in endurance capacity (the time to exhaustion at small speed on a treadmill) has been explained by lower level attributes, such as body size, muscle mass, or aerobic scope (e.g., Garland, 1984). Attempts to separate the performance gradient of endurance capacity between genetic and non genetic effects have also been conducted because evolutionary responses rely on heritable interindividual variation. In several species of lizards, significant broad-sense heritabilities have been detected for endurance capacity (e.g., Garland, 1988; Jayne & Bennett, 1990a; Tsuji et al., 1989; van Berkum & Tsuji, 1987). However, broad-sense heritability includes not only additive genetic effects, but also non additive genetic effects, non genetic maternal effects, and common environmental effects (Falconer, 1989). Although the contribution of non additive genetic effects is usually small, maternal effects can have considerable effects on offspring phenotype at birth (Mousseau & Fox, 1998), and can inflate broad-sense heritabilities of locomotor performances in lizards (Shine & Harlow, 1996; Sorci & Clobert, 1997). The extent to which maternal effects influence variation on endurance capacity at birth has nevertheless been usually neglected (but see Meylan & Clobert submitted).

Related to this issue is whether variation at birth is consistent during ontogeny. Consistency over time of individual's performance within a population is important because a lack of repeatability limits the opportunities for natural selection (Bennett & Huey, 1990). In several species, significant repeatabilities of locomotor performances have been found on both the short and long term (e.g. Elphick & Shine, 1998; van Berkum et al., 1989). Most studies have searched for repeatability of locomotor performances after growth cessation, hence when consistency is likely high, rather than during natal growth (but see van Berkum et al., 1989). Furthermore, despite the plasticity of locomotor performance traits (e.g., John-Adler & Bennett, 1981), repeatability has not been compared between environments (Garland & Losos, 1994). We predict that poor environments would lead to high repeatability because restricted growth preserves interindividual variation against compensatory changes.

Fitness gradient

Different alternatives have been used to explain a link between locomotion and fitness. A first hypothesis is that sustained activity in the field and social dominance are limited by endurance capacity, leading to a positive link between performance and fitness (Bennett & Huey, 1990). This idea is substantiated by the positive correlation between behavioural activity and maximal endurance capacity among and within species of lizards (Clobert et al., 2000; Garland, 1999). Second, elevated performances and activity can be associated with higher energy expenditure, greater risks of predation,

or higher parasitism, leading to a negative link between performance and fitness (Clobert et al., 2000). Third, locomotor capacities might be well above the scope of most field activities or can be bypassed by behavioural shifts, leading to a neutral relationship between performance and fitness (e.g., Hertz, Huey & Garland, 1988; Irschick & Garland, 2001). Indeed, behaviours, such as 'increase your wariness if you are a slow runner', can compensate physiological differences in performance (Brodie III, 1989a). Clearly, studies of ongoing selection on locomotor performances could help to clarify between these alternatives (Bennett & Huey, 1990; Garland & Losos, 1994).

However, few field studies have reported direct fitness gradients on locomotor performances in squamates (Bennett & Huey, 1990; Clobert et al., 2000; Jayne & Bennett, 1990b; Miles, 1989; Miles et al., 2000). Of those, two have found directional selection favouring higher sprint speed (Jayne & Bennett, 1990b; Miles, 1989), and only one detected directional selection favouring higher endurance capacity in adults (Miles et al., 2000). Because some of these studies were conducted separately from proximate analysis of natural variation, it was difficult to distinguish the map linking performance to fitness from the map linking morphology to fitness (review in Garland & Losos, 1994). Multivariate selection analysis on both locomotor performance and its lower-level correlates provides a solution to this controversy (Arnold, 1983; Lande & Arnold, 1983). However, all studies applying this technique have suffered from two methodological pitfalls. First, they were unable to control for capture and movement heterogeneity (Clobert, 1995). Second, they relied on wild animals released in heterogeneous habitats, which could have hidden or confound selection gradients (Scheiner et al., 2002), especially if locomotor performances change plastically in response to local environmental conditions (Losos et al., 2001).

Endurance capacity at birth in a lizard

In this article, we evaluate three aspects of the morphology-performance-fitness paradigm: (i) the *performance gradient* from morphology to performance, (ii) the *ontogenic consistency* of individual differences in performance, and (iii) the *fitness gradient* from morphology and performance to fitness. We used cross-sectional and longitudinal studies of endurance capacity in a viviparous lizard without parental care, *Lacerta vivipara* (Jacquin 1787). We study endurance capacity (i) because this species is an active forager with poor sprinting abilities (Bauwens et al., 1995), suggesting that endurance is more important to fitness than locomotor speed; and (ii) because broad-sense heritability has been found for endurance in a previous study (Sorci et al., 1995). First, we analyse morphological, maternal and sibship effects on interindividual variation. Second, we investigate ontogenic consistency of endurance capacity at two different levels of food availability. Third, we study natural selection on endurance capacity and its lower-level morphological determinants. Contrary to other studies, we minimised environmental differences by releasing individuals in standardised environments, and did not confound our measure of survival with capture or movement heterogeneity.

MATERIAL AND METHODS

The common lizard *Lacerta vivipara* is a small, ground-dwelling, and actively foraging species (offspring snout-vent length 15-27 mm). Reproduction is ovoviviparous, and hatching occurs in few minutes following parturition (modal clutch size: 5-6 shell-less eggs). Offspring are autonomous at birth and patrol over a home range of a few hundred square meters (Massot, 1992). At this stage, survival can depend on the ability to move within a foraging area and among basking sites and refuges, hence probably on endurance capacity.

Endurance trials

Endurance was measured by running lizards on a circular treadmill closed with plastic walls and covered with cork to ensure traction (external diameter 64 cm, internal diameter 52 cm). Circular and motorised treadmills are two commonly used techniques to measure endurance capacity (Bennett & Huey, 1990; Garland, 1984). Lizards were heated at 31-32°C before trials, and the circular belt was maintained between 29-32°C with two heat lamps. This temperature matches the average body temperature in the field (modal range: 30-33°C, see van Damme, Bauwens & Verheyen, 1990). Lizards were motivated to run at a constant speed (c.a. 0.36 km.h⁻¹) by gently tapping the basis of their tail with a soft paint brush, and the number of stimulations during the trial was recorded. The trial speed was chosen because it was ecologically relevant, and agreed with typical values used to exhaust small lizards (Garland, 1994), including other studies on the same species (Clobert et al., 2000; Sorci et al., 1995). Each trial was concluded upon exhaustion of the animal, estimated by the loss of a righting response after 10 consecutive taps on the tail (Huey et al., 1984). Offspring were measured once at the same age by the same person in a random order. The time to exhaustion (to the closest s) measured endurance capacity. The number of stimulations per unit distance was used to measure behavioural resistance, with higher values indicating a lower motivation to run (Bennett & Huey, 1990). This was accounted for because it has been found that motivation can affect stamina (Sorci et al., 1995; van Berkum & Tsuji, 1987).

Repeatability of these trials was estimated using 70 offsprings from 14 families measured at one day old and at three days old. Endurance did not change significantly between trials (first trial: 212.2 s ± 10.8 SE, second trial: 217.6 s ± 9.9 SE; paired Student's t-test, P = 0.37), and measurements were repeatable (ANOVA, log-transformed endurance capacity, $F_{69,70} = 10.18$, P < 0.001). The high repeatability coefficient indicates consistency of individual differences on a short time scale (intraclass correlation coefficient: $r = 0.78$, Lessels & Boags, 1987).

Proximate determinants at birth

We measured endurance capacity in 2001 on 447 offsprings of 90 families obtained from one natural population of a upland area (Lozère, 1500 m a.s.l., 44°27'N, 3°44'E) in the south of France

(Clobert et al., 1994), and from enclosures located in a lowland area (Ecological Research Station of Foljuif, 60 m a.s.l., 48°17'N, 2°41'E). This lowland sample contained lizards translocated from upland populations to outdoor enclosures in 1999, and maintained at the lowland site during an experiment investigating the effects of population density on demography (Le Galliard, Ferrière & Clobert, 2003). These outdoor enclosures are similar and can sustain a small local population matching the age and sex structure of natural populations (see details in Boudjemadi, Lecomte & Clobert, 1999). In 1999, density of outdoor enclosures was manipulated by releasing either 20 adults plus 36.5 offspring (± 2.4 SE) in 8 low-density enclosures, or 40 adults plus 71.2 offspring (± 3.9 SE) in 8 high-density enclosures (see Le Galliard et al., 2003 for more details). In Spring 2001, the population size was 9.6 individuals (± 3.6 SE) in the low-density enclosures and 21.3 individuals (± 4.4 SE) in the high-density enclosures, meaning persistent differences between treatments ($\chi^2 = 9.0$, $P = 0.002$). Therefore, all gravid females from the lowland sample were assigned to a low- or a high-density group.

Gravid females removed from the upland area (25 May to 28 May) and the lowland area (28 May to 3 June) were maintained in the laboratory of the lowland site under standard conditions until laying. Females were measured for snout-vent length (body size) and weighed regularly during gestation. After parturition, females were weighed and neonates were isolated. Offspring sex was determined based on the counting of ventral scales (Lecomte, Clobert & Massot, 1992). We measured offspring tail size and body size to the nearest mm, and offspring body mass to the nearest mg. In this study, offspring were given a unique code by toe-clipping, which has no effect on survival (Massot et al., 1992). The day after birth, we measured endurance capacity.

Natural selection

Offspring measured in 2001 were released in nine similar outdoor enclosures at the lowland site after a day of rest in the laboratory. Each outdoor enclosures has a 10 × 10 m size to mimic a natural home range, and is protected from predators by plastic walls and by nylon nets. Populations were initiated during July 2001 with 9 families, 21 adults (including the mother of each family), and 16 yearlings. Offspring presence was then monitored by hand recaptures in August 2001 and in June 2002. During these censuses, the recapture probability p estimated by the modelling of individual life histories was approximately equal to one (August 2001, $p > 0.95$; June 2002: $p = 1$, see Lebreton et al., 1992). Therefore, individuals not caught in August 2001 and June 2002 can be thought as dead before the census.

Post-hatching effects of food availability

We manipulated food availability during one month after birth in 2002. Two levels of food intake were calibrated with body growth data obtained from a longitudinal study at the lowland site (Le Galliard *unpub. data*) and with physiological data obtained from (Avery, 1971). Body growth data

were used to calibrate a distribution of natal growth rates. The physiological data from (Avery, 1971) were used to translate these growth rates into expected food intakes in the laboratory. The resulting food intake distribution was normally distributed with a mean of 37.6 mg.day⁻¹ and a standard deviation of 12.2 mg.day⁻¹. During the first week, we therefore chose 15 mg.day⁻¹ of house crickets larvae (*Acheta domesticus*, 3-5mm size) as a low-food treatment to mimic food deprivation. The high-food level was chosen as three times this quantity. The food intake was then raised each following week, while maintaining a constant 1 : 3 ratio between low-food and high-food treatments (see Table 1 for details). This gave an average food intake of 20.5 mg.day⁻¹ in the low-food treatment versus 61.5 mg.day⁻¹ in the high-food treatment.

Table 1. Food intake (mg.day⁻¹ of house crickets larvae) given per lizard per day during the four weeks of the experimental manipulation of food availability. The weekly change was justified by the fact that energetic demands increase during early ontogeny.

	First week	Second week	Third week	Fourth week	Average
Age (day)	4-10	11-17	18-24	25-31	4-31
Low-food treatment	15	17	21	29	20.5
High-food treatment	45	51	63	87	61.5

We selected 2 males and 2 females from 32 families, and allocated one individual of each sex to one feeding treatment (split-clutch design). At the age of one day, we recorded endurance capacity. The evening following endurance trials, we isolated offspring in small individual terraria (17 × 11 × 12 cm). Each terrarium was warmed with a single heating lamp (25 W) from 8:00 to 18:00 local time, and UV light was added once every two days (Iguana Light 5.0 UV-B, ZooMed, 40 W). Terraria were distributed in a rearing room according to a randomised block design. Each block consisted of a tray with three heating lamps under which the same family was pooled. Feeding was initiated at the age of four days. Food was weighted prior to each feeding and was deposited in the early morning. At the end of the experiment, endurance was measured for the second time (33 days old).

Statistical analyses

We used mixed-effects models including fixed (e.g., morphology) and random effects (e.g., family). Endurance was log-transformed to ensure normality. Estimates were derived from a restricted maximum likelihood approach using SAS software (Littell et al., 1996). Statistical inferences for the fixed effects were obtained from type III statistics. Random effects were tested with conservative likelihood ratio tests (Stram & Lee, 1994). Results are presented as mean ± SE.

The effects of offspring and maternal characteristics on endurance capacity at birth were investigated with a multivariate regression. Offspring characteristics included body size (snout-vent

length), residual tail size (residual from a linear regression of tail length against body size), body condition (residual from a linear regression of body mass against body size), and sex. Maternal characteristics included maternal body size, residual fecundity (obtained as the residual of total clutch size on maternal body size), residual relative clutch mass (obtained as the residual on maternal body size of the clutch mass ratio to post-parturition body mass), post-parturition body condition, and geographical origin. Moreover, offsprings from the lowland site were classified according to maternal age (2 years old, 3 years old, or greater than 3 years old) and density (low- or high-density treatment). The family effect was included as a random effect, and the variance among families was used to compute broad-sense heritability (Falconer, 1989).

The post-hatching effect of food intake was investigated by modelling the change in endurance capacity during one month as a function of food availability, sex, initial endurance and their interactions. In this analysis, we modelled block (laboratory tray) and family as random effects. One observation was removed because the lizard lost its tail during the rearing.

A multivariate analysis of natural selection on performance (endurance capacity) and its morphological determinants (body size, body condition) was conducted. All covariates were standardised (zero mean, unit variance). The survival probability was modelled with mixed-effects logistic regressions using the GLIMMIX macro in SAS (Littell et al., 1996). We used linear terms to test for patterns of directional selection on each trait, quadratic terms to test for patterns of stabilising or disruptive selection on each trait, and interaction terms to test for correlational selection on morphology and performance (Lande & Arnold, 1983). Standardised selection gradients associated with these terms were derived from logistic regression estimates following on Janzen & Stern (1998). Lizards from the two geographical origins were pooled together because we found no difference in heights and slopes of fitness between origins ($P > 0.05$). Also, behavioural resistance during the trial was not included because we found no significant effect of behaviour on survival ($P > 0.10$). The non-independence of offspring from the same population and the same family was accounted for with random effects of enclosure and family. We used the deviance as a chi-square statistic to test the goodness of fit of these models, and found no evidence of lack of fit (McCullagh & Nelder, 1989). Furthermore, we observed qualitative concordance between these models and non parametric functions implemented from a cubic spline regression (Schluter, 1988).

RESULTS

Morphology, family and maternal effects

Endurance varied from 36 s to 1677 s in 2001, a 45-fold increase (average 222 ± 7.3 s, $n = 447$, Figure 1A). Residual maternal fecundity, post-parturition maternal body condition, offspring sex, residual relative clutch mass, and offspring residual tail size were not correlated with offspring

endurance at birth (all $P > 0.17$). Furthermore, there was no difference between families originating from the upland and lowland areas (Lowland area: 232.7 ± 11.5 s, $n = 257$; Upland area: 207.6 ± 7.11 s, $n = 190$; $F_{1,85} = 1.69$, $P = 0.20$). The final model indicated that endurance at birth was influenced by offspring size, offspring body condition, offspring behaviour during the trial, and maternal body size (Table 2). Partial regressions showed that endurance capacity at birth (i) increased with offspring body condition and offspring body size (Figure 1B, C), (ii) decreased with maternal body size (Figure 1D), and (ii) decreased with the number of stimulations given per unit distance during the trial (not illustrated). Behaviour had more influence on endurance capacity than offspring morphology and maternal effects (Table 2). Also, a significant family effect was detected in the final model, and the broad-sense heritability of endurance capacity at birth was $h^2 = 0.40$.

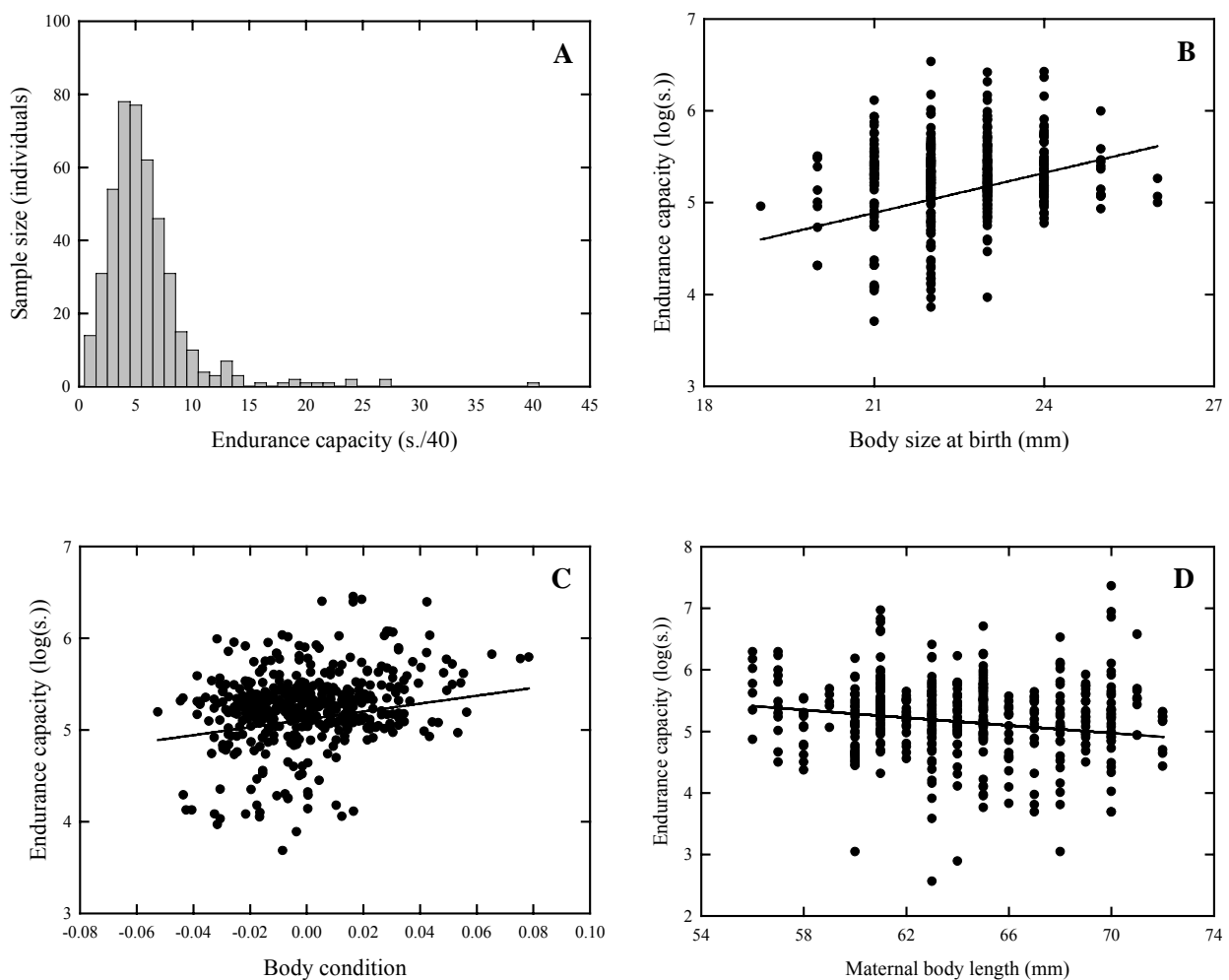


Figure 1. Natal determinants of endurance capacity at birth in offspring common lizards *Lacerta vivipara*. A. Frequency distribution of endurance capacity at birth for all offspring (447 offspring). Distribution is skewed on the right with few offspring displaying exceptional endurance. B. Relationship between offspring body size and endurance capacity at birth. C. Relationship between offspring condition and endurance capacity at birth. D. Relationship between maternal body size and offspring endurance capacity at birth. The endurance capacity has been log-transformed to ensure normality.

The influences of maternal age, density manipulation, and their interaction on offspring endurance at birth were tested on the lowland sample (257 offsprings from 51 families). These effects were not significant (ANOVA with family included as a random factor nested within Age and Density effects, Age effect: $F_{2,45} = 0.88$, $P = 0.42$; Density effect: $F_{1,45} = 0.10$, $P = 0.75$; Age \times Density effect: $F_{2,45} = 0.17$, $P = 0.84$).

Table 2. Effects of offspring body size, offspring body condition, offspring behaviour, maternal body size and family on endurance capacity at birth in offspring *Lacerta vivipara*. Test statistics, parameter estimates (\pm SE) and partial regression are derived from a mixed-effect analysis of variance (447 observations, 89 families).

	Test statistics	Parameter estimates	Partial regression r^2
<i>Fixed effects</i>			
Offspring body size	$F_{1,355} = 14.6$ **	0.098 ± 0.026	<i>0.041</i>
Offspring body condition	$F_{1,355} = 40.4$ ***	8.725 ± 1.373	<i>0.070</i>
Offspring behaviour	$F_{1,355} = 86.1$ ***	-0.031 ± 0.012	<i>0.233</i>
Maternal body size	$F_{1,355} = 7.1$ **	-0.953 ± 0.103	<i>0.046</i>
<i>Random effects</i>			
Family	$\chi^2 = 105.1$ ***	0.125 ± 0.026	-

** $P < 0.01$, *** $P < 0.001$

Post-hatching effect of food availability

Endurance varied from 105 to 1337 s (average 465 ± 15.8 s, $n = 128$) during the first trial, and from 219 to 1179 s (average 622 ± 17.7 s, $n = 127$) during the second trial. A significant individual increase between the two trials was detected (paired Student's t-test, $P < 0.001$; average change: 158 ± 19.4 s). Also, there was a significant ontogenic repeatability (ANOVA on subject effect, $F_{126,127} = 1.46$, $P = 0.02$; intraclass correlation coefficient: $r = 0.19$; interclass Pearson's correlation coefficient: $r = 0.40$, $P < 0.001$). Endurance at birth and at the age of one month were negatively correlated with the behavioural resistance of the lizard ($P < 0.01$). Therefore, when testing for an effect of food manipulation, the effect of behaviour was controlled by including the change in behavioural resistance between measurements as a covariate.

Ontogenic increase in endurance capacity was not related to change in individual behaviour ($F_{1,90} = 2.29$, $P = 0.13$) nor to offspring sex ($F_{1,90} = 2.70$, $P = 0.10$). The food by sex interaction, which tests for different effects of treatment on males and females, was also not significant ($F_{1,90} = 1.10$, $P = 0.30$). The effect of food availability was state dependent, as shown by a significant interaction between treatment and endurance at birth ($F_{1,90} = 10.9$, $P = 0.001$). Within the low-food treatment, change in endurance capacity was unaffected by initial endurance ($F_{1,28} = 1.34$, $P = 0.26$), but it decreased with performance at birth in the high-food treatment ($F_{1,29} = 58.9$, $P < 0.001$, Fig. 2). The

ontogenic repeatability of individual differences was then not significant in the good environment (ANOVA on subject effect, $F_{62,63} = 0.99$, $P = 0.51$), and significant in the poor environment ($F_{63,64} = 2.17$, $P = 0.001$, intraclass correlation coefficient: $r = 0.37$). The Pearson product-moment correlation coefficient between endurance capacity at birth and at the age of one month was higher in the low-food ($r = 0.57$) than in the high-food treatment ($r = 0.21$, Student-test on z -transformation, $P = 0.018$; Sokal & Rohlf, 1998).

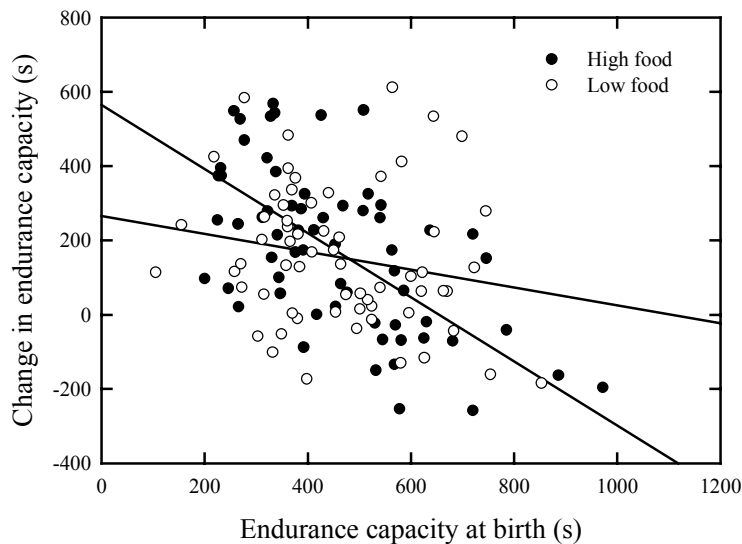


Figure 2. Ontogenic change in endurance capacity in offspring common lizards depending on food availability and endurance at birth. Change in endurance capacity during ontogeny decreases significantly with endurance capacity at birth in the high-food treatment ($P < 0.001$).

Natural selection on performance and morphology

From the 447 offspring measured for endurance at birth, 16 individuals died before release, 316 survived summer selection, and 192 survived annual selection. No pattern of correlational selection between body size, body condition, and endurance capacity was detected in all survival analyses ($P > 0.13$). This suggests that natural selection acted independently on morphology and performance. The additive survival model describing summer selection indicated a directional selection on body size at birth favouring larger body sizes, a directional selection on endurance capacity at birth for larger endurance capacities, and a tendency for directional selection on body condition favouring heavier offspring (see Table 3, Fig. 3). Especially, all individuals with endurance capacities above values of 500 s (14 observations, 3 % upper range) survived after one month in outdoor enclosures. When additive natural selection was studied from the summer to the spring of the next year, no selection on endurance capacity at birth ($F_{1,234} = 0.01$, $P = 0.92$) or body size at birth ($F_{1,234} = 2.86$, $P = 0.09$) was detected, but the quadratic body condition term was significant (Body condition² effect: $F_{1,234} = 5.77$, $P = 0.02$). The positive average standardised selection gradient ($\beta = 0.10$) associated with this term indicated a disruptive selection favouring both leaner and heavier offspring at birth.

Table 3. Effects of body size, endurance capacity, and body condition on survival of offspring *Lacerta vivipara* during summer and during the first year of life. Enclosure where offspring were released and family are also included as random effects. Test statistics and parameter estimates (\pm SE, logit scale) are derived from a mixed-effect logistic regression (431 observations, 9 enclosures, 84 families). The average standardised selection gradient is calculated following equation (4) in Janzen & Stern (1998).

	Summer survival			Annual survival		
	Test statistics	Estimates	Gradient	Test statistics	Estimates	Gradient
<i>Fixed effects</i>						
Endurance	$F_{1,344} = 6.42$ *	0.465 ± 0.183	0.104	$F_{1,343} = 4.43$ *	0.268 ± 0.127	0.120
Body size	$F_{1,344} = 7.17$ **	0.341 ± 0.127	0.077	$F_{1,343} = 7.45$ **	0.335 ± 0.123	0.150
Body condition	$F_{1,344} = 3.3$ †	0.249 ± 0.137	0.056	$F_{1,343} = 1.27$	0.146 ± 0.130	0.065
Body condition ²	-	-	-	$F_{1,343} = 5.92$ *	0.228 ± 0.094	0.102
<i>Random effects</i>						
Enclosure	$\chi^2 = 39.39$ ***	0.491	-	$\chi^2 = 60.83$ ***	0.743	-
Family	$\chi^2 = 52.56$ ***	0.531	-	$\chi^2 = 52.63$ ***	0.441	-

† $0.05 < P < 0.10$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

To summarise these analyses, we pooled the two selection episodes and investigated additive natural selection during the first year of life. Directional selection on endurance capacity was significant in this model, and the strength of the selection gradient was of the same order of magnitude than during summer selection (Table 3). However, removing some individuals from this analysis indicated that the relationship between survival and endurance was extremely sensitive to a few individuals with the lowest endurance capacities at birth (Table 4). This shows that the overall pattern of selection on endurance reflects mostly selection acting against the lowest endurance capacities, while selection is neutral at other levels of endurance capacities (see Fig. 3). In addition to this directional pattern on endurance, there was a directional selection favouring larger body size at birth, and a disruptive selection on body condition (Table 3). In the latter case, natural selection favoured both offspring leaner and heavier at birth than the average body condition (Fig. 3).

DISCUSSION

Similar to previous studies in lizards, we detected strong interindividual variation on endurance capacity at birth (Garland & Losos, 1994), which allowed us to address the three related issues that we raised in the introduction: the proximate basis, the ontogenic consistency, and the natural selection on endurance capacities at birth.

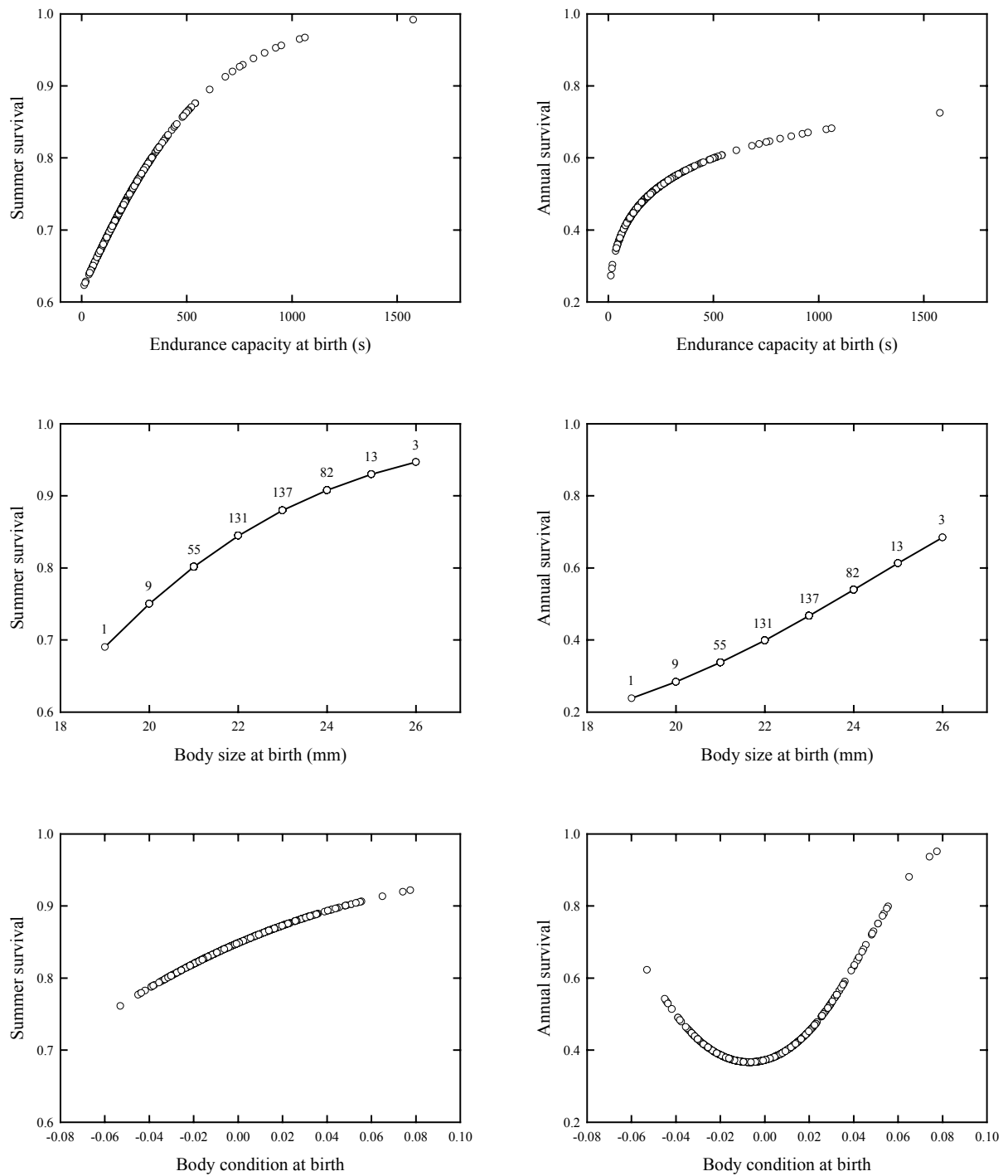


Figure 3. Fitness functions predicted by mixed-effect logistic regressions of natural selection on endurance capacity, body size and body condition during summer (left panels) and during the first year of life (right panels) in offspring common lizards. Data have been back-transformed from the predicted values of the models. In the case of body size, the numbers inside the panel indicate sample size; otherwise, each circle corresponds to a single individual.

Table 4. Effect of removing individuals with the lowest endurance capacities on the relationship between annual survival, morphology, and performance in offspring common lizards. The first sample contains 424 observations and 83 families. The second sample contains 409 observations and 83 families. The third sample contains 385 observations and 78 families. Test statistics are derived from a mixed-effect logistic regression.

	Annual survival			
	Initial sample	First sample	Second sample	Third sample
Endurance	$F_{1,343} = 4.43 *$	$F_{1,337} = 3.00 †$	$F_{1,322} = 1.86$	$F_{1,303} = 0.09$
Body size	$F_{1,343} = 7.45 **$	$F_{1,337} = 7.30 **$	$F_{1,322} = 5.94 *$	$F_{1,303} = 4.93 *$
Body condition	$F_{1,343} = 1.27$	$F_{1,337} = 1.59$	$F_{1,322} = 0.27$	$F_{1,303} = 1.59$
Body condition ²	$F_{1,343} = 5.92 *$	$F_{1,337} = 5.54 *$	$F_{1,322} = 6.47 *$	$F_{1,303} = 5.96 *$

† $0.05 < P < 0.10$, * $P < 0.05$, ** $P < 0.01$

Proximate basis of individual differences

We observed that longer and heavier offspring displayed higher endurance capacities at birth, as expected from the ‘bigger is better’ hypothesis (Garland, 1994). Biomechanical and physiological considerations can explain these correlations. Body size increases the strength of the lateral trunk bending used for forward propulsion in squamates (Farley & Ko, 1997), is linked to limb cycling frequencies (Garland, 1994), and is correlated with limb dimensions and muscle development, therefore reducing movements costs (Garland, 1993). Furthermore, the positive relationship between body condition and endurance indicates effects of stockiness, such as the relative mass of the musculature (increasing the capacity to utilise oxygen) or the relative mass of the heart and the lung (increasing the maximal oxygen consumption).

Motivation of the lizard during the trial also influenced locomotor performance. Whether such motivational issues bias our measurements or is inherent to the natural behaviour of lizards is difficult to assess (Garland & Losos, 1994). We could have tried to measure maximal locomotor performances with repeated observations on the same subjects and to exclude individuals performing sub-optimally (Losos, Creer & Schulte II, 2002). However, this procedure was prohibitive with our sample size, the multiple measurements could induce deleterious effects due to fatigue, and we had no obvious reason to reject some individuals since all lizards reached complete exhaustion as estimated from the loss of a righting response. Alternatively, motivational variation could act as filter between maximal performances and realised performances, and determine patterns of locomotor activities in the field. Some studies have indeed suggested that natural locomotor activities depend on complex interactions between morphology, physiology and also behaviour (Brodie III, 1989b; Irschick & Garland, 2001).

Endurance capacities at birth had a significant broad-sense heritability as in most studies on squamates (reviews in Bennett & Huey, 1990; Garland & Losos, 1994). Without breeding experiments, it is difficult to know whether this is due to strong additive genetic, non additive genetic, maternal or common environment effects (Falconer, 1989). Common environmental and maternal

effects were reduced by our rearing protocol. Moreover, we found few evidences of maternal effects: geographical origin, maternal age, and habitat density did not influence endurance capacity at birth. The lack of any origin effect suggests the absence of long-term maternal effects and similar selective pressures on endurance capacity in the two habitats (Sinervo & Losos, 1991; van Damme, Aerts & Vanhooydonck, 1998), despite the fact that these sites differ widely with respect to climatic conditions and many life-history traits (Bauwens, Heulin & Pilorge, 1986). Similarly, although low- and high-density treatments induce different levels of intraspecific competition in this species (Massot et al., 1992), density did not affect endurance at birth. The same conclusion was reached when long and short-term maternal effects on endurance at birth were jointly investigated in the common lizard (Meylan & Clobert submitted). It was found that a social perturbation of the maternal population and a maternal hormonal perturbation during gestation did not influence endurance capacities of offspring.

Ontogenic consistency of individual differences

Endurance capacity increased from birth to the age of one month. This ontogenic increase in stamina and activity capacity has been previously described in snakes (Garland, 1988; Pough, 1977) and in one lizard (Garland & Else, 1987), where it was related to changes in aerobic scope after birth. Unexpectedly, food availability had no effect on this ontogenic change. Such an effect could have been mediated by influence of food on morphology, muscle, glycogen reserves, or aerobic metabolism. In our case, design features were indeed positively affected by food availability (Le Galliard *unpub data*). However, these positive effects could have been compensated by the development of non contractile, fat tissues increasing the costs of locomotion without providing force generation (e.g., Schwarzkopf & Shine (1992) for lizards and Cureton & Sparling (1980) for humans).

A significant repeatability of individual differences on endurance capacity was detected during one month of growth in the laboratory. Similarly, ontogenic repeatability has been reported for endurance of hatchling lizards *Sceloporus occidentalis* across several months (van Berkum et al., 1989), and our estimate of repeatability matched the values obtained in this study during one month of field activity. Moreover, by rearing offspring in both poor and good environments, we found that ontogenic repeatability was only significant in the poor environment. Environmental dependent expression of ontogenic repeatability has also been found for morphological traits in birds. For example, correlation between size of nestling collared flycatchers and size at fledging is higher in poor environments resulting from clutch size enlargement than in good environments (Merilä, 1997). The fact that ontogenic repeatability of endurance capacity differed between the two environments could mean constraints on ontogeny. Alternatively, the differential effect of feeding on good and bad runners at birth could reflect an adaptive trade-off between allocating resources to muscles and metabolism to increase locomotor capacity versus allocating resources to fat and stocks at the expense of locomotor performances. To distinguish between constraints and adaptation, investigations of the physiological

consequences of food intake, studies of the relationship between physiology and endurance capacity, and measurements of natural selection on endurance in the two environments will be needed.

The ultimate consequences of a low ontogenic repeatability on endurance capacity in a good environment are twofold. First, the lack of ontogenic repeatability questions the heritability of endurance performance capacities at the yearling and adult stages in this species, and therefore the quantitative response to selection on performances of mature individuals (Falconer, 1989). Second, because selection acts on current differences among individuals within populations, low ontogenic repeatability in a good environment places a strong limit on the predictability of natural selection on hatchling performances over time (van Berkum et al., 1989).

Natural selection on individual differences

We found directional selection for larger endurance capacities at birth during summer and during the study year, contrary to other field studies on squamates (Bennett & Huey, 1990; Clobert et al., 2000; Jayne & Bennett, 1990b). However, endurance capacity at birth had no detectable effect on survival from summer to the following year, and therefore most selection occurred quickly after birth. This temporal change could be explained by a reduction of natural variation due to the first selection episode and/or a low ontogenic consistency of endurance capacity. A closer inspection of annual survival further also indicated that the directional selection was due to selection against poorly performing individuals, while natural selection on higher performances was neutral. This suggests either that the advantages of stronger performance levels are bypassed by behavioural compensations (Irschick & Garland, 2001), trade-offs (Clobert et al., 2000) and ontogenic changes (this study), or that the maximal performances are not used under field activities (Bennett & Huey, 1990). High performances abilities could be modulated by behavioural shifts in activity pattern, habitat use, or social interactions. For example, high performance individuals may rely on active foraging strategy, while lower performance individuals could use sit-and-wait behaviours (Huey et al., 1984). Also, low endurance capacities may be traded against a higher sprint speed or lower risks of mortality. In the same species, one field study has indeed suggested that low endurance was compensated by lower predation risks and lower susceptibility to parasites (Clobert et al., 2000).

The multivariate analysis of natural selection revealed (i) that morphology and performance affected natal survival additively, and (ii) that selection gradients were as strong for morphological traits than for locomotor performance. The occurrence of joint and additive selection on morphology and endurance capacity indicates either a direct path from morphology to fitness, or an indirect path from morphology to fitness through alternative (unmeasured) performance indexes (Arnold, 1983; Pough, 1989). For example, directional selection for larger body sizes could be due to an association between size and social dominance, food intake or sprint speed (Ferguson & Fox, 1984; Sinervo et al., 1992). Also, for a given size, a larger body mass at birth could reflect fat storage or another performance that acts positively on survival. However, the disadvantage of leaner individuals reversed

during winter and spring, resulting in an overall pattern of disruptive selection. Whether this pattern of multivariate selection is unique to our study can be evaluated by collecting information on selection on both morphology and performance in other systems. Nevertheless, the fact that our estimates of linear and quadratic selection gradients matched the average values found by (Kingsolver et al., 2001) in a survey of phenotypic selection in natural populations is suggestive that our case is not atypical.

Conclusion

We evaluated the adaptive basis of variation on endurance capacity at birth. On the one hand, we found that (i) the performance gradient from morphology to performance supports the 'bigger is better' hypothesis; (ii) endurance capacity varied strongly among families, indicating the possibility of narrow sense heritability; (iii) individual differences on endurance capacity were consistent over one month of life, and (iv) the fitness gradient from endurance to survival was positive, with selection gradients of the same magnitude as those acting on morphological traits. On the other hand, ontogenic consistency depended on the environment. The ranking of individual differences vanished during ontogeny in a good environment, placing a strong limit on the predictability of natural selection over time. Also, patterns of natural selection were not strictly concordant with the expectation: low-performance individuals were quickly selected against after birth, while natural selection on high-performance individuals was weak and inconsistent over time.

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