Original Article

The importance of a good neighborhood: dispersal decisions in juvenile common lizards are based on social environment

Elodie Vercken,[a] Barry Sinervo,[b] and Jean Clobert[c]
[a]Laboratoire Fonctionnement et Evolution des Systèmes Ecologiques, Université Pierre et Marie Curie, UMR 7625, Bâtiment A, 7 quai Saint Bernard, 75252 Paris Cedex 05, France, [b]Department of Ecology and Evolutionary Biology, Earth and Marine Sciences Building, Red Hill Road, University of California, Santa Cruz, CA 95064, USA, and [c]Station d'Ecologie Expérimentale du CNRS à Moulis, USR 2936, Moulis, 09200 Saint-Girons, France

Within a population, dispersers are likely to differ in their motivation and adaptations to disperse; yet individual heterogeneity in dispersal decisions is still poorly documented. In the common lizard, females can be classified into 3 types of ventral color (yellow, orange, and mixed) that signal alternative strategies in reproduction and behavior. The reproductive success of these alternative strategies depends on the frequency of each color type in their local environment. Therefore, we predicted that adaptive emigration and settlement decisions should differ between color types and respond to the social composition of the environment. To test this prediction, we analyzed juvenile local dispersal decisions in response to an experimental manipulation of the local color type frequencies. Offspring from orange or mixed females showed decreased dispersal rate in populations where the frequency of yellow females was increased, and those who dispersed chose to settle in environments with lower female density but higher frequency of yellow females. Our results demonstrate that the composition of the social environment is used as a direct cue for dispersal decisions that provides information on resource competition and environment quality. The frequency of female color types is thus a key parameter of the social environment that influences habitat choice decisions. However, the pattern of spatial autocorrelation of adult females was not consistent with these color-related dispersal patterns, which suggest that other processes also participate in shaping the distribution of individuals at the population scale. *Key words:* color polymorphism, frequency dependence, ideal free distribution, natal dispersal, public information, spatial niche partitioning. *[Behav Ecol]*

INTRODUCTION

Dispersal has been recognized as a key parameter in population persistence and species evolution (Hanski 2001). Dispersal is a common adaptive response to many different selective pressures: dispersers may avoid inbreeding, competition with kin and nonkin, or escape low-quality environments (Johnson and Gaines 1990). Therefore, dispersal is often open to the influence of many environmental factors (Clobert et al. 2001, 2004; Bowler and Benton 2005), which allows individuals to respond adaptively to spatial variations of their abiotic, biotic, and social environment (Clobert et al. 2004). Recently, several studies suggested that dispersers are a heterogeneous set of individuals (Clobert et al. 2009) who leave their natal area for different reasons and therefore have developed different adaptations to cope with the dispersal process (emigration, transience, and settlement). However, few studies so far have documented different dispersal patterns related to the phenotypic characteristics of individuals (but see Cote and Clobert 2010; Solmsen et al. 2011). Indeed, such heterogeneity at the individual scale is difficult to detect in natural populations due to lack of information on individual phenotype and history.

Alternative strategies describe major heterogeneity in life-history and/or behavioral traits between individuals (Sinervo and Svensson 1998; Zera and Harshman 2001), often associated with discrete conspicuous signals (e.g., morphological or color polymorphism; Gross 1996; Brockmann 2001; Roulin 2004). Because information on individual phenotypic differences is made directly available through the existence of such signals, alternative strategies thus provide a convenient framework to study the relationship between individual heterogeneity and dispersal decisions. In particular, dispersal decisions of alternative strategies are expected to be strongly influenced by the social composition of the local environment. Indeed, the fitness of alternative strategies depends on the frequency of the interactions, they have with one another (Henson and Warner 1997; Gross and Repka 1998; Brockmann 2001; Bleay et al. 2007). Therefore, adaptive habitat choice decisions at the intrapopulation scale should aim at minimizing the frequency of costly interactions and maximizing the frequency of beneficial ones for each strategy. As a result, both emigration and settlement decisions are predicted to depend on the interaction between an individual's strategy and the social composition of his environment at the spatial scale over which most individual interactions occur (Murren et al. 2001). At

Address correspondence to E. Vercken, Institut National de la Recherche Agronomique, 400 route des Chappes, BP 167, 06903 Sophia Antipolis, France. E-mail: elodie.vercken@sophia.inra.fr.

a larger scale, the spatial structure of the populations is also expected to reflect this heterogeneity in habitat choice decisions, with a phenomenon of spatial niche partitioning between strategies (e.g., Sinervo and Clobert 2003; Formica et al. 2004; Formica and Tuttle 2009).

The common lizard *Lacerta vivipara* is a model system that allows us to test such theoretical expectations about the relationship between alternative strategies and dispersal patterns. Previous studies have demonstrated that local dispersal in this species is sensitive to both kin competition and general competition (Léna et al. 1998; Ronce et al. 1998; Le Galliard et al. 2003; Meylan et al. 2007; Cote and Clobert 2010), through a multiplicity of cues (maternal effects: Massot and Clobert 1995, 2000; Massot et al. 2002; Meylan et al. 2004; Vercken, de Fraipont, et al. 2007; relatedness: Léna et al. 1998; de Fraipont et al. 2000; Léna et al. 2000; Le Galliard et al. 2003; density: Léna et al. 1998; Le Galliard et al. 2003; Lecomte et al. 2004; Cote and Clobert 2007b; public information: Aragón, Massot, et al. 2006; Aragón, Meylan, and Clobert 2006; Cote and Clobert 2007a; Cote, Boudsocq, and Clobert 2008). In addition, a recent work documented that individuals dispersing in response to different selective pressures were characterized by different phenotypes (Cote and Clobert 2010). Dispersal is thus a highly plastic adaptive trait in this species that impacts significantly the distribution of individuals at the local population scale.

In addition, female common lizards display variation in ventral color, which can be classified into 3 color types: yellow, orange, and mixed (Vercken, Massot, et al. 2007; Vercken et al. 2008). This color polymorphism was proposed to signal alternative strategies in reproduction (Vercken, Massot, et al. 2007) and behavior (Vercken and Clobert 2009), and female reproductive success was found to depend on the interaction between female color and her social environment (Vercken et al. 2010). More precisely, the frequency of yellow, dominant females affected negatively the reproductive success of all females, with an increased effect on mixed females (Vercken et al. 2010). Therefore, the dispersal patterns of individuals of different colors at the intrapopulation scale are expected to depend on the composition of their social environment, that is, the frequency of color types in a local neighborhood. However, because natal dispersal in common lizards takes place within the first days of life, before individuals express their ventral color, we assumed that the dispersal patterns of juveniles could be predicted by the ventral color of their mother.

First, we predicted that the decision to leave the natal territory should depend on the interaction between maternal phenotype and the relative frequency of color types in the natal environment (i.e., fitness prospects in the natal territory). As female reproductive success was found to be negatively impaired by the frequency of yellow females in the population (Vercken et al. 2010), we predicted that juveniles should disperse more when their mother had a high frequency of yellow neighbors. This effect was expected to be especially strong for offspring from mixed females, who suffered the highest fitness costs from an increased frequency of yellow females (Vercken et al. 2010). Second, we predicted that the determinants of the settlement decision should also depend on maternal phenotype because dispersers of different colors would have left their natal territory for different reasons. Finally, we predicted that the spatial distribution of adult females should be influenced by these habitat choice decisions and reflect some degree of spatial niche partitioning between color types.

In order to test these predictions, we studied juvenile local dispersal patterns in 4 natural populations. To test whether dispersal responded to the composition of the social environment, we experimentally manipulated color type frequency at the local scale in all populations, and we analyzed the effect of the interaction between maternal color and the color of the social environment on dispersal probability. Then, to identify which elements of the social landscape affected settlement decisions in the different color types, we tested how the post-dispersal environment of dispersing juveniles differed from their natal environment. Finally, to test whether dispersal decisions based on the social environment resulted in significant spatial patterns within populations, we analyzed the distribution of females within these populations before the experimental manipulation to reveal potential color-related spatial structure.

MATERIALS AND METHODS

The species

Lacerta vivipara is a small (adult snout–vent length from 50 to 70 mm) live bearing lacertid lizard, found throughout Europe and Asia. All the study populations are located on Mont Lozère (Southern France, altitude 1420 m). These populations are peatbog or heathland areas surrounded by forest, prairie, or pasture. The distribution of individuals within the populations is relatively homogeneous, with hotspots of density around specific landscape structures like rocks or tree stumps that provide efficient basking spots. As the surrounding habitat is relatively unsuitable for common lizards, the populations are unlikely to experience high levels of emigration or immigration, and we consider them as isolated.

In these populations, adult males emerge from hibernation in mid-April, followed by yearlings, and adult females in mid-May. Mating occurs at female emergence, and gestation lasts for 2 months. Parturition starts in mid-July and lasts for 2 or 3 weeks. Females lay an average clutch of 5 soft-shelled eggs (range 1–12). Offspring hatch within 1 or 2 h after laying and are immediately independent of their mother. The activity season ends in late September, and juveniles are the last to enter hibernation.

In these populations, female ventral color is variable between individuals and ranges from pale yellow to bright orange, whereas males are almost always orange. Juveniles start by being melanic and slowly turn to a pale green ventral coloration when yearlings. Stability of ventral color arises with sexual maturity (usually at 2 years in the Mont Lozère populations). We chose to analyze female color as a discrete variable (yellow, orange, or mixed) because

(i) unlike spectrum components like chroma and hue that vary along time and seem to be open to short-term environmental influences (Cote, Le Galliard, et al. 2008; Vercken et al. 2010), visual classification of females into 3 discrete color classes is stable throughout adult life and heritable within female lineages (Vercken, Massot, et al. 2007), which makes it more likely to correlate with structural differences between individual's phenotype or genotype (Vercken et al. 2008) and

(ii) these color classes were found to correlate with differences in life-history (Vercken, Massot, et al. 2007) and behavioral traits (Vercken and Clobert 2008, 2009) and were proposed to reflect alternative strategies, characteristic of a hawk–dove–bully game (Vercken et al. 2010). Ventral color is not actively displayed by individuals, yet it has been shown to affect social interactions between unfamiliar females in an experimental context (Vercken and Clobert 2009). Such differences between color classes are nonlinear (i.e., mixed individuals do not have intermediate profiles between yellow and orange individuals) and thus are better described by a nonordinal variable.

Juvenile dispersal takes place within the first 10 days of life (Léna et al. 1998), before individuals express their definitive ventral color and is definitive (i.e., juveniles will remain as

adults on their natal or their dispersing site). However, ventral color is partly heritable within female lineages (Vercken, Massot, et al. 2007), thus maternal color could be used as a proxy for the future coloration of female juveniles. Moreover, juvenile dispersal is open to many maternal effects (e.g., Ronce et al. 1998; de Fraipont et al. 2000; Massot and Clobert 2000; Vercken, de Fraipont, et al. 2007), and we could expect females to influence the dispersal pattern of their offspring depending on their own strategy.

Dispersal data

The 4 populations we studied experimentally are distributed along a linear axis (road), 2 nearby populations being separated by 1.2 km on average (minimum: 800 m, maximum: 2 km).

From 2004 to 2006, 773 females were temporarily removed from the 4 populations (251 females in 2004, 282 in 2005, and 240 in 2006). Forty-eight females were captured at least 2 years and 1 female was captured in each of 3 years. Each year, from the end of June, females were captured and kept in the laboratory until parturition. Females were housed in plastic terraria with damp soil, a shelter and received sprayed water 3 times a day. Females were exposed to natural daylight and were heated 6 h/day with an electric bulb. All animals were treated in accordance with "The National Institutes of Health Guide for Care and Use of Laboratory Animals."

We obtained 3029 living juveniles over the 3 years of study. At birth, offspring were marked individually by toe clipping and sexed by counting ventral scales (Lecomte et al. 1992). Toe clipping is known to have no influence on probability of recapture (Massot et al. 1992) and maximal sprint speed in the common lizard (Sorci G, personal communication). Offspring and their mother were then released either in their population of origin or transplanted into another population (see Frequency experiment). Recapture sessions in fall and spring allowed us to map the location of juveniles after dispersal. We recaptured 629 juveniles. Juvenile survival is about 40% during the first 2 months of life (Vercken E, unpublished results), and we achieved about 50% recapture rate on juveniles. Dispersers were defined as individuals for whom the distance moved between the release point and the last recapture point was greater than 30 m (upper 95% confidence limit of the home range diameter). Philopatric individuals were defined as individuals that had moved less than 20 m (average home range diameter) (Clobert et al. 1994; Massot and Clobert 2000). Indeed, the distributions of dispersal distances for the 4 study populations, all show a strong mode around 10–15 m, and a second, smaller mode around 30–40 m (Supplementary File 1). In addition, individuals moving more than 30 m were never found to return to their natal territory. Juveniles that had moved between 20 and 30 m were not assigned any dispersal status and were excluded from the analysis. We obtained effective dispersal status for 503 juveniles (80% of recaptured individuals).

Frequency experiment

There is little evidence of genetic differences between the 4 populations described above based on the analysis of 6 microsatellite markers (Richard M, unpublished data). As the maximum dispersal distance for a lizard is around 100 m, the study populations cannot be connected through direct migration. Female density and relative frequency of color types have been estimated by mark–recapture analyses. Several recapture sessions occurred in 2004, which allowed us to estimate female density with the Lincoln–Petersen index for closed populations. Density estimates in 2005 and 2006 were based on recaptures between years and were calculated from the Cormack–Jolly–Seber model ("mra" package in R, R Development Core Team 2008; McDonald 2012). At the beginning of the study, the 4 study populations differed in female density and in female color type frequencies (Table 1). We distinguished 2 populations with high frequency of orange females ("high-orange" populations, A and B) from 2 populations with high frequency of yellow females ("high-yellow" populations, C and D).

In 2004 and 2005, yellow females captured in high-yellow populations were released with their offspring in high-orange populations, whereas orange females captured in high-orange populations were released with their offspring in high-yellow populations (for sample sizes, see Table 1). Thus, initially high-yellow populations had the frequency of orange females increased (O+ treatment) and initially high-orange populations had the frequency of yellow females increased (Y+ treatment). Frequency of mixed females and total population densities were not modified. In their new population, immigrant females were released at the capture point of a native female that had been transplanted in order not to modify female density at the local scale. There was no effect of transplantation on female survival or body condition, and transplanted females were found to remain on their release site, which confirms the successful settlement of transplanted females (Vercken et al. 2010).

Because the reciprocal transplants were performed in 2004 and 2005, females experienced an "undisturbed" environment in 2004, a "moderately disturbed" environment in 2005, and a "strongly disturbed" environment in 2006 (for the annual estimations of color type frequency, see Table 1). The dispersal rates observed in 2004 were used as references as they were obtained in undisturbed populations, before any experimental manipulation. We analyzed the difference between the dispersal patterns in 2004 and the following years to estimate the effect of the experimental manipulation (see Statistical analyses), independently of annual effects related to the natural variations of the environment that are expected to be the same for all populations regardless of their experimental treatments. This experimental design has been used in this species with success at several occasions (Lorenzon et al. 2001; Massot et al. 2002; Meylan et al. 2007), and the limited number of experimental replicates is compensated by the large sample sizes within each replicate, maximizing the probability that a significant treatment effect will not result from a population effect. In this type of design, the power for detecting a significant effect is relatively weak because we have a strong power to detect interpopulation differences to the detriment of intertreatment effects. Hence, any significant treatment effect should reflect important experimental differences.

Statistical analyses

Response of dispersal rate to the experimental manipulation
Statistical tests were conducted using R (R Development Core Team 2009). Dispersal status was considered as a binomial variable (0: philopatric offspring; 1: disperser). Dispersal was analyzed using generalized linear models and generalized linear mixed-effects models with maximum likelihood estimation (package "lme4"; Bates et al. 2011). We tested 2 different random structures to account for differences between populations: 1) random intercept or 2) random intercept and slope of the relationship with year. Fixed effects included juvenile sex and snout-vent length (SVL), ventral color of the mother, year, and frequency treatment in the population of origin and the interactions of year by treatment and year by ventral color. Interactions between ventral color and treatment were not analyzed because of unbalanced design (few yellow females in O+ populations and few orange females in Y+ populations). A significant year effect alone

Table 1
Description of the experimental manipulation and its consequences on the social environment

Population	A	B	C	D
Adult female population size (SE) in 2004/2005/2006	160(18)/175(51)/135(38)	140(9)/180(61)/105(40)	175(29)/165(72)/140(51)	100(12)/155(50)/120(31)
Orange/yellow female frequency in 2004	0.42/0.36	0.4/0.25	0.2/0.37	0.21/0.42
Number of transplanted females in 2004	25 orange females and 125 juveniles to population D	26 orange females and 93 juveniles to population C	26 yellow females and 90 juveniles to population B	25 yellow females and 105 juveniles to population A
Orange/yellow female frequency in 2005	0.34/0.44	0.31/0.34	0.33/0.3	0.27/0.3
Number of transplanted females in 2005	19 orange females and 128 juveniles to population D	23 orange females and 78 juveniles to population C	23 yellow females and 105 juveniles to population B	19 yellow females and 120 juveniles to population A
Orange/yellow female frequency in 2006	0.28/0.5	0.25/0.4	0.44/0.19	0.31/0.26

Female population size was estimated from the Lincoln–Petersen Index in 2004 and from the Cormack–Jolly–Seber model using "mra" package in R in 2005 and 2006. SE, standard error.

would mean that only annual effects related to the natural variations of the environment are responsible for differences between the parameters observed in 2004 and the parameters observed in 2005 or 2006. A significant year by treatment effect would mean that the frequency treatments have affected juvenile dispersal in comparison with the reference year, with different effects for the 2 treatments that cannot be explained by annual variation only. A significant year by mother's ventral color would mean that the annual trend in juvenile dispersal differs between offspring from mothers of different color types.

Following Zuur et al. (2009), we selected random structure first by comparing models, including all fixed effects (Table 2), then we selected fixed effects by comparing models, including the best random structure (Supplementary File 1). For transplanted females, frequency treatment could be defined either as the prenatal environment (population of origin) or the postnatal environment (population of release). We used either one or the other (Table 2; Supplementary File 2a,b) in all analyses: postnatal environment gave consistently better fit, but all trends were conserved between analyses. The same results were obtained when excluding the offspring of transplanted females from the analyses. When comparing the models including different combinations of fixed effects, individual sex and SVL were always included or removed at the same time, considering they describe individual phenotype.

All model comparisons were based on lowest Akaike's Information Criterion (AIC). The selected model included no random effects, and overdispersion was not significant, thus we used classical generalized linear models. Likelihood ratio tests (χ^2 values) and type III sum of squares were used to interpret fixed effects.

Comparison of predispersal and postdispersal environments
Because the composition of the population had been modified between female gestation and offspring dispersal in 2004 and 2005, we used only data from 2006 for this analysis. We described the composition of the predispersal and postdispersal environment of juveniles as the number of females and the frequency of yellow and orange females within a 20, 15, or 10-m range around the mother's release point (predispersal environment) or the juvenile recapture point (postdispersal environment).

All analyses gave consistent results over this distance range, with higher significance for the 15-m range, which also correspond to the core of a female's home range (Clobert et al. 1994; Meylan et al. 2007). Therefore, we report only the results for the 15-m distance range, which likely reflects the scale of most repeated social interactions. We analyzed the difference in predispersal and postdispersal environments for each color type (total number of females and the frequency of yellow and orange females) with nonparametric paired Wilcoxon signed-rank tests.

Juveniles make active dispersal and settlement decisions based on their experience of the environment (Léna et al. 1998; de Fraipont et al. 2000), therefore, the determinants of habitat choice can be inferred from the comparison between their natal environment and the environment they settle in. Females are direct competitors of juveniles and yearlings, thus the total number of females is an indicator of the overall level of intraspecific competition at the local scale (Léna et al. 1998), whereas the frequency of yellow and orange females reflects specialized competition between strategies (Vercken et al. 2010).

Spatial distribution of females
We analyzed the distribution of females in 2004 (before any manipulation of the social environment) using a bivariate

Table 2

Selection of random structure for models of juvenile dispersal response

Random structure	Treatment: postnatal environment		Treatment: prenatal environment	
	AIC	ΔAIC	AIC	ΔAIC
Random intercept and slope (year)	647.3	6.2	649.9	8.8
Random intercept	643.4	2.3	646.0	4.9
No random structure	641.1	0	643.4	2.3

Fixed effects: year + color + treatment (prenatal or postnatal environment) + sex + length + year:treatment + year:color.

point pattern analysis (Programita software, Wiegand and Moloney 2004). We calculated Ripley's L function (Ripley 1981) with a 1-m^2 grid for the distribution of each color morph (class 1) in comparison with the distribution of the other 2 morphs (joined in class 2). The difference $L_{11} - L_{12}$ evaluates whether individuals of class 1 tend to be surrounded by other individuals of class 1 at different distances. A positive difference $L_{11}(r) - L_{12}(r)$ indicates that circles of radius r around individuals of class 1 contain relatively more class 1 than class 2 individuals. We calculated confidence intervals (CIs) using a null model of random labeling, which assumes that the 2 classes of individuals have a random structure within the given spatial structure of the joined pattern (Bailey and Gatrell 1995; Goreaud and Pélissier 2003). Because preliminary analyses revealed no difference in patterns between populations, we analyzed the 4 populations as combined replicates in order to increase the sample size (Diggle 2003; Illian et al. 2008).

RESULTS

Response of dispersal rate to the experimental manipulation

Juvenile dispersal was affected by the interactions between year and 1) frequency treatment ($\chi_1^2 = 5.41$, $P = 0.020$) and 2) maternal color ($\chi_2^2 = 11.72$, $P = 0.003$). Juveniles from orange or mixed mothers tended to disperse less in Y+ populations in comparison with O+ populations, whereas the opposite pattern was found for juveniles from yellow mothers (Figure 1). Although the same trend was present in 2005, this difference became significant in 2006 only, when the manipulation of color type frequencies was maximal.

Comparison of predispersal and postdispersal environments

The experimental treatment at the population level had no effect on individual settlement decisions: the same results were obtained when analyzing Y+ and O+ populations separately or together, thus we pooled individuals from different populations in the final analysis to increase statistical power.

First, dispersing offspring from females of all color types settled in local environments where there were fewer females than in their prenatal environment (offspring from yellow females: $V = 137.5$, $P = 0.002$, $n = 19$; offspring from orange females: $V = 70$, $P = 0.008$, $n = 13$; offspring from mixed females: $V = 96$, $P = 0.003$, $n = 16$; Figure 2, top). In a heterogeneous environment, such a pattern could result from random distribution of individuals: if individuals tend to leave from most crowded areas, they are likely to settle in less crowded areas just by chance. To rule out this hypothesis, we simulated the random distribution of 10 000 individuals within the populations while eliminating the locally empty areas considered as unsuitable habitat. The 95% CI of the number of female neighbors in these simulations
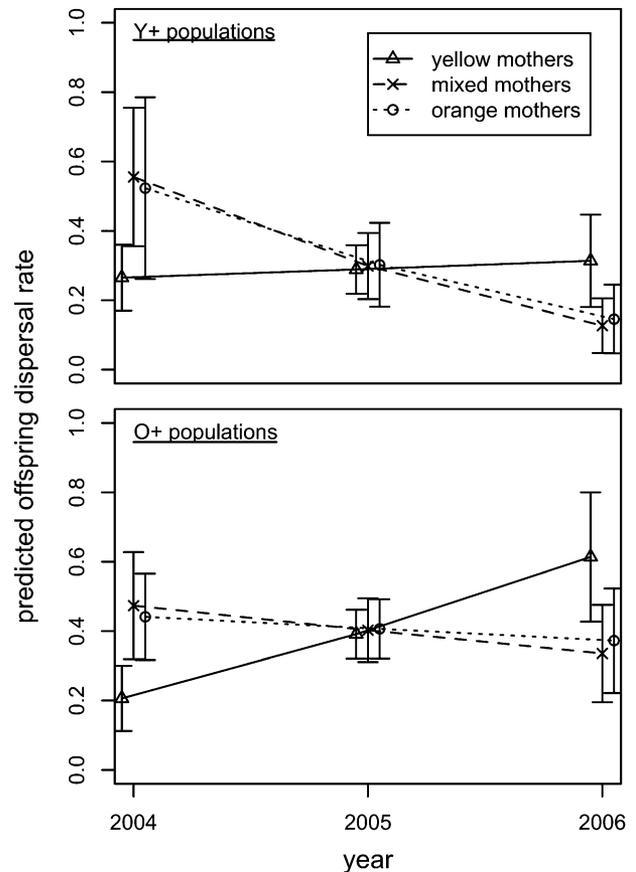
Figure 1
Model fit for offspring dispersal for yellow, mixed, and orange mothers in O+ (increased frequency of orange females) and in Y+ (increased frequency of yellow females) populations in 2004, 2005, and 2006. Error bars are 95% CIs.

was significantly higher than the number of female neighbors we observed for dispersing individuals, thus indicating active habitat selection by dispersers.
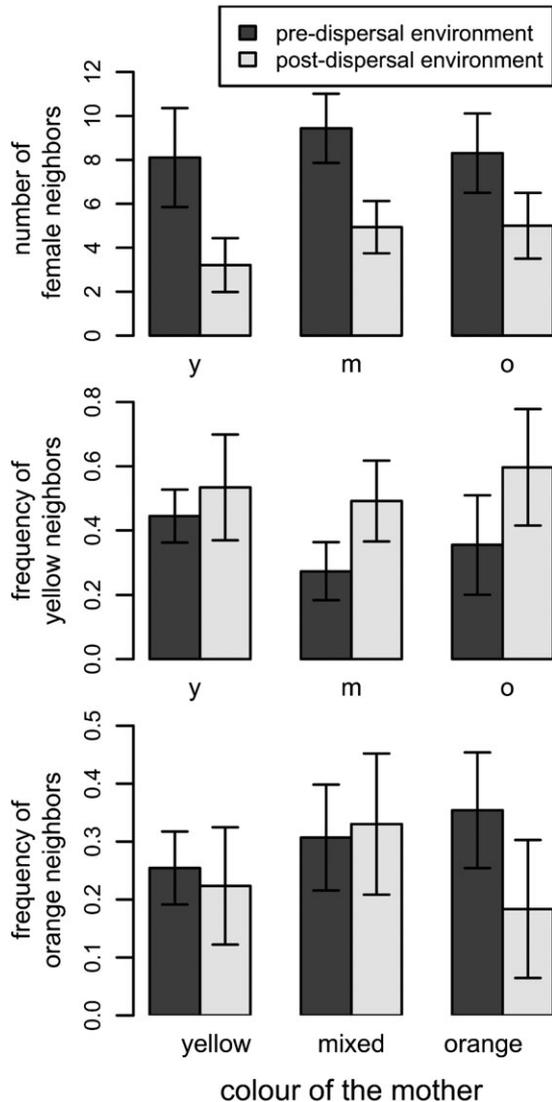
Figure 2, middle, shows that offspring from orange and mixed females tended to settle in environments with higher frequency of yellow females (offspring from orange females: $V = 16$, $P = 0.039$, $n = 13$; offspring from mixed females: $V = 12.5$, $P = 0.007$, $n = 16$), whereas it was not the case for offspring from yellow females ($V = 53$, $P = 0.138$, $n = 19$). Offspring from orange females also tended to settle in environments with lower frequency of orange females ($V = 64$, $P = 0.027$, $n = 13$), whereas it was not the case for offspring from yellow ($V = 77$, $P = 0.500$, $n = 16$) or mixed females ($V = 44$, $P = 0.714$, $n = 19$; Figure 2, bottom).

Spatial distribution of females

Yellow and mixed females showed no pattern of spatial autocorrelation, either positive or negative (Figure 3, top, middle). For orange females, the difference $L_{11} - L_{12}$ was significantly positive for distances between 2 and 4 m (Figure 3, bottom), which indicates positive autocorrelation within this distance, that is, orange females are spatially associated at small spatial scale.

DISCUSSION

By manipulating the composition of the social environment, we demonstrated that its interaction with individual phenotype
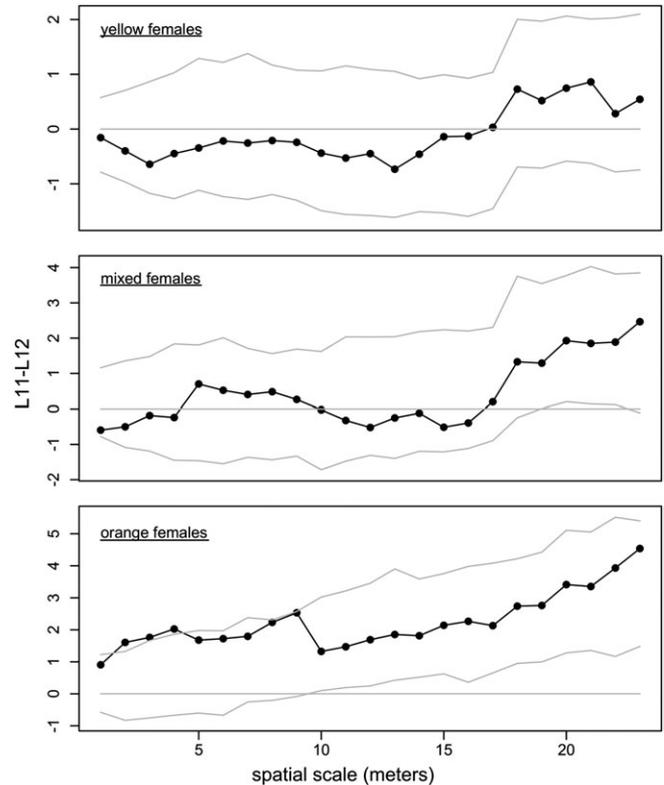
Figure 2
Average number of neighbors (top) and frequency of yellow (middle) and orange females (bottom) in predispersal (dark bars) and postdispersal environments (light bars) for offspring from each color type in 2006. Error bars are 95% CIs.

affected dispersal decisions. All individuals who dispersed chose to settle in less crowded environments than their natal ones. General competition for space and resources is thus a strong determinant of habitat choice. In addition, offspring from orange or mixed females dispersed less when the frequency of yellow females in the population had been increased, and those who dispersed chose to settle in environments with higher frequency of yellow females than their natal neighborhood. Because the frequency of yellow females was manipulated experimentally, we can conclude that the local frequency of yellow females was used as a direct cue for dispersal decisions. This result confirms the importance of the frequency of female color types as a key parameter of the social environment in this species.

Habitat choice: a trade-off between environment quality and competition intensity?

Female ventral color is thought to indicate dominance status (Vercken and Clobert 2008, 2009), and yellow females were

Figure 3
Evolution of the difference $L_{11} - L_{12}$ and its 95% CI for increasing spatial scales for yellow, mixed, and orange females (combined analysis of the 4 populations). A positive difference indicates spatial aggregation.

proposed to be the strongest competitors (hawk strategy, Vercken et al. 2010). If weaker competitors like orange and mixed females suffer high costs from competition with yellow females, we would expect offspring from orange or mixed females to avoid environments where yellow females are frequent. However, we observe the opposite pattern, with dispersing offspring from orange and mixed females selecting environments with high frequency of yellow females and low density. A potential explanation for this result is based on the ideal free distribution theory: when individuals differ in their competitive ability in a heterogeneous environment, it is predicted that the best competitors will be more frequent in high-quality habitats (Parker and Sutherland 1986; Sutherland 1996; Doncaster et al. 1997). According to this theory, dominant yellow females are expected to occupy the highest quality territories: in this case, if dispersing offspring from orange or mixed females select high-quality habitats they should settle in environments with high frequency of yellow females. By also choosing low-density habitats, offspring from orange or mixed females might be able to compensate for the increased competitive pressure due to the high frequency of yellow females. Such heterogeneous distribution of unequal competitors according to environment quality was found in several systems with 2 competing species (Pimm et al. 1985; Berec et al. 2006; Franke et al. 2006). At the intraspecific level, several examples exist where continuous variation in a phenotypic trait determines the competitive ability of individuals (e.g., size-dependent habitat choice, Primicerio 2003; Hammond et al. 2007), yet this is one of the first examples that we know of involving a discrete polymorphism of strategies.

Public information and dispersal decisions

In addition, it seems that the presence of yellow females is used directly as an indicator of environment quality for juveniles from orange or mixed females (public information, Bell 1991; Danchin et al. 2004). If the presence of yellow females is used as cue for habitat quality, then we expect dispersal rate to decrease in populations where the frequency of yellow females was increased. This is exactly what we observe, which suggests that offspring born in populations where the frequency of yellow females was increased experienced a positive signal of environment quality that affected their dispersal decisions. Public information is recognized as a common way to assess habitat quality at low costs for the individual, yet in most cases, habitat quality is estimated from the reproductive success of neighboring conspecifics (Danchin et al. 1998; Parejo et al. 2007; Boulinier et al. 2008; Calabuig et al. 2008), alone or in combination with environmental predictors (Part et al. 2011; Robinson et al. 2011). In contrast, this study is the first to suggest that heterogeneity in individual phenotypes can be used as an indicator of environment quality, independently of other cues directly related to reproductive success.

The use of public information related to habitat quality for dispersal decisions in our system is further supported by the fact that, although offspring from yellow females are expected to select the highest quality habitats, they were the only ones not to settle in environments with higher frequency of yellow females than their natal environment. On the contrary, if yellow female frequency is to be a reliable indicator of environment quality for orange and mixed females, then yellow females must select actively their habitat using more direct cues, and the dispersal or settlement decisions of offspring from yellow females should not be based on yellow female frequency. In this scenario, offspring from yellow females would be more likely to colonize new, less crowded territories, where they would avoid competition with other dominant individuals ("colonizer strategy"; Cote and Clobert 2007a). On the other hand, offspring from orange or mixed females would follow secondarily the distribution of yellow females ("joiner strategy"; Clobert et al. 2009), thus avoiding the costs of direct exploration of the environment and assessment of its quality. Such alternative colonization behaviors have been suggested in other vertebrate species (Ebenhard 1990), sometimes in association with other behavioral traits (e.g., aggression, Duckworth and Badyaev 2007; boldness, Kurvers et al. 2010). However, this study provides the first evidence for such colonization behaviors coexisting within populations in association with larger alternative strategies, with potential consequences on population spatial dynamics.

Spatial structure of natural populations

Dispersal distances in common lizards are typically between 30 and 100 m, whereas the areas of the populations we studied range between 5500 and 8000 m^2 (95–115 m long, 50–70 m wide). Individual dispersal behavior is thus on the same scale as maximal intrapopulation distances and has the potential to affect directly distribution patterns at the population level (Lima and Zollner 1996). However, although we found that dispersal and settlement decisions responded to the composition of the social environment, color-related dispersal patterns are not a direct predictor of the spatial distribution of color morphs in the field. We found that juveniles from orange females tended to settle in environments with a lower frequency of their own color type than their natal environment, which should result in negative spatial autocorrelation for this color morph. Contrary to this expectation, we found a positive spatial autocorrelation of orange females.

A first hypothesis to explain this discrepancy between habitat choice decisions and effective spatial distribution of individuals is that spatial structure is more strongly impacted by philopatry than by dispersal (Solmsen et al. 2011). Indeed, ventral color in the common lizard was found to be maternally heritable (Vercken, Massot, et al. 2007) so that related females are relatively likely to have the same ventral color. In this study, basal juvenile dispersal rate was found to depend on maternal color (color effect on dispersal in 2004 $\chi_2^2 = 11.91$, $P = 0.003$). In the first year of the study, before the manipulation of color type frequencies, offspring from yellow females were the most philopatric (average dispersal rate around 20–30%), whereas offspring from mixed or orange females were more likely to disperse (average dispersal rate around 50–60%; Figure 1). Therefore, if spatial autocorrelation resulted mostly from high philopatry, we would rather expect this pattern to occur in yellow females, which was not the case. Alternatively, different dispersal distances between color types (with lower distance for offspring from orange females) could also result in different autocorrelation patterns (Gauffre et al. 2009). However, juvenile dispersal distances are independent of maternal color in all study populations ($\chi_2^2 = 4.54$, $P = 0.103$), which rules out this potential explanation.

These results imply that dispersal behavior cannot be the only process shaping the distribution of individuals at the population scale. Even if offspring from orange females are not more philopatric than others, orange females could be more closely associated spatially if they produce more offspring on average and/or if their offspring sex ratio is biased toward females. In this study, we found a marginal effect of female color on fecundity ($\chi_2^2 = 6.47$, $P = 0.039$) and no effect on clutch sex ratio ($\chi_2^2 = 1.24$, $P = 0.538$). Yellow females produced less offspring (3.8 on average) than mixed or orange females (4.2 for both color types). Relatively high offspring philopatry associated with high fecundity in orange females is thus the most likely explanation at present for positive spatial autocorrelation at short distances in this color type. Such a phenomenon would result in fine-scale relatedness structure, which could also be related to the existence of different degrees of kin interactions between color types (Radespiel et al. 2003; Duncan et al. 2010; Davis 2012). Indeed, nonrandom genetic structure between females was reported in other populations of common lizard (Hofmann 2008), but color-related differences were not investigated. Studies to come should focus on elucidating fine-scale genetic spatial structure for the different color types, as a potential component of their alternative strategies.

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REFERENCES

Aragón P, Massot M, Gasparini J, Clobert J. 2006. Socially acquired information from chemical cues in the common lizard, Lacerta vivipara. Anim Behav. 72:965–974.

Aragón P, Meylan S, Clobert J. 2006. Dispersal status-dependent response to the social environment in the Common Lizard, Lacerta vivipara. Funct Ecol. 20:900–907.

Bailey T, Gatrell T. 1995. Interactive spatial data analysis. Harlow (UK): Longman.

Bates D, Maechler M, Bolker B. 2011. lme4: Linear mixed-effects models using S4 classes R package version 0.999375–42. [cited 2012 April 18]. Available from: http://CRAN.R-project.org/package=lme4.

Bell WJ. 1991. Searching behaviour. The behavioural ecology of finding resources. New York: Chapman and Hall.

Berec M, Krivan V, Berec L. 2006. Asymmetric competition, body size, and foraging tactics: testing the ideal free distribution in two competing fish species. Evol Ecol Res. 8:929–942.

Bleay C, Comendant T, Sinervo B. 2007. An experimental test of frequency-dependent selection on male mating strategy in the field. Proc R Soc B Biol Sci. 274:2019–2025.

Boulinier T, Mccoy KD, Yoccoz NG, Gasparini J, Tveraa T. 2008. Public information affects breeding dispersal in a colonial bird: kittiwakes cue on neighbours. Biol Lett. 4:538–540.

Bowler DE, Benton TG. 2005. Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. Biol Rev. 80:205–225.

Brockmann HJ. 2001. The evolution of alternative strategies and tactics. Adv Study Behav. 30:1–52.

Calabuig G, Ortego J, Cordero PJ, Aparicio JM. 2008. Causes, consequences and mechanisms of breeding dispersal in the colonial lesser kestrel, Falco naumanni. Anim Behav. 76:1989–1996.

Clobert J, Danchin E, Dhondt AA, Nichols JD. 2001. Dispersal. Oxford: Oxford University Press.

Clobert J, Ims RA, Rousset F. 2004. Causes, mechanisms and consequences of dispersal. In: Hanski I, Gaggiotti OE, editors. Ecology, genetics and evolution of metapopulations. San Diego (CA): Academic Press. p. 307–335.

Clobert J, Le Galliard J-F, Cote J, Meylan S, Massot M. 2009. Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. Ecol Lett. 12:197–209.

Clobert J, Massot M, Lecomte J, Sorci G, de Fraipont M. 1994. Determinants of dispersal behavior: the common lizard as a case study. In: Vitt LJ, Pianka ER, editors. Lizard ecology: historical and experimental perspectives. Princeton (NJ): Princeton University Press. p. 183–206.

Cote J, Boudsocq S, Clobert J. 2008. Density, social information, and space use in the common lizard (Lacerta vivipara). Behav Ecol. 19:163–168.

Cote J, Clobert J. 2007a. Social information and emigration: lessons from immigrants. Ecol Lett. 10:411–417.

Cote J, Clobert J. 2007b. Social personalities influence natal dispersal in a lizard. Proc R Soc B Biol Sci. 274:383–390.

Cote J, Clobert J. 2010. Risky dispersal: avoiding kin competition despite uncertainty. Ecology. 91:1485–1493.

Cote J, Le Galliard J-F, Rossi J-M, Fitze PS. 2008. Environmentally induced changes in carotenoid-based coloration of female lizards: a comment on Vercken et al. J Evol Biol. 21:1165–1172.

Danchin E, Boulinier T, Massot M. 1998. Conspecific reproductive success and breeding habitat selection: implications for the study of coloniality. Ecology. 79:2415–2428.

Danchin E, Giraldeau L-A, Valone TJ, Wagner RH. 2004. Public information: from nosy neighbors to cultural evolution. Science. 305:487–491.

Davis AR. 2012. Kin presence drives philopatry and social aggregation in juvenile Desert Night Lizards (Xantusia vigilis). Behav Ecol. 23:18–24.

Diggle PJ. 2003. Statistical analysis of spatial point patterns. 2nd ed. London: Arnold.

Doncaster CP, Clobert J, Doligez B, Gustafsson L, Danchin E. 1997. Balanced dispersal between spatially varying local populations: an alternative to the source-sink model. Am Nat. 150:425–445.

Duckworth RA, Badyaev AV. 2007. Coupling of dispersal and aggression facilitates the rapid range expansion of a passerine bird. Proc Natl Acad Sci U S A. 104:15017–15022.

Duncan SI, Riechert SE, Fitzpatrick BM, Fordyce JA. 2010. Relatedness and genetic structure in a socially polymorphic population of the spider Anelosimus studiosus. Mol Ecol. 19:810–818.

Ebenhard T. 1990. A colonization strategy in field voles (Microtus agrestis): reproductive traits and body size. Ecology. 71:1833–1848.

Formica VA, Gonser R, Ramsay S, Tuttle E. 2004. Spatial dynamics of alternative reproductive strategies: the role of neighbors. Ecology. 85:1125–1136.

Formica VA, Tuttle EM. 2009. Examining the social landscapes of alternative reproductive strategies. J Evol Biol. 22:2395–2408.

de Fraipont M, Clobert J, John-Alder H, Meylan S. 2000. Increased pre-natal maternal corticosterone promotes philopatry of offspring in common lizards Lacerta vivipara. J Anim Ecol. 69:404–413.

Franke HD, Gutow L, Janke M. 2006. Flexible habitat selection and interactive habitat segregation in the marine congeners Idotea baltica and Idotea emarginata (Crustacea, Isopoda). Marine Biol. 150:929–939.

Gauffre B, Petit E, Brodier S, Bretagnolle V, Cosson JF. 2009. Sex-biased dispersal patterns depend on the spatial scale in a social rodent. Proc R Soc B Biol Sci. 276:3487–3494.

Goreaud F, Pélissier R. 2003. Avoiding misinterpretation of biotic interactions with the intertype K12-function: population independence vs. random labelling hypotheses. J Veg Sci. 14:681–692.

Gross MR. 1996. Alternative reproductive strategies and tactics: diversity within sexes. Trends Ecol Evol. 11:92–98.

Gross MR, Repka J. 1998. Game theory and inheritance in the conditional strategy. In: Dugatkin LA, Reeve HK, editors. Game theory and animal behavior. New York: Oxford University Press. p. 168–187.

Hammond JI, Luttbeg B, Sih A. 2007. Predator and prey space use: dragonflies and tadpoles in an interactive game. Ecology. 88:1525–1535.

Hanski I. 2001. Population dynamic consequences of dispersal in local populations and in metapopulations. In: Clobert J, Danchin E, Dhondt AA, Nichols JD, editors. Dispersal. Oxford: Oxford University Press. p. 283–298.

Henson SA, Warner RR. 1997. Male and female alternative reproductive behaviors in fishes: a new approach using intersexual dynamics. Ann Rev Ecol Syst. 28:571–592.

Hofmann S. 2008. Who is sitting next to me? Relatedness between next neighbours in common lizards. Amphib Reptil. 29:19–24.

Illian J, Penttinen A, Stoyan H, Stoyan D. 2008. Statistical analysis and modelling of spatial point patterns. Chichester (UK): Wiley.

Johnson ML, Gaines MS. 1990. Evolution of dispersal: theoretical models and empirical tests using birds and mammals. Ann Rev Ecol Syst. 21:449–480.

Kurvers RHJM, van Oers K, Nolet BA, Jonker RM, van Wieren SE, Prins HHT, Ydenberg RC. 2010. Personality predicts the use of social information. Ecol Lett. 13:829–837.

Lecomte J, Boudjemadi K, Sarrazin F, Cally K, Clobert J. 2004. Connectivity and homogenisation of population sizes: an experimental approach in Lacerta vivipara. J Anim Ecol. 73:179–189.

Lecomte J, Clobert J, Massot M. 1992. Sex identification in juveniles of Lacerta vivipara. Amphib Reptil. 13:21–25.

Le Galliard J-F, Ferrière R, Clobert J. 2003. Mother-offspring interactions affect natal dispersal in a lizard. Proc R Soc B Biol Sci. 270:1163–1169.

Léna J-P, Clobert J, de Fraipont M, Lecomte J, Guyot G. 1998. The relative influence of density and kinship on dispersal in the common lizard. Behav Ecol. 9:500–507.

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.

Lima SL, Zollner PA. 1996. Towards a behavioral ecology of ecological landscapes. Trends Ecol Evol. 11:131–135.

Lorenzon P, Clobert J, Massot M. 2001. The contribution of phenotypic plasticity to adaptation in Lacerta vivipara. Evolution. 55:392–404.

Massot M, Clobert J. 1995. Influence of maternal food availability on offspring dispersal. Behav Ecol Sociobiol. 37:413–418.

Massot M, Clobert J. 2000. Processes at the origin of similarities in dispersal behaviour among siblings. J Evol Biol. 13:707–719.

Massot M, Clobert J, Lorenzon P, Rossi J-M. 2002. Condition-dependent dispersal and ontogeny of the dispersal behaviour: an experimental approach. J Anim Ecol. 71:253–261.

Massot M, Clobert J, Pilorge T, Lecomte J, Barbault R. 1992. Density dependence in the common lizard: demographic consequences of a density manipulation. Ecology. 73:1742–1756.

McDonald T. 2012. Package mra: analysis of mark-recapture data R package version 2.2. [cited 2012 April 18]. Available from: http://CRAN.R-project.org/package=mra.

Meylan S, Clobert J, Sinervo B. 2007. Adaptive significance of maternal induction of density-dependent phenotypes. Oikos. 116:650–661.

Meylan S, de Fraipont M, Clobert J. 2004. Maternal size and stress and offspring philopatry: an experimental study in the common lizard (Lacerta vivipara). Ecoscience. 11:123–129.

Murren CJ, Julliard R, Schlichting CD, Clobert J. 2001. Dispersal, individual phenotype, and phenotypic plasticity. In: Dispersal. Oxford: Oxford University Press. p. 261–272.

Parejo D, White J, Clobert J, Dreiss A, Danchin E. 2007. Blue tits use fledgling quantity and quality as public information in breeding site choice. Ecology. 88:2373–2382.

Parker GA, Sutherland WJ. 1986. Ideal free distributions when individuals differ in competitive ability: phenotype-limited ideal free models. Anim Behav. 34:1222–1242.

Part T, Arlt D, Doligez B, Low M, Qvarnstrom A. 2011. Prospectors combine social and environmental information to improve habitat selection and breeding success in the subsequent year. J Anim Ecol. 80:1227–1235.

Pimm SL, Rosenzweig ML, Mitchell W. 1985. Competition and food selection: field tests of a theory. Ecology. 66:798–807.

Primicerio R. 2003. Size-dependent habitat choice in Daphnia galeata Sars and size-structured interactions among zooplankton in a subarctic lake (lake Lombola, Norway). Aquat Ecol. 37:107–122.

Radespiel U, Lutermann H, Schmelting B, Bruford MW, Zimmermann E. 2003. Patterns and dynamics of sex-biased dispersal in a nocturnal primate, the grey mouse lemur, Microcebus murinus. Anim Behav. 65:709–719.

R Development Core Team. 2009. R: a language and environment for statistical computing. [Internet]. Vienna: R Foundation for Statistical Computing. [cited 2012 April 18]. Available from: http://www.R-project.org.

Ripley BD. 1981. Spatial statistics. New York: Wiley.

Robinson BG, Larsen KW, Kerr HJ. 2011. Natal experience and conspecifics influence the settling behaviour of the juvenile terrestrial isopod Armadillidium vulgare. Can J Zool. 89:661–667.

Ronce O, Clobert J, Massot M. 1998. Natal dispersal and senescence. Proc Natl Acad Sci U S A. 95:600–605.

Roulin A. 2004. The evolution, maintenance and adaptive function of genetic colour polymorphism in birds. Biol Rev. 79:815–848.

Sinervo B, Clobert J. 2003. Morphs, dispersal behavior, genetic similarity, and the evolution of cooperation. Science. 300:1949.

Sinervo B, Svensson E. 1998. Mechanistic and selective causes of life history trade-offs and plasticity. Oikos. 83:432–442.

Solmsen N, Johannesen J, Schradin C. 2011. Highly asymmetric fine-scale genetic structure between sexes of African striped mice and indication for condition dependent alternative male dispersal tactics. Mol Ecol. 20:1624–1634.

Sutherland WJ. 1996. From individual behaviour to population ecology. Oxford: Oxford University Press.

Vercken E, Clobert J. 2008. Ventral colour polymorphism correlates with alternative behavioural patterns in female common lizards (Lacerta vivipara). Ecoscience. 15:320–326.

Vercken E, Clobert J. 2009. The role of colour polymorphism in social encounters among female common lizards. Herpetol J. 18:223–230.

Vercken E, Clobert J, Sinervo B. 2010. Frequency-dependent reproductive success in female common lizards: a real-life hawk-dove-bully game? Oecologia. 162:49–58.

Vercken E, de Fraipont M, Dufty AM, Clobert J. 2007. Mother's timing and duration of corticosterone exposure modulate offspring size and natal dispersal in the common lizard (Lacerta vivipara). Horm Behav. 51:379–386.

Vercken E, Massot M, Sinervo B, Clobert J. 2007. Colour variation and alternative reproductive strategies in females of the common lizard Lacerta vivipara. J Evol Biol. 20:221–232.

Vercken E, Sinervo B, Clobert J. 2008. Colour variation in female common lizards: why we should speak of morphs, a reply to Cote et al. J Evol Biol. 21:1160–1164.

Wiegand T, Moloney KA. 2004. Rings, circles, and null-models for point pattern analysis in ecology. Oikos. 104:209–229.

Zera AJ, Harshman LG. 2001. The physiology of life-history trade-offs in animals. Ann Rev Ecol Syst. 32:95–126.

Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM. 2009. Mixed effects models and extensions in ecology with R. New York: Springer.