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Effect of patch occupancy on immigration in the common lizard

JEAN-FRANÇOIS LE GALLIARD*, RÉGIS FERRIÈRE*† and JEAN CLOBERT*

**Laboratoire Fonctionnement et Evolution des Systèmes Ecologiques, Ecole Normale Supérieure, 46 rue d'Ulm, 75005 Paris, France; and †Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, Arizona 85721, USA*

Summary

1. Colonization is critical to invasion propensity and the viability of fragmented populations. This study evaluates the behavioural and demographic effects of patch occupancy on immigration in the common lizard (*Lacerta vivipara*).
2. We manipulated connected two-patch systems during one year. Two treatments were contrasted: both patches initially occupied vs. one occupied patch connected to one empty patch. Effects of manipulation were measured on emigration from occupied patches, on settlement in arrival patches and on demographic parameters in residents and immigrants.
3. Settlement probability was not influenced by the presence of conspecifics, but unsettled lizards stayed longer in initially empty than in occupied patches. The relationship between yearlings' body condition and emigration probability was affected by the manipulation, indicating that different yearlings disperse depending upon metapopulation structure.
4. Growth and maturation rate were influenced positively in juveniles colonizing empty patches, whereas there was no difference between immigrants to occupied patches and residents. Faster growth allowed female juvenile immigrants to reproduce earlier during colonization. No effect on growth or reproduction was detected in yearlings and adults. Selective benefits of colonization at the juvenile stage may provide an ultimate explanation for why natal dispersal prevails over breeding dispersal in this species.
5. At the population level, immigration and increased reproductive recruitment led to higher population growth in colonized patches. This may contribute to the species' capacity to develop and maintain a wide geographical distribution.

Key-words: colonization, habitat selection, *Lacerta vivipara*, metapopulation.

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Introduction

Dispersal is under the influence of multiple selective pressures (Perrin & Goudet 2001). Identifying these pressures is important because dispersal is key to the persistence of fragmented populations and to the invasion of new habitats (Levins 1969; Ebenhard 1991; Hanski 1999). Even in uniform landscapes, selection for dispersal can occur as a result of spatial and temporal variation in local population size and structure (Cadet *et al*. 2003). Levins' notion of a metapopulation offers the simplest approximation of this variation by assuming that patches can switch between empty states (following on extinction and prior to colonization) and occupied states (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* when the arrival patch is initially empty of congeners (Ebenhard 1991; Ims & Yoccoz 1997). Understanding the proximate and ultimate factors of dispersal therefore requires comparing immigration between these two cases.

The presence of conspecifics can be beneficial to immigrants if residents decrease the costs of settlement in unfamiliar habitats [review in Greene & Stamps (2001), 'costly colonization' scenario]. For example, immigrants can cue on residents to select suitable sites (Stamps 1987). Similarly, augmentation can yield benefits to adult immigrants through positive density dependence arising

Correspondence: Jean-François Le Galliard, University of Oslo, Centre for Ecological and Evolutionary Synthesis, PO Box 1050 Blindern, NO-0316 Oslo, Norway. Tel: +47 22857289; Fax: +47 22854605; E-mail: j.f.l.galliard@bio.uio.no

from reproductive interactions, i.e. Allee effects (e.g. Veit & Lewis 1996). However, augmentation entails that immigrants will face accrued competition for limiting resources directly with individuals already present in the patch and later with other immigrants [review in Lambin, Aars & Piertney (2001), 'beneficial colonization' scenario]. Immigrants may even suffer from asymmetric competition due to a prior-resident advantage explained by familiarity with the habitat or social dominance (Anderson 1989; Massot *et al*. 1994). For example, enclosed prairie voles (*Microtus ochrogaster* Wagner) immigrating into empty patches survive and reproduce better than residents (Johnson & Gaines 1985, 1987). To our knowledge, however, no experiment has attempted to evaluate the potential benefits and costs of immigration by measuring specifically the demographic consequences of immigration associated with colonization vs. augmentation.

The settlement behaviour of dispersers may also differ during augmentation vs. colonization (Smith & Peacock 1990; Doligez *et al*. 2003). Specifically, individuals may adopt three distinct patch-choice strategies. First, settlement could be independent of patch occupancy, as most metapopulation models assume (Levins 1969; 'random settlement' scenario). Secondly, settlement could involve a preference for occupied sites ('social attraction' scenario), as a response to the presence of conspecifics (Stamps 1991) or to the public information on local reproductive performance, assessed by the density of juveniles present in a patch (Danchin, Heg & Doligez 2001). A contrasting, third settlement strategy could involve aggressive interactions or competition with residents and result in repulsion from already occupied sites. This phenomenon has been described as the 'social fence' scenario by Hestbeck (1982). Within a population, immigrants can use the presence of conspecifics as a cue for territory choice (Stamps 1987). Among local populations, patch selection based on public information has been suggested in several birds (e.g. Doligez, Danchin & Clobert 2002). Only two population-level experiments have addressed the effect of presence of conspecifics on settlement in vertebrates and they supported a social-fence mechanism (Danielson & Gaines 1987; Gundersen, Andreassen & Ims 2002). However, both studies were based on the translocation of individuals into either empty or occupied populations, meaning that they investigated emigration behaviour following artificial transfer rather than immigration behaviour following voluntary dispersal (*sensu* Ims & Yoccoz 1997). Extrapolating these results to predict the effects of presence of conspecifics on settlement in natural populations is problematic. Indeed, dispersers are not a random subset of the population and have been shown to interact with conspecifics differently from residents (Swingland 1983). Therefore, a better understanding of the effect of presence of conspecifics on habitat-choice strategies raises the need for population-level experiments comparing the settlement behaviour of natural immigrants depending on patch occupancy.

Here, we report on the short-term behavioural and demographic consequences of presence of conspecifics on immigration in the common lizard (*Lacerta vivipara* Jacquin). We designed two types of experimental two-patch systems: an 'augmentation' treatment, in which both patches were populated initially with lizards; and a 'colonization' treatment, in which one occupied patch is connected to an initially empty patch. Movements were then allowed between the two patches of each system during 1 year. We studied the effect of presence of conspecifics on the probability to settle and the time spent in a patch. We analysed the dependence of several life-history traits (growth, survival and reproduction) upon immigration status (resident or immigrant) and treatment. Because differences in metapopulation structure may also influence departure behaviour, we studied the effects of treatment on the emigration pattern.

Materials and methods

STUDY ORGANISM

The common lizard is a small viviparous species inhabiting most humid habitats across northern Eurasia (Surget-Groba *et al*. 2001). Three age classes can be distinguished according to size and secondary sexual characters: juveniles (year-born individuals), yearlings and adults. In our study site, individuals are active from mid-February to November. Mating occurs in March during 2–3 weeks. Mated females complete gestation in almost 3 months and lay on average five shell-less eggs (range 1–12). Hatchlings are autonomous at birth and parents do not provide care. Natal dispersal starts a few days after birth and is five to 10 times more prevalent than breeding dispersal in natural populations (Massot *et al*. 2002).

EXPERIMENTAL SYSTEM

The experimental system consisted of seven units of two patches located at the Ecological Research Centre of Foljuif (Seine et Marne, France, 48°17′N, 2°41′E). Each unit is made of two enclosed patches (10 m × 10 m) connected by 20-m long one-way corridors used by lizards to disperse from one patch to the other within the same unit (Fig. 1). The scale of this system is consistent with dispersal distances in natural populations (Clobert *et al*. 1994; Lecomte & Clobert 1996; Le Galliard, Ferrière & Clobert 2003). The experimental system is described in more detail in Boudjemadi *et al*. (1999).

EXPERIMENTAL DESIGN

The experiment was started in June 2001 and the early colonization process was studied by monitoring all experimental patches until June 2002. Two types of units were established at the start of the experiment: two connected, occupied patches (augmentation treatment, two

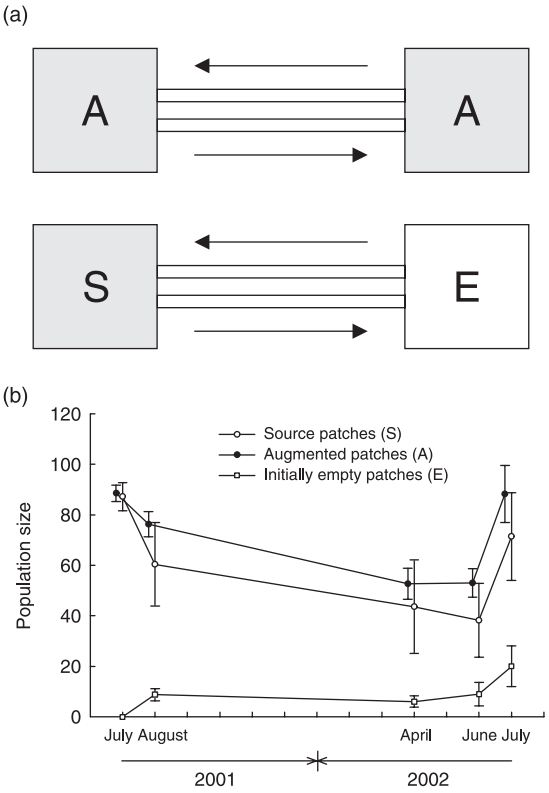

Fig. 1. Experimental design and population dynamics. (a) Augmentation units connect two occupied patches (A). Colonization units connect a source patch (S) with an initially empty patch (E). The two patches are connected by one-way corridors. (b) Population dynamics in the three types of patch during the study year (mean population size ± SD). The data point in July 2002 corresponds to the number of individuals surviving until June 2002 plus the number of newborn.

replicates), or one occupied patch connected to one empty patch (colonization treatment, five replicates). Thus, there were three different types of patches (Fig. 1): augmented patches, occupied initially and connected to similar, occupied patches (denoted by A, four replicates); source patches, occupied initially and connected to an initially empty patch (S, five replicates); and initially empty patches (E, five replicates).

Lizards were originally captured in May 2001 in two populations. One sample came from populations maintained at the Research Centre since 1999 (60 m asl, sample called Fo, $n = 175$). Another sample came from a natural population in the Cévennes, Southern France (1400–1600 m asl, sample called Cv, $n = 164$). All lizards were kept in individual terraria until females gave birth. Body size (from snout to vent, to the nearest mm) and body mass (to the nearest mg) were recorded. Offspring sex was determined by counting ventral scales (Lecomte, Clobert & Massot 1992). A body-condition index was measured as the residual of the linear regression of body mass against body size. We released all individuals during June and July 2001 into units with which they had no prior familiarity. Sixteen yearlings were introduced into each population, involving three Fo and five Cv males, and three Fo and five Cv females. Also, five adult males from each sample, 10 postgravid females along with their offspring, and one non-reproductive female were released per patch (seven to eight Fo and three to four Cv females per patch). All lizards were given a unique code by toe-clipping. Body size, body condition, sex ratio and litter size did not differ between treatments at the start of the manipulation (ANOVAS of treatment effect, all $P > 0{\cdot}3$).

CENSUS AND SAMPLING EFFORT

Movements were monitored daily from July to November 2001 (summer 2001) and from March to June 2002 (spring 2002) by inspecting pitfall traps at the end of each corridor. Dispersers were released into the patch to which they were heading. Individuals were also captured in all patches in August 2001 (3 recapture days), September 2001 (1 recapture day) and April 2002 (2 recapture days). All individuals were captured in June 2002 and females were isolated in individual terraria to study reproduction characteristics. In summer 2001 and spring 2002 we defined three classes of individuals: *residents* (lizards captured at least once during the period and never caught in a pitfall trap), *immigrants* (dispersers that settled down in their arrival patch) and *transients* (dispersers that moved at least twice between patches).

Because statistical comparisons of individual movements and life-history traits between treatments assume unbiased capture probabilities, we modelled capture probability as a function of treatment, census season and unit using multistrata models (Nichols *et al*. 1992). Models indicated significant seasonal changes in capture probability in all age classes (all $P < 0{\cdot}01$). Capture probabilities were high in August 2001 (> 90%) compared with September 2001 (> 60%) and April 2002 (> 75%). However, there was no bias between treatments (all $P > 0{\cdot}36$).

STATISTICAL METHODS

Colonization dynamics

We estimated population size per age and sex classes from capture–recapture models in August 2001 and April 2002 (Otis *et al*. 1978). Population size and population age and sex structures were then modelled with repeated-measures models with population size in August 2001, April 2002 and June 2002 as repeats. Patch was included as a random effect. Temporal variation was modelled as a within-patch effect using a variance–covariance structure minimizing the Akaike index criterion of a MIXED model in SAS (Littell *et al*. 1996).

Movements

We tested the effects of treatments on settlement in arrival patches and departure from introduction patches. We compared the settlement probability and the time

spent by transient individuals (an index of preference for one type of habitat; see Stamps 2001) between occupied and initially empty patches. We also tested for effects of treatments on departure probability and timing of movements from introduction patches. Settlement and departure probabilities were studied with mixed-effects logistic regressions in SAS (procedure GLIMMIX), including patch as a random effect (Littell *et al*. 1996).

Demographic parameters of immigrants

We studied the consequences of dispersal taking place during summer 2001 in the two treatments (augmentation vs. colonization) on post-summer growth, reproduction in 2002 and postsummer survival. In these analyses, we excluded transients and individuals dispersing in spring 2002. Daily growth rates were calculated for body size and body condition. In the case of body condition, females were excluded because of the confounding effect of reproductive burden. Four descriptors of female reproduction in 2002 were analysed: probability of being gravid, assessed by palpation of the abdominal cavity; total clutch size, measured as the total number of eggs produced; proportion of viable eggs, calculated from the number of aborted eggs within total clutch, and offspring characteristics, i.e. clutch sex ratio, neonate body size and body condition. Thirdly, we measured post-summer survival from dispersal to the end of the experiment assuming that lizards not captured in June 2002 were dead. Data were analysed in SAS with the procedure MIXED for continuous traits and with the procedure GLIMMIX for ratios (Littell *et al*. 1996). In both cases, unit was modelled as a random effect. Residuals of the MIXED models were tested for normality and equality of variances. Results are given as mean ± SE unless otherwise stated.

Results

COLONIZATION DYNAMICS

All initially empty patches were colonized within 1 month (Fig. 1). No colonized patch went extinct during the experiment. From 1 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 (log-linear model, $F_{2,11} = 31{\cdot}4$, $P < 0{\cdot}001$, contrast between initially empty and occupied patches: $P < 0{\cdot}001$). There was no detectable difference between population sizes of source and augmented patches (S: 47·4 ± 18·2 SD, A: 60·7 ± 12·6 SD, contrast: $P = 0{\cdot}23$). From 1 month after introduction, sex and age structure were similar in initially empty, source and augmented patches (logistic models; proportion of males: $F_{2,11} = 0{\cdot}93$, $P = 0{\cdot}42$; proportion of juveniles: $F_{2,11} = 1{\cdot}37$, $P = 0{\cdot}29$).

Population growth rate was calculated as the log-ratio of population size in June 2002 to population size in August 2001. Populations declined in augmented patches (per capita growth rate: $r = -0{\cdot}37 \pm 0{\cdot}08$) and in source patches ($r = -0{\cdot}49 \pm 0{\cdot}06$), while colonized populations increased at the same time ($r = 0{\cdot}26 \pm 0{\cdot}26$; effect of patch type: $F_{2,11} = 5{\cdot}34$, $P = 0{\cdot}02$). Reproductive recruitment, measured as the number of juveniles produced per female in each patch, 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: $P = 0{\cdot}04$). Therefore, the population-growth differential between colonized and other patches was even higher after reproduction took place in 2002 ($F_{2,11} = 6{\cdot}95$, $P = 0{\cdot}01$).

Table 1. Effects of treatments (augmentation or colonization) and patch types (augmented, source or initially empty) on departure and settlement probabilities

Source of variation	*F*-statistic	*P*-value
Summer departure probability		
Age	$F_{2,633} = 1{\cdot}49$	0·23
Sex	$F_{1,633} = 7{\cdot}47$	0·006
Treatment	$F_{1,7} = 0{\cdot}47$	0·51
Spring departure probability		
Age	$F_{2,457} = 3{\cdot}14$	0·04
Sex	$F_{1,457} = 8{\cdot}63$	0·003
Patch type	$F_{2,11} = 1{\cdot}44$	0·28
Summer settlement		
Age	$F_{2,103} = 0{\cdot}81$	0·45
Sex	$F_{1,103} = 2{\cdot}01$	0·16
Treatment	$F_{1,7} = 0{\cdot}32$	0·59

EMIGRATION BEHAVIOUR

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 during summer 2001. Overall, males were 1·8 times more likely to disperse than females, but departure probabilities were not different between treatments (Table 1). The timing of departure was also similar between augmentation and colonization units (effects of age: $F_{2,102} = 12{\cdot}01$, $P < 0{\cdot}001$; sex: $F_{1,102} = 5{\cdot}90$, $P = 0{\cdot}02$; age × sex: $F_{2,102} = 3{\cdot}19$, $P = 0{\cdot}04$; treatment: $F_{1,7} = 0{\cdot}56$, $P = 0{\cdot}48$). Males dispersed earlier in adults and yearlings (contrast between males and females = −17·8 days ± 5·65, $P = 0{\cdot}002$), but not in juveniles (contrast = −3·9 days ± 6·48, $P = 0{\cdot}55$). We also compared departure probability between source, augmented and colonized patches in spring 2002 (Table 1). Of the 474 individuals captured, 45 moved at least once (12 juveniles, 13 yearlings and 20 adults). Yearlings and adults dispersed more than juveniles (odds yearlings and adults : odds juveniles = 2·31, $P = 0{\cdot}02$), and dispersal was male-biased (odds male : odds female = 2·86). However, departure probability was not affected by patch type (Table 1).

In juveniles, there was a positive correlation between departure probability and body condition at birth

irrespective of treatment ($F_{1,303} = 8{\cdot}74$, $P = 0{\cdot}003$). In yearlings, departure probability was influenced by an interaction between body condition at introduction and treatment ($F_{1,120} = 4{\cdot}96$, $P = 0{\cdot}03$). Yearling dispersers tended to be more corpulent than residents in augmentation units (odds ratio per condition unit = 2·19, $P = 0{\cdot}19$, $n = 59$), while they tended to be leaner in colonization units (odds ratio = −3·77, $P = 0{\cdot}07$, $n = 72$). In adults, departure probability was correlated with body size, sex and geographical origin, irrespective of treatment. Adult dispersers were larger than residents (odds ratio per mm = 1·22, $F_{1,170} = 7{\cdot}72$, $P = 0{\cdot}006$), adult males dispersed more than females (odds males : odds females = 10·7, $F_{1,170} = 11{\cdot}95$, $P < 0{\cdot}001$) and adults from the local area dispersed more than adults translocated from the mountain area (odds Fo : odds Cv = 3·25, $F_{1,170} = 6{\cdot}53$, $P = 0{\cdot}01$).

IMMIGRATION BEHAVIOUR

Among the 116 individuals dispersing in 2001, 87 immigrants settled in their patch of arrival and 29 transients returned to their patch of introduction. Across all age and sex classes, settlement probability was not different between occupied and initially empty patches (Table 1). However, the timing of dispersal in the colonization process could have influenced settlement decisions, as predicted by the social attraction hypothesis (Stamps 1991). Against this prediction, late dispersers were not more likely to settle in an initially empty patch than early dispersers (logistic regression on the arrival rank in an empty patch, $F_{1,44} = 0{\cdot}25$, $P = 0{\cdot}62$). None the less, the time spent by transients within a patch of arrival was affected by the manipulation (effects of age: $F_{2,19} = 0{\cdot}94$, $P = 0{\cdot}41$; sex: $F_{1,19} = 1{\cdot}53$, $P = 0{\cdot}23$; treatment: $F_{1,7} = 7{\cdot}35$, $P = 0{\cdot}04$). Transients stayed longer in initially empty patches than in augmented patches (31·1 ± 5·9 days, $n = 12$ vs. 10·8 ± 4·8 days, $n = 17$).

DEMOGRAPHIC PARAMETERS IN IMMIGRANTS

Growth

In juveniles, an interaction between treatment and immigration status affected growth in body size (Table 2). As predicted by the 'beneficial colonization' scenario (Fig. 2), the annual growth rate was higher for immigrants in colonization units than for immigrants in augmentation units and for residents (independent contrasts, all adjusted $P < 0{\cdot}05$), and immigrants' growth in augmentation units was not different from residents ($P > 0{\cdot}13$). This was not due to intrinsic differences between immigrants from augmentation and colonization units. Indeed, the growth rates of juvenile immigrants were similar in both units before dispersal ($F_{1,6} = 1{\cdot}02$, $P = 0{\cdot}35$, $n = 52$), whereas growth from dispersal to settlement was higher in empty than in occupied patches ($F_{1,5} = 31{\cdot}45$, $P = 0{\cdot}002$, $n = 19$). A similar effect of

Table 2. Effects of treatments on annual growth in body size in juveniles, yearlings and adults. Statistical models included a random family effect in the case of juveniles

Source of variation	*F*-statistic	*P*-value
Juveniles growth		
Sex	$F_{1,118} = 10{\cdot}2$	0·002
Immigration status	$F_{1,118} = 0{\cdot}85$	0·36
Treatment	$F_{1,5} = 7{\cdot}47$	0·04
Immigration status × treatment	$F_{1,118} = 7{\cdot}08$	0·009
Yearlings growth		
Sex	$F_{1,73} = 46{\cdot}75$	< 0·0001
Immigration status	$F_{1,73} = 0{\cdot}31$	0·58
Treatment	$F_{1,5} = 2{\cdot}06$	0·21
Immigration status × treatment	$F_{1,73} = 3{\cdot}54$	0·06
Adults growth		
Sex	$F_{1,113} = 86{\cdot}6$	< 0·0001
Immigration status	$F_{1,113} = 6{\cdot}92$	0·01
Treatment	$F_{1,5} = 0{\cdot}45$	0·53
Immigration status × treatment	$F_{1,113} = 0{\cdot}20$	0·66

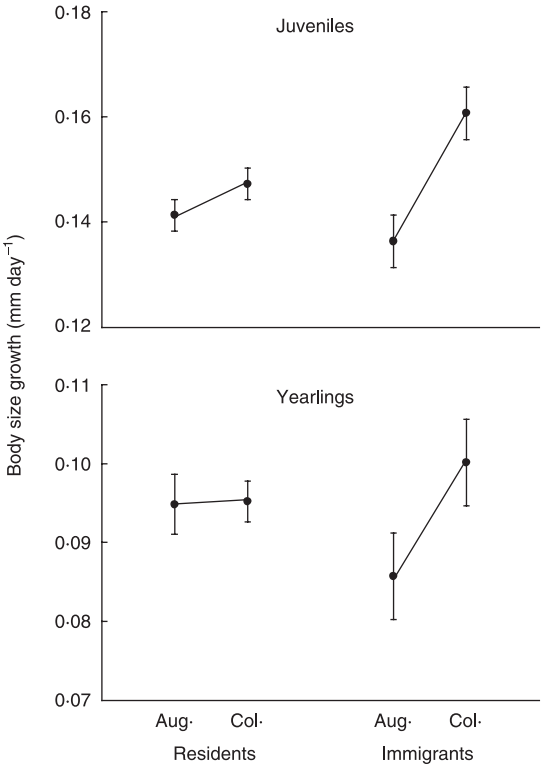

Fig. 2. Annual growth rates in body size per immigration class (residents or immigrants) and treatment (augmentation or colonization) in juveniles and yearlings. Data are given as means ± SE. Aug: augmentation units. Col: colonization units.

treatment was detected on growth in body size among yearlings (Fig. 2), but the trend was only marginal (Table 2). In adults, manipulation had no effect on growth in body size: immigrants grew more than residents irrespective of treatment (Table 2, contrast between immigrants and residents = 1·23 mm per year ± 0·47).

Manipulation and immigration status had no effect on change in body condition among male juveniles ($P > 0{\cdot}11$) and male yearlings ($P > 0{\cdot}20$). However, the

change in body condition in adult males was influenced by an interaction between immigration status and treatment ($F_{1,47} = 8{\cdot}39$, $P = 0{\cdot}006$, 57 observations). Body condition of immigrants increased more in colonization compared to augmentation units (contrast between colonization and augmentation = $0{\cdot}56 \pm 0{\cdot}18$, $P = 0{\cdot}016$), while treatment had no effect in residents ($P = 0{\cdot}95$).

Reproduction

The proportion of juvenile females that were gravid in June 2002 was affected by an interaction between treatment and immigration status ($\chi^2_1 = 5{\cdot}84$, $P = 0{\cdot}02$). The proportion of gravid juvenile females was independent of treatment in residents (Fisher's exact test, $P = 0{\cdot}50$, $n = 94$), but was higher in immigrants of colonized patches than in immigrants of occupied patches (Fisher's exact test, $P = 0{\cdot}01$, $n = 11$, see Table 3). Growth rates were correlated positively with the probability of being gravid in juveniles ($\chi^2_1 = 34{\cdot}52$, $P < 0{\cdot}001$). Furthermore, when postnatal growth rates were accounted for, the interaction between treatment and immigration status was not significant ($\chi^2_1 = 1{\cdot}28$, $P = 0{\cdot}26$). In older females, the probability of being gravid was not affected by treatment ($F_{1,5} = 1{\cdot}03$, $P = 0{\cdot}36$), immigration status ($F_{1,97} = 0{\cdot}87$, $P = 0{\cdot}35$) or their interaction ($F_{1,97} = 1{\cdot}72$, $P = 0{\cdot}19$, Table 3). Other brood characteristics (clutch size, hatching success, sex ratio, offspring size and condition) were not influenced by the manipulation or the immigration status of the mother (all $P > 0{\cdot}23$).

Survival

The post-summer survival of juveniles, yearlings or adults was not influenced by treatment or immigration status (all $P > 0{\cdot}38$). Survival was age-specific ($F_{2,595} = 15{\cdot}43$, $P < 0{\cdot}001$): juveniles had lower survival than yearlings and adults (odds juveniles : odds yearlings and adults = $0{\cdot}49$, $P < 0{\cdot}001$).

Discussion

Our manipulation allowed us to investigate the behavioural and demographic effects of patch occupancy on immigration in the common lizard. Our main results are summarized in Table 4 and compared with the hypotheses stated in the Introduction.

COSTS AND BENEFITS OF IMMIGRATION

Two fitness components (body growth and maturation) were enhanced in offspring immigrating into initially empty patches, whereas offspring dispersing into occupied patches did not differ from residents. No significant difference between colonization and augmentation was detected in yearling and adult immigrants, except that adult male immigrants gained more condition in the colonization treatment. These results support the 'beneficial colonization' scenario for juveniles.

Such effects of colonization can be related to intraspecific competition. It has been shown in the common lizard that density-dependent interactions for food and space primarily affect post-natal growth (Massot *et al.* 1992). Competition for food and social stress were probably relaxed during colonization, resulting in enhanced body growth. Prey availability was indeed affected by initial patch occupancy: at the end of the experiment, the abundance of spiders (one of the main prey of the common lizard, Avery 1962) was twice as high along 10 m transects in initially empty patches ($22{\cdot}2 \pm 1{\cdot}7$ spiders per transect) than in initially occupied patches

Table 3. Probability of reproduction in two age classes of females per treatment. Results are given as means and 95% CI

Age cohort	Type	Augmentation	Colonization
Juvenile females	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] ($n = 6$)
Older females	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] ($n = 9$)

Table 4. Summary of predicted and observed effects of presence of conspecifics on immigration behaviour and demographic parameters in immigrants

Hypothesis	Prediction	Observed effects
Immigration behaviour		
Random dispersal	No effect	No effect on settlement probability
Social fence	Repulsion from occupied patches	Longer transience time in empty patches
Social attraction	Preference for occupied patches	
Demographic parameters in immigrants		
Neutral colonization	No effect	No effect in yearlings and adults
Beneficial colonization	Immigrants perform better in empty patches	Increased growth in juveniles in colonization units Earlier reproduction of females in colonization units
Costly colonization	Immigrants perform better in occupied patches	

(11·2 ± 1·2; $F_{1,10}$ = 22·2, P < 0·001). The higher growth during colonization caused most female juvenile immigrants to reach a critical body size before the age of 1 year, enabling them to reproduce earlier than females immigrating into occupied patches. The fact that growth and maturation of yearlings and adults were not influenced in the same way as in juveniles may reflect the lower plasticity or sensitivity to competition of older lizards.

The short-term benefits of colonization evidenced here could, however, be offset by several fitness costs (e.g. Olsson & Shine 2002). First, compared to older females, young females laid their clutches significantly later during the summer (contrast = 12·5 ± 2·5 days, P < 0·001) and produced smaller (contrast = −0·94 ± 0·33 mm, P < 0·001) and leaner offspring (contrast = −0·019 ± 0·006, P = 0·001). Delayed parturition and lower offspring condition and size are likely to be associated with reduced offspring survival (Sorci & Clobert 1999). Secondly, females maturing before the age of 1 year could suffer from reduced annual survival as a result of a cost of early reproduction. However, only strong survival costs are likely to compensate the observed benefit of early reproduction in this species (Caswell 2001; Lorenzon, Clobert & Massot 2001).

The significant short-term increase in offspring immigrant fitness associated with colonization has implications for our understanding of dispersal patterns. Theory suggests that favourable conditions for the evolution of dispersal are met if population density fluctuates and if colonization relaxes competition (e.g. Olivieri, Michalakis & Gouyon 1995). The first condition is likely to be fulfilled in our species because there is significant variation of population density at the spatial scale over which most dispersal occurs (Manuel Massot, personal communication). This experiment provides evidence that the second condition applies to juveniles, suggesting that opportunity 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 may explain further why dispersal occurs primarily at the juvenile stage in this species (Clobert *et al*. 1994).

SETTLEMENT AND DEPARTURE BEHAVIOUR

Settlement probability was not influenced by presence of conspecifics, although transient individuals stayed longer in colonized than in augmented patches (Table 4). This has two consequences. First, our results support the hypothesis of a 'random settlement' probability (Levins 1969) rather than the scenarios of conspecifics' attraction (Stamps 1991) or social fence (Hestbeck 1982). Secondly, the signal of a putative social fence detected by the lower time that transient individuals spent in occupied patches is not found to translate into changes in settlement probabilities. This questions the relevance of using local stopping-over times as measures of immigration potential in fragmented populations (Smith & Peacock 1990; Stamps 1991).

Social-fence phenomena have been illustrated by studies of saturated populations of small mammals and cooperatively breeding birds (Lambin *et al*. 2001). In these species, habitat saturation increases the frequency of aggressive social interactions, raises the risk of predation during dispersal and decreases the opportunities of independent breeding (e.g. Jones *et al*. 1988; Gundersen *et al*. 2002). Here, the absence of any sign of a social fence is somewhat puzzling in the light of previous studies in the common lizard, showing that competition increases with habitat saturation and that local density reduces transience (Massot *et al*. 1992). Conspecifics' attraction has received support from studies of habitat selection at different spatial scales, ranging from territory to patch or colony (Stamps 1991; Danchin *et al*. 2001). Recent models have shown that cueing on conspecifics can bring some benefits (Greene & Stamps 2001; Doligez *et al*. 2003). However, these models do not account for the spatial and temporal constraints acting on settlement and for the fitness costs of habitat exploration. Thus, random settlement as observed here may actually reflect constraints on habitat choice (Stamps 2001).

Our treatments can be categorized in terms of overall density (low in colonization units, high in augmentation units) and interpatch flow (mostly unidirectional in colonization units, bi-directional in augmentation units). Behavioural processes acting at the unit level might therefore affect emigration. In our study, the relationship between body condition and departure probability was influenced by treatments in yearlings, meaning that different yearlings dispersed depending on metapopulation structure. It is possible that the arrival of unfamiliar immigrants induced specific social interactions within the connected patches belonging to the augmentation units and played a significant role in the dispersal of different individuals.

COLONIZATION AND PATCH DEMOGRAPHY

Colonized patches had a higher per capita growth rate from early colonization to the end of the study than the other types of patches. This was because immigration from source patches more than compensated for local mortality and also because of a higher reproductive recruitment in recently colonized patches. Thus, immigration can be regarded here as a rescue effect as it enhances growth in a population far below its carrying capacity (Brown & Kodric-Brown 1977). Furthermore, this rescue effect observed was not cancelled out by a subsequent reduction in reproduction resulting from Allee effects within colonized patches. Such dynamics may contribute to the species' capacity to colonize new habitats and to maintain a large geographical distribution. The common lizard is indeed one of the most widespread lizard species on Earth, with populations distributed from northern Spain up to the Arctic Circle,

from Western Europe to the Sakhalin Island, and from sea level up to 3000 m elevation (Heulin & Guillaume 1989). This distribution has been established during several Quaternary invasion dynamics, where the species spread between the ice ages over the whole Eurasia from its south-eastern refuges (Surget-Groba *et al*. 2001).

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