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Individual dispersal status influences space use of conspecific residents in the common lizard, *Lacerta vivipara*

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Abstract The effects of immigration on the behaviour of residents may have important implications for the local population characteristics. A manipulative laboratory experiment with yearlings of the common lizard (*Lacerta vivipara*) was performed to test whether the introduction of dispersing or philopatric individuals influences the short-term spacing behaviour of resident individuals. Staged encounters were carried out to induce interactions within dyads. The home cage of each responding individual was connected by a corridor to an unfamiliar “arrival cage” to measure the latency to leave their own home cage after each encounter. Our results showed that the time that pairs spent in close proximity was longer when a dispersing individual was introduced in the home cage. The latency to leave the home cage was longer after the introduction of a dispersing individual. These response variables were not influenced by the relative body sizes of contestants nor by the level of aggression towards each other. In contrast, the

aggressive response was significantly influenced by the residency asymmetry established experimentally (“owner” of the home cage vs introduced individual). Our results suggest that the space use by resident individuals is influenced by the dispersal status of conspecifics. The potential ultimate causes driving this effect are discussed.

Keywords Dispersal · Immigration · Social interactions · Space use · Lizards · *Lacerta vivipara* · Reptile

Introduction

Dispersal has important implications for the structure of populations via demographic, genetic and phenotypic flow (Hamilton and May 1977; Johnson and Gaines 1990; Whitlock 2001). The study of the causes and consequences of dispersal has therefore become an important issue in evolutionary biology (Bullock et al. 2002; Clobert et al. 2001; Lidicker and Stenseth 1992). Both the departure from the natal/breeding site and the settlement in a novel environment may affect local population characteristics such as inter-individual variability. Thus, local structure may not only be affected by the number of exchanges among areas but also by the nature of the individuals exchanged (Murren et al. 2001; Clobert et al. 2004).

For example, dispersal is often sex- and age-dependent (Bullock et al. 2002; Clobert et al. 2001), but the social consequences of this pattern are poorly known (Andreassen et al. 2002). Gundersen et al. (2002) pointed out not only the potential demographic consequences (reproduction, survival and local recruitment) but also the behavioural impact of different types of new individuals on the resident population. Among the most likely consequences is that the arrival of new individuals to a given area should induce local spacing readjustments. These spacing readjustments could modify the accessibility of resources, therefore affecting individual fitness. Furthermore, if the readjustments on the spatial structure modulate the type and number of neighbours, this may in turn influence future mating opportunities.

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To understand interactions between residents and immigrants, it is necessary to acquire a better knowledge of the phenotypic correlates of dispersal (Clobert et al. 2004; Dingemans et al. 2003). There is a recent accumulation of studies comparing dispersing and philopatric phenotypic attributes (Clobert et al. 2004; Murren et al. 2001). It turns out that dispersers can differ from philopatric individuals in morphology (Meylan et al. 2002; O'Riain et al. 1996), physiology (Dufty and Belthoff 2001; Holekamp and Smale 1998) and behaviour (boldness: Fraser et al. 2001; Wilson et al. 1994; aggressiveness: Pastschniak-Arts and Bendel 1990; or exploratory capacity: Dingemans et al. 2003). Little is known, however, about the outcomes of interactions between residents and recently dispersed immigrants, although this type of interactions has been hypothesised to prompt both dispersal and recruitment (Krebs 1978; Pastschniak-Arts and Bendel 1990; Rosenberry et al. 2001).

Dispersing and philopatric individuals are likely to display different behavioural strategies (Clobert et al. 2004; Dingemans et al. 2003), and the outcome of their social interactions cannot be limited to the study of social dominance. For instance, individuals may take cues from conspecifics to learn the location of suitable habitats (Stamps 1991). More specifically, it has recently been hypothesised that the presence of newly arrived dispersing individuals (immigrants) might be a good indicator of the suitability of an area to conspecifics (Clobert et al. 2004; Lecomte et al. 2004). In addition, morphological, physiological or behavioural differences between dispersers and philopatric individuals might serve as indirect sources of information about the surrounding environment (Clobert et al. 2004). For example, immigrants into a population already carry the information that some other populations exist elsewhere. The phenotype of the immigrants can furthermore serve as a cue about the characteristics of the habitat of origin, just as the reproductive success of conspecifics serves as a cue for habitat selection in birds (Doligez et al. 2002). Thus, if animal movements are not only due to the social environment but also to the habitat quality, then both processes can often induce interacting effects (Clobert et al. 1994).

In this study, we performed an experiment to compare the response of philopatric individuals to a space use challenge when induced to interact with a philopatric or a dispersing individual. We used the common lizard (*Lacerta vivipara*) because recent studies on this species have shown that philopatric and dispersing individuals differ in their behavioural profile (activity rate: Clobert et al. 1994, affinity towards maternal odour: Léna et al. 2000, condition-dependent escape attempts: De Fraipont et al. 2000 and foraging strategy: Meylan et al. submitted). Furthermore, in this species, dispersal has been found to correlate either positively (Léna et al. 1998; Boudjemadi et al. 1999) or negatively (Léna et al. 1998; Le Galliard et al. 2003) to conspecific density, suggesting that the presence of conspecifics might modulate spatial movements in interaction with other more subtle cues from conspecifics. For example, a field study showed that individuals of the

lizard species *Uta stansburiana* do not settle randomly but rather show either attraction towards or repulsion from conspecifics of different colour morphs, suggesting that individuals might use the colouration of conspecifics as a cue to decide where to settle (Sinervo and Clobert 2003). Taking all these together, we hypothesised that, in *L. vivipara*, the spacing behaviour of residents may be influenced not only by the presence of conspecifics but also by other subtle cues such as the dispersal status of conspecifics.

Yearlings were selected as experimental individuals after their emergence from hibernation, as this should be a stage when the number of local spacing readjustments are frequent because: (1) the departure phase occurs mainly at the end of the activity season (Clobert et al. 1994), which might mean a short time frame to decide on a definitive neighbourhood; (2) the survival rate after the first winter is low in this species (Le Galliard et al. 2005), which may give survivors the opportunity to readjust their areas moving into newly freed spaces; and (3) dispersal occurs not only at the juvenile stage but also after hibernation (Clobert et al. 1994; Boudjemadi et al. 1999; Le Galliard et al. 2003, 2005; Lecomte et al. 2004). Thus, substantial differences in the neighbourhood before and after the winter should occur. Furthermore, behavioural differences between philopatric individuals and dispersers remain for at least 1 year after birth (Clobert et al. 1994, Meylan et al. unpublished data), which may be a source of information to conspecifics.

Materials and methods

Study species

L. vivipara is a small, live-bearing lacertid species (50 to 70 mm adult snout-vent length), which is widely distributed across Eurasian peat bogs and heath lands. In our study population (44°30'N, 3°45'E, Mont Lozère, France, elevation of 1,420 m), adult males emerge from hibernation in late March or April, followed by yearlings and adult females in early May. The activity season ends in late September. The departure phase of dispersal occurs mainly within the first 10 days after birth (Clobert et al. 1994). Sexual maturity is reached at the age of 2 years (Pilorge and Castanet 1981).

Measurement of dispersal

The study area is a 9,000-m² moor whose population has been monitored since 1986 using a grid system to study dispersal (Clobert et al. 1994). It is mainly covered by grass and heath patches, but its physical heterogeneity is enhanced by trees and rocks scattered across the study site. The study area is surrounded by wooded areas that greatly limit emigration (Clobert et al. 1994).

To study natal dispersal, 77 pregnant females were removed from the field in early July 2002. Females were

maintained individually until parturition in plastic terrariums (18×12×12 cm) with about 1 cm of soil and a shelter. This is an adequate size for terrariums, according to standardised rearing conditions (Massot and Clobert 2000), since 94.8% of females successfully achieved parturition. Females were exposed to natural daylight and heated 6 h per day with an electric bulb (25 W). These females were held in captivity for a maximum of 1 month and were fed with meal moth larvae, *Pyralis farinalis*.

At birth, juveniles were sexed using a discriminant function based on the counting of ventral scales (Lecomte et al. 1992). This method gives more than 95% of success in gender determination. In addition, this rate was improved upon by observing sexual dimorphism that some individuals begin to show at the yearling stage. Juveniles were individually marked by toe-clipping. Natural toe loss was observed in this species and toe-clipping has been shown to have no effect on behaviour or fitness (Dodd 1993; Ott and Scott 1999). To obtain the dispersal status in the field, 375 juveniles (73 clutches) and mothers were released immediately after birth at the mother's capture point. Because pregnant females are highly sedentary (Bauwens and Thoen 1981), the juvenile natal site is considered to be the mother's capture point (Clobert et al. 1994). All individuals were healthy when released and immediately showed typical behaviours in this species such as exploration (tongue flicking and walking). Yearling movements were determined by hand recaptures during a 2-week capture session in June 2003. The distances moved were measured by comparing the coordinates of the release (July 2002) and the last recapture point (June 2003). Recapture points were located to a precision of 1 m using a grid of markers spaced every 3 m. The recapture rate of yearlings born in the laboratory was 18% (67 yearlings). We defined as dispersers those yearlings that moved a distance greater than 30 m (upper 95% confidence limit of the yearling/adult range diameter), and as philopatric ones those yearlings that moved less than 20 m (average of the home range diameter). This definition of dispersal is consistent because, in the same population, individuals classified as dispersers were never observed to return to their natal site (Clobert et al. 1994; Massot and Clobert 1995, 2000, more than 400 observations). In our experiment, five yearlings that moved distances between these

two values were not used to avoid confounding effects between home range exploration and dispersal.

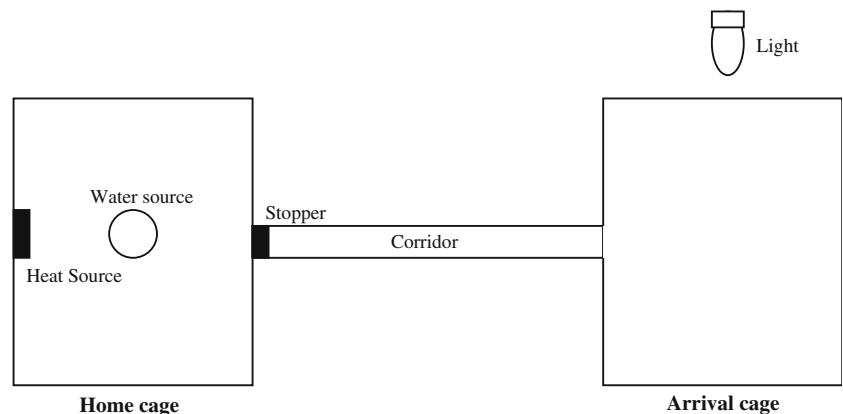
Experimental procedure

In June 2003, 62 yearlings (representing 40 clutches) of known dispersal status (46 philopatric yearlings and 16 dispersers) were removed from the field. In the laboratory, yearlings were measured (snout-vent length) with a ruler, weighed with a digital weight and individually housed in plastic cages (25×15×15 cm) to carry out the experiment. To facilitate thermo-regulation, an incandescent lamp was provided as a resource of heat for 5 h per day, and a shelter and ad libitum water were also available. A piece of absorbent paper constituted the floor of the terrarium as a means of increasing humidity and retaining scent-marks (De Fraipont et al. 2000). To allow individuals to establish residency, individuals were maintained in these conditions for 2 days after capture. In lizards, chemical senses play an important role in intra-specific communication (Mason 1992; Cooper 1994). Thus, according to the scent-matching hypothesis, individuals can assess asymmetries in residency by comparing the scents of a conspecific with those found in the substrate, a mechanism that has been documented in lacertids (Edsman 2001). This mechanism is compatible with either site defence or territoriality systems, which have been described in the genus *Lacerta* (Stamps 1977; Aragón et al. 2004, 2006).

On the third day of captivity, the cages in which individuals were kept for 2 days (hereafter 'home cage') was connected to an empty clean terrarium (hereafter 'arrival cage') by a transparent plastic tube measuring 20 mm in diameter and 45 cm in length (hereafter 'corridor') (Fig. 1). Each trial consisted of two phases.

In the first phase of the experiment, another yearling, acting as an intruder, was introduced in the home cage. Hereafter, those individuals that interacted in their own home cages with an introduced partner are referred to as "residents", and those individuals that were introduced in the home cage of the resident individual as "intruders". Thus, 31 residents and 31 intruders were used in this experiment. In contrast, philopatric and dispersing individuals are classified with regard to their dispersal status as

Fig. 1 Experimental design. In the first phase, one yearling was introduced in the home cage of the experimental resident to induce resident–intruder interactions. Residents in the home cage were philopatric in the field and intruders were either philopatric or dispersers. In the second phase, intruders were removed and the home cage was connected to an arrival cage to record the latency of residents to leave their home cage



defined from the field data. Thus, in our experimental manipulation, the intruder was either a philopatric or a dispersing individual from the field. The resident (the “owner” of the cage) was always a philopatric individual from the field. With this design, a natural situation was mimicked in which one individual acts as the resident and the other as an intruder (López and Martín 2001; Aragón et al. 2006). More specifically, 31 philopatric individuals acting as residents were faced with two different individual intruders chosen with regard to their dispersal status profile. Thus, 16 unfamiliar disperser intruders resembled immigrants in a natural situation and 15 unfamiliar philopatric intruders resembled individuals performing an excursive activity further from their core area (as has been documented in lacertids, Aragón et al. 2004, 2006). When individuals move out of their most commonly used areas within home ranges (core areas), they are likely to encounter unfamiliar conspecifics. Another non-exclusive scenario is that some home ranges and neighbours are not yet established due to local spacing readjustments in the early stages of the ontogeny. Thus, first encounters between animals in this age class may in fact occur among unfamiliar philopatric individuals. This last scenario is congruent with a previous study on lacertids which showed that only older residents discriminated between neighbour and non-neighbour conspecifics (Aragón et al. 2000).

To increase the level of intra-specific interaction, access to the heat source was limited by a 3-cm-long resistor placed at the edge of the terrarium (Fig. 1). The heating surface allowed for the thermo-regulation of only one individual. The heat source was selected from among the potential resources to limit because it is known that lizards compete for basking platforms in the wild, from birth (Phillips et al. 1993) on to adulthood (Stamps 1977). Besides the obvious thermo-regulatory advantages, it has been demonstrated in lizards (Pratt et al. 1992; Downes and Bauwens 2004) that access to basking sites may affect growth rates at the juvenile stage and future fitness attracting potential mates when sexual maturity is reached. The intruder and resident were placed individually into two small boxes (2.5×6 cm) at opposite ends of the resident’s home cage equidistant from the heat source, which also controlled for handling effects. They were left inside for 30 s and then carefully released from the boxes to begin the trial. The first phase of the experiment lasted 20 min. Trials were videotaped to avoid observer effects. A small white spot placed in different positions on an individual’s tail served as an identification mark. Two types of behaviour were recorded: the time that yearlings spent in close proximity (less than 1 cm apart) with no sign of aggressiveness, and the number of aggressive responses (chases or chases with quick bites) initiated by each individual. Time spent in close proximity has been interpreted as an indication of social tolerance in lizards (Downes and Bauwens 2004; Aragón et al. unpublished data). Agonistic interactions never came to the point of persistent attacks or injuries and did not lead to sustained attempts to escape. During this first phase of the experi-

ment, the extremity of the tube connected to the home cage was closed.

After 20 min, the second phase of the experiment began by removing the intruder from the resident’s home cage leaving the resident individual alone for 5 min. After this time period, the connection between the arrival and home cages was attached. Both the heat and water source were then suppressed in the home cage. In addition, water and a heat source (a light bulb) were put in the arrival cage. With this procedure, a situation in which declining conditions of humidity and thermo-regulation opportunities was emulated. In this species, a low humidity rate at the ground level has a negative effect on presence and density (Lorenzon et al. 2001). In nature, animal movements are often simultaneously influenced by different factors, which can interact being additive or counteracting effects. Dispersal decisions in this species have been recurrently found to be influenced by habitat quality (Boudjemadi et al. 1999; Massot et al. 2002; Lecomte et al. 2004) and social environment (Léna et al. 1998; Le Galliard et al. 2003). Therefore, we modified local conditions in the second phase to present a realistic scenario in which individuals should encompass indirect information through conspecifics and direct assessment of patch quality within their areas. Thus, if there were a differential response to the social environment (philopatric intruders vs disperser intruders) even when local conditions are declining, such a conservative result would reveal that the social information manipulated in this experiment played an important role in this species.

We then measured the time it took for resident individuals to enter the arrival cage (latency) to examine whether the degree of avoidance of an area was dependent on the dispersal status of the conspecific previously presented. Latency to leave patches in semi-natural conditions has been previously used as a response variable for dispersal experiments in this species (Léna et al. 1998; Boudjemadi et al. 1999; Le Galliard et al. 2003). The maximum duration of the second phase of the experiment was 3 h.

Thirty-one trials (31 residents faced with 31 intruders) were performed. Individuals were randomised to obtain similar differences in body size (resident–intruder) through the treatments (philopatric intruder vs dispersing intruder), ensuring all of the sex combinations within pairs. Furthermore, yearlings were matched within pairs according to their capture date. Lizards were allowed to bask under the light for only 1 h before each trial, which was enough to initiate lizard activity but not to fully reach their thermo-regulatory requirements (Aragón et al. 2000). The only heat source during trials, however, was the resistor. All of the trials were performed in June 2003 between 0900–1600 h GMT. Room temperature was between 23.1 and 23.8°C. No lizard was used in more than one trial. Those few yearlings from the same clutch were distributed between the resident and intruder categories but were not paired in trials. After trials, yearlings were released at their capture point.

Statistical analysis

We first checked that the differences in morphometry within each pair were similar in both treatments using one-way ANOVAs (Procedure GLM, SAS Institute 1999).

We analysed different response variables: the aggressive response displayed by individuals, the time that the intruder and the resident spent together and the resident's latency to leave the home cage. The explanatory variables were the intruder's dispersal status, the sex of the resident and intruder, and the difference in snout-vent-length (DIFSVL) between the resident and intruder. The variable DIFSVL was included in the model because it has been widely demonstrated that body size plays an important role in determining dominance in lizards (e.g. López and Martín 2001; Olsson 1992; Aragón et al. 2006). The starting models (see below) included the first-order interactions between all effects, but only the second-order interactions with the continuous covariable (DIFSVL) to avoid an over-parameterisation.

To verify whether our experimental design reliably induced asymmetries in residency independent of field dispersal status, the level of aggressive responses displayed by residents and intruders within each pair was compared. Because the statistical unit for this type of analysis is the pair, a Wilcoxon matched-pairs test (procedure NPAR1WAY; SAS Institute 1999) was used. To test whether contest competition was dependent on the field dispersal status of the experimental intruder, the score obtained from the difference between the aggressive response displayed by the resident and the intruder (dominance score) was analysed. For this analysis, we performed a maximum likelihood-based approach (procedure GENMOD; SAS Institute 1999), using a Poisson distribution and a log link term.

Variance analyses were used for continuous dependent variables (Procedure GLM, SAS Institute 1999) using a log

transformation to meet the model assumptions. A backward selection procedure was used to explore the effects of the independent variables (McCullagh and Nelder 1989). The final model contained all significant effects and those main non-significant effects that were part of a significant interaction term. For other non-significant effects, the statistics associated with the model before dropping these effects are also shown.

To examine whether there was a relationship between the aggressive response and time spent together or latency, we used regression analysis (Procedure REG, SAS Institute 1999).

Results

The difference in SVL within each pair (i.e. resident's SVL–intruder's SVL) did not differ significantly between treatments (i.e. resident's SVL–dispersing intruder's SVL vs resident's SVL–philopatric intruder's SVL) (one-way ANOVA, $F_{1,29}=0.338$, $P=0.56$, philopatric intruder: mean±SE=0.20±0.93 mm, dispersing intruder: mean±SE=0.93±0.86 mm). Similarly, the difference in weight within pairs did not differ significantly between treatments ($F_{1,25}=0.355$, $P=0.55$, philopatric intruder: mean±SE=0.01±0.09 g, dispersing intruder: mean±SE=0.08±0.06 g). There was a strong significant relationship between SVL and weight (Pearson's correlation, $r=0.91$, $F_{1,56}=280.7$, $P<0.0001$). We also tested for differences using a relative measure of weight (corpulence) which was estimated by taking the residual score of the linear regression of body weight on the SVL. The difference in corpulence within pairs did not differ significantly between treatments ($F_{1,24}=0.110$, $P=0.74$, philopatric intruder: mean±SE=0.01±0.02, dispersing intruder: mean±SE=−0.004±0.03). There were no significant differences

Table 1 The effects on the time spent together and latency to leave the home cage of SR (sex of residents), SI (sex of intruders), DST (dispersal status of intruders) and DIFSVL (SVL difference between the individuals of each pair) and interactions in yearlings of *Lacerta vivipara* (* $P<0.05$, ** $P<0.01$)

Effects	Time spent together			Latency		
	df	F	P-value	df	F	P-value
DST	1.29	6.25	0.01*	1.24	8.92	<0.01**
SI	1.28	<0.01	0.97	1.22	0.59	0.44
SR	1.26	0.96	0.33	1.24	5.43	0.02*
DIFSVL	1.25	<0.01	0.95	1.23	2.86	0.10
SI*DST	1.27	2.90	0.10	1.19	1.41	0.24
DIFSVL*SR	1.24	3.05	0.09	1.17	0.49	0.49
SR*SI	1.23	1.11	0.30	1.16	0.29	0.59
DIFSVL*DST	1.22	0.05	0.82	1.18	0.61	0.44
SR*DST	1.21	<0.01	0.94	1.21	2.73	0.11
DIFSVL*SI	1.20	<0.01	0.96	1.20	1.39	0.25
DIFSVL*SI*DST	1.19	0.75	0.39	1.14	0.36	0.55
DIFSVL*SR*DST	1.18	0.63	0.43	1.15	2.43	0.13
DIFSVL*SR*SI	1.17	0.11	0.73	1.13	0.08	0.78

Sample sizes are 31 for the time spent together and 27 for the latency

between residents and intruders either in SVL ($F_{1,60}=0.619$, $P=0.43$) or weight ($F_{1,56}=0.976$, $P=0.32$).

During the first phase of the experiment, both residents and intruders emitted tongue flicks to the substrate and to the other individual; a behaviour associated with chemical exploration (Cooper 1994) and therefore with the scent-matching mechanism. Around 68% of the agonistic interactions consisted of chases that ended with a single bite given by the chaser, whereas the rest of these interactions were chases involving no bites. In every case, the chasers provoked the withdrawal of the other individual. Residents displayed more agonistic behaviours than intruders, independently of the dispersal status obtained from the field (Wilcoxon matched-pairs test: $n=31$, $Z=2.58$, $P<0.01$; residents: mean \pm SE=1.61 \pm 0.35 acts/20 min, intruders: mean \pm SE=0.54 \pm 0.23 acts/20 min). The difference between the agonistic interactions initiated by the resident and those by the intruder in each pair (dominance score) was not affected by the dispersal status of the intruders ($X^2_1=0.04$, $P=0.83$), their relative size ($X^2_1=0.50$, $P=0.47$) nor by other factors or interactions ($P>0.16$ in all cases).

The time that the pairs of lizards spent together was longer when the intruder was a dispersing individual (Table 1, Fig. 2a), whereas none of the other factors or their interactions significantly influenced this variable (Table 1). There was no significant relationship between the time that yearlings spent together and the aggressive response of residents (philopatric intruders: $F_{1,13}=0.380$, $P=0.54$, $r=0.169$; dispersing intruders: $F_{1,14}=0.013$, $P=0.90$, $r=0.031$) or intruders (philopatric intruders: $F_{1,13}=1.724$, $P=0.21$, $r=-0.34$; dispersing intruders: $F_{1,14}=1.995$, $P=0.17$, $r=-0.35$).

The time taken to leave the home cage (latency) was longer when residents were faced with dispersing intruders than when faced with philopatric intruders (Table 1, Fig. 2b). Only four individuals did not leave the home cage after 3 h, and all of them had been paired with disperser intruders. Latency was also longer for resident males than for resident females, but not in interaction with the intruder's dispersal status or its sex (Table 1). There was no significant relationship between latency and the aggressive response of residents (philopatric intruders: $F_{1,13}=0.237$, $P=0.63$, $r=-0.13$; dispersing intruders: $F_{1,10}=0.070$, $P=0.79$, $r=0.08$) or intruders (philopatric intruders: $F_{1,13}=0.131$, $P=0.72$, $r=0.10$; dispersing intruders: $F_{1,10}=0.337$, $P=0.57$, $r=-0.18$).

Discussion

At least three lines of evidence demonstrate an ability of resident lizards to distinguish among intruders that were dispersers vs philopatric. First, the time that lizard pairs spent in close proximity was longer when a dispersing individual was introduced into the home cage. Second, the latency for lizards to leave the home cage was longer after the introduction of a dispersing individual. Third, the four resident individuals that did not leave the home cage after

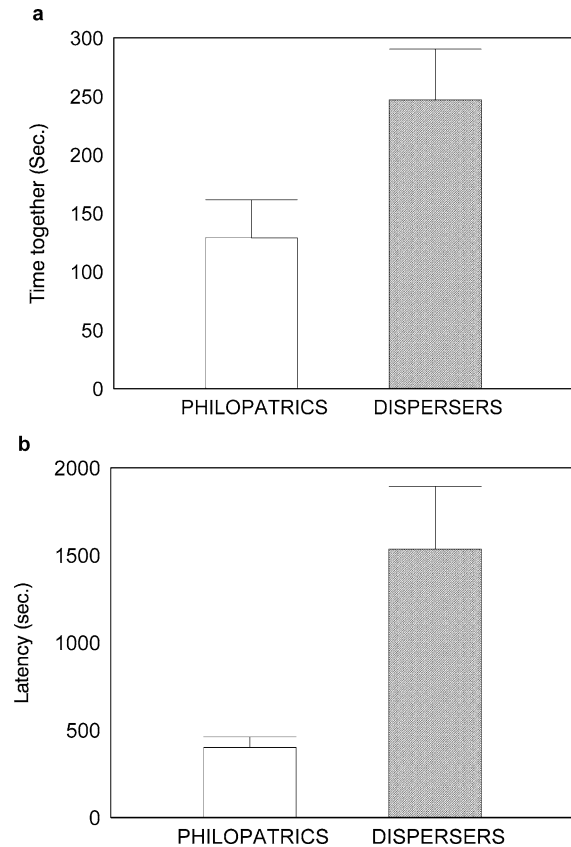


Fig. 2 **a** Time (mean \pm 1SE) that the pairs of yearling common lizards (*Lacerta vivipara*) spent together during trials depending on the field dispersal status of the intruders in the experimental conditions. **b** Latency (mean \pm 1SE) of resident philopatric yearlings to leave their home cage depending on the field dispersal status of the intruders in the experimental conditions

3 h had all been paired with disperser intruders. Thus, decisions about space use depended on information related to the dispersal status of the individuals encountered.

Latency to leave the home cage was sex dependent, but did not interact with a lizard's dispersal status. For both response variables (time together and latency), the interaction between the sex of the residents and the intruders was not significant; however, because this was a four-level effect, the power of the tests might be low due to sample size. These response variables were not influenced by relative body size nor by aggressive responses. The relative size of a lizard also did not influence the aggressive response, which may be because the difference in body size within dyads was small (average less than 1 mm), the effect of size is less important in this age class or a significant effect of the experimental asymmetry in residence ("owner" of the home cage vs introduced individual) on the aggressive response could have over-ridden other effects.

Intra-specific competition has been documented as one of the forces affecting avoidance and spacing behaviour (Huntingford and Turner 1987) in several species including our study lizard (Lecomte et al. 1994). Several studies with other species showed that philopatric individuals were more dominant or aggressive than dispersers (Holekamp

and Smale 1998; McShea 1990; Rosenberry et al. 2001). However, none of these studies disentangled the effect of uncorrelated asymmetries, such as the “owners win” rule (Riechert 1998), and other differences correlated with the dispersal status profile. In nature, it is difficult to know whether these differences are due to a disperser profile or simply to asymmetries in residence, because dispersers are often intruders during the transient and settlement phase.

Our study disentangles these factors by presenting both dispersers and philopatric individuals as intruders; we did not find differences in patterns of dominance between these situations. Residents, in contrast, initiated more agonistic interactions than experimental intruders, independently of the field dispersal status. It has been hypothesised that the owner of a resource has an advantage when engaged in agonistic interactions with an intruder, which may constitute an evolutionary stable strategy (Maynard Smith 1982) because the value of winning should be higher for individuals that have invested more into familiarization with the area (Stamps and Krishnan 1994). There is now accumulating evidence for such a rule in lacertids (López and Martín 2004; Aragón et al. 2006).

To what extent the information carried by these individuals is related to space, competition or other correlated factors remains open to discussion. Although no evidence was found supporting the notion that direct competition differs between treatments (dispersing vs philopatric intruders), our results on time spent together and latency indicate a greater tolerance that may reflect lower competition between individuals of different dispersal status. A slight niche differentiation in resource exploitation between philopatric individuals and dispersers might in fact decrease scramble competition as indicated by their difference in boldness (Fraser et al. 2001), foraging strategy (Meylan et al. submitted), exploratory behaviour (Dingemans et al. 2003) or activity (Clobert et al. 1994). This scenario would be compatible with the conclusion from a previous field study with the lizard *U. stansburiana*, whose findings showed that patterns of juvenile settlement are not merely due to selection at the individual level but that group selection might also evolve (Sinervo and Clobert 2003).

On the other hand, there is growing evidence for the assessment of source quality through conspecific cues in different taxa (reviewed in Valone and Templeton 2002; Giraldeau et al. 2002). Thus, when considering our results, an alternative but non-exclusive explanation is that the quality or type of information on source quality given via conspecific signals may depend on the dispersal status of individuals. For instance, the presence of an immigrant intruder (the disperser) in the first phase of the experiment might indicate that the local conditions elsewhere are less suitable. In this case, even when faced with a decline in local resources, philopatric individuals might delay their departure because of a conflict of information (own experience vs the presence of a disperser conspecific as a cue). This last possibility is interesting because it might give individuals indirect information about the suitability of their own area in relation to other areas through

information carried by dispersers. The presence or absence of such information might explain part of the variation in the relationship between density and dispersal in this species (Lecomte et al. 2004) because it has been found to correlate either positively (Léna et al. 1998; Boudjemadi et al. 1999) or negatively (Léna et al. 1998; Le Galliard et al. 2003).

In the same way, to what extent the proximal cues that support this information are based on behaviour, physiology or other yet unknown differences between dispersers and philopatric individuals remains to be studied. Differences between dispersing and philopatric conspecifics (e.g. hormone levels, chemical signals and behavioural profile) might serve as honest signals and, consequently, constitute a source of information on which strategic decisions could be based. For instance, higher levels of testosterone were associated to higher dispersal rates in adults of the spotted hyena (*Crocuta crocuta*) (Holekamp and Smale 1998) and juveniles of Belding’s ground squirrels (*Spermophilus beldingi*) (Nunes et al. 1999). In *L. vivipara*, juveniles from corticosterone treated mothers dispersed in lower rates (De Fraipont et al. 2000).

In conclusion, the results of this study show that the dispersal status of conspecifics influences the individual space use in yearlings of *L. vivipara*. These findings highlight the need for further studies to test whether these behavioural responses modulate the spatial structure in the field.

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