

Are Dispersal-Dependent Behavioral Traits Produced by Phenotypic Plasticity?

SANDRINE MEYLAN^{1,2*}, MICHÈLE DE FRAIPONT³, PEDRO ARAGON⁴,
ELODIE VERCKEN¹, AND JEAN CLOBERT³

¹Laboratoire d'Ecologie, Université de Paris, Paris, France

²IUFM de Paris-Université Sorbonne, Paris, France

³Station d'Ecologie Expérimentale du CNRS à Moulis, Saint-Girons, France

⁴Departamento de Ecología Evolutiva, Museo Nacional de Ciencias Naturales, CSIC, Madrid, Spain

ABSTRACT Dispersal is a common response to deteriorating conditions such as intense competition, food limitation, predation or parasitism. Although it provides obvious advantages, dispersal is often assumed to be costly. Selection is therefore likely to have acted to decrease these costs, and indeed several studies demonstrated that dispersers and philopatric individuals differ in their morphology, physiology and/or behavior. Using the common lizard (*Lacerta vivipara*) as our model system, we examined the contribution of phenotypic plasticity to the establishment of dispersal-dependent behavioral traits. We used a reciprocal transplant experiment in which conditions at the maternal site of origin, during offspring development in utero, and at the release site were manipulated. We then compared activity, social interactions and foraging behavior between individuals that stayed philopatric and those that dispersed. Most behavioral traits were also measured at birth and after the dispersal phase.

This study demonstrates that (a) 10 months after the dispersal phase, there were still marked behavioral differences between dispersing and philopatric individuals, (b) the reaction when confronted to another individual was also dispersal-status dependent, a result which strongly suggests that individuals are able to recognize the dispersal status of same-age conspecifics and (c) none of the behavioral characteristics were found to be dependent on the environmental conditions (maternal and natal environment) indicating a lack of phenotypic plasticity in the building of the dispersal-dependent behavioral traits examined. *J. Exp. Zool.* 311A, 2009. © 2009 Wiley-Liss, Inc.

How to cite this article: Meylan S, de Fraipont M, Aragon P, Vercken E, Clobert J. 2009. Are dispersal-dependent behavioral traits produced by phenotypic plasticity? *J. Exp. Zool.* 311A:[page range].

In a majority of situations, dispersal has been proved theoretically to evolve even in the presence of high costs (Lemel et al., '97; Murren et al., 2001). For example, traveling across unfamiliar habitats or through an hostile matrix makes individuals prone to predation or starvation (energetic costs due to transience), and settling into a new population might render an individual less successful in searching for refuges and food owing to a lack of familiarity with the habitat and conspecifics (Johannesen and Andreassen, '98; Aars et al., '99). Although these costs are compensated by benefits accrued by changing habitat or social group, it has been suggested that some of

these costs might also be decreased by dispersing individuals having some morphological, physiological or behavioral pre-adaptations to dispersal (Ims and Hjermann, 2001; O'Riain and Braude, 2001; Clobert et al., 2004, 2009). For example, the dispersal ability of individuals to rapidly travel

Grant sponsor: The CNRS; Grant number: 98N62/0120.

*Correspondence to: Sandrine Meylan, Laboratoire d'Ecologie, CNRS-UMR 7625, Université de Paris VI, Case 237, 7 quai Saint Bernard, 75252 Paris, France. E-mail: smeylan@snv.jussieu.fr

Received 11 July 2008; Revised 23 December 2008; Accepted 10 February 2009

Published online in Wiley InterScience (www.interscience.wiley.com). DOI: 10.1002/jez.533

long distances has been enhanced by the development of morphological structures such as winged seeds in plants or winged forms in insects (Dixon, '85; Denno and Peterson, '95; Venable et al., '98). Other types of extreme morphological adaptation are found in a wide range of organisms, from ciliates (Nelson and DeBault, '78) to mammals (O'Riain et al., '96). In fact, the appearance of dispersal-specialized forms is likely to correspond to particular ecological situations (discontinued or heterogeneous habitats), but, in most situations, decreasing the cost of dispersal apparently requires only small quantitative shifts in the phenotype, such as differences in body size or in energy reserves (Nunes and Holekamp, '96; Dufty and Belthoff, 2001).

Most of the above specializations are likely to concern primarily the transience phase, and it might be predicted that decreasing the cost at settlement requires other types of adaptation, such as habitat recognition (Edelaar et al., 2008) and social integration (Cote and Clobert, 2007a, Cote et al., 2008). For instance, young females of the gray-sided voles (Ims, '90), which show asocial behavior against unfamiliar females were the most likely to disperse. In naked mole rats, dispersers participate little to cooperative maintenance tasks, but display important locomotor and feeding activities (O'Riain et al., '96). In the common lizard (de Fraipont et al., 2000), individuals that showed a higher exploratory rate in novel environments were those found to disperse later on. Finally, two other studies found similar results using "novel environment test" (Verbeek et al., '94), a variant of the classical open field test of animal psychologists (Walsh and Cummins, '76): Dingemans et al. (2003) in the great tit, and Fraser et al. (2001) in fishes. Fraser and colleagues demonstrate that boldness, expressed as the propensity to explore unfamiliar habitat, predicts initial dispersal in the field. All these studies provide direct evidence for a behavioral polymorphism that underlies dispersal behavior. These behavioral modifications were demonstrated, in some cases, to have an underlying physiological component (Woodroffe et al., '93; Dufty and Belthoff, 2001). In most cases, only pre-dispersal differences in behavior are correlated with dispersal propensity, but the extent to which they reflect short-term behavioral modifications or more profound changes remains questionable. Two studies have reported on post-dispersal differences in behavior among philopatric and dispersing individuals: in mole rats (O'Riain

et al., '96), individuals that had dispersed had a reduced participation in social activities of the colony they joined, and in the great tit (Dingemans et al., 2003), individuals that immigrated into a population were faster explorers than locally born birds. In the two above studies, dispersers and residents already behave differently before dispersal. In the great tit case, a comparison of exploratory behavior between parents and offspring has led these authors to suggest a strong heritability of dispersal through its behavioral component.

Dispersal behavior has been found to be a fixed trait in only a few species (Ims and Hjermann, 2001; Roff and Fairbairn, 2001; Sinervo et al., 2006). Instead, most studies have documented the important role of phenotypic plasticity in shaping dispersal patterns (Davis and Stamps, 2004), and the few models that addressed this question all found support for the predominance of plastic over fixed dispersal decisions (Ronce et al., '98; Clobert et al., 2001, 2009). Indeed it was demonstrated that dispersal behavior was strongly influenced by maternal effects (MacKay and Wellington, '77; Massot and Clobert, '95; Lorenzon et al., '99; de Fraipont et al., 2000; Meylan et al., 2002) or even by grand-maternal effects (Dixon, '85).

The aims of this study are first to examine the nature of the differences in behavioral traits between dispersing and philopatric individuals, second to assess the stability of these differences in a 10-month period, and finally to determine the contribution of phenotypic plasticity to the development of dispersal-dependent behavioral traits.

We selected the common lizard as our model system because it has been demonstrated that in this species: (1) dispersal was strongly environmentally driven (Massot et al., '92; Lorenzon et al., 2001) even in the presence of a strong family effect (Massot and Clobert, 2000), (2) juveniles that showed a strong attraction toward their mothers' odor at birth were found to be philopatric later on (Léna et al., 2000), (3) dispersers confronted with a novel environment were less stressed than philopatric individuals (de Fraipont et al., 2000) and (4) social tolerance was found to influence density-dependent settlement (Cote and Clobert, 2007a). If dispersal decision seems to be influenced by many environmental factors, we have no information on the plasticity of the "behavioral profile" associated to dispersal decision. Indeed, the dispersal tendency can be plastic but the behavioral profile associated to dispersers and philopatrics can be fixed. To study the

contribution of phenotypic plasticity to the establishment of dispersal-dependent behavioral traits (also called dispersal syndromes, Sih et al., 2004), we conducted a reciprocal transplant experiment in which conditions at the site of origin, during offspring development in utero, and at the release site were manipulated. We then compared activity patterns, social interactions and foraging behavior between individuals that remained philopatric and those that dispersed.

METHODS

Species

Lacerta vivipara is a small, live bearing lacertid species (50–70 mm adult snout–vent length) inhabiting peat bog and heath land. This species is widely distributed across Europe and Asia (from Spain to the Pacific coast of Russia, and from Scandinavia to southern Romania). In our study populations (Mont Lozère, 44° 30' N 3° 45' E, Southern France), mating takes place in May. Parturition occurs after a 2-month gestation, when young are fully developed. Females lay a clutch of five soft-shelled eggs, on average, and offspring hatch within 1 hr of oviposition. Juveniles (snout–vent length up to 18 mm) are

independent of their mother immediately after birth. Dispersal occurs within the first 10 days of activity after birth (Clobert et al., '94).

Experimental design: manipulation of pre- and post-natal conditions

To study phenotypic plasticity in behavioral traits, we selected four populations located in the same geographical area (called A, B, C, and D, distant by less than 4–5 km at a same elevation of 1450 m), that display comparable population structure and density (sex ratio, proportion of age classes, for more details see Meylan and Clobert, 2004; Meylan et al., 2007).

We decided to manipulate the environmental conditions at different stages of juvenile development (Fig. 1 and Table 1 to assess the chronology of the different manipulations). We focused on two factors that earlier studies on this species have shown to strongly influence dispersal probability and the production of dispersal-dependent phenotype: density (Léna et al., '98, Le Galliard et al., 2003; Lecomte et al., 2004; Cote and Clobert, 2007a; Meylan et al., 2007), and maternal levels of corticosterone during pregnancy (de Fraipont et al., 2000; Meylan and Clobert, 2004, 2005).

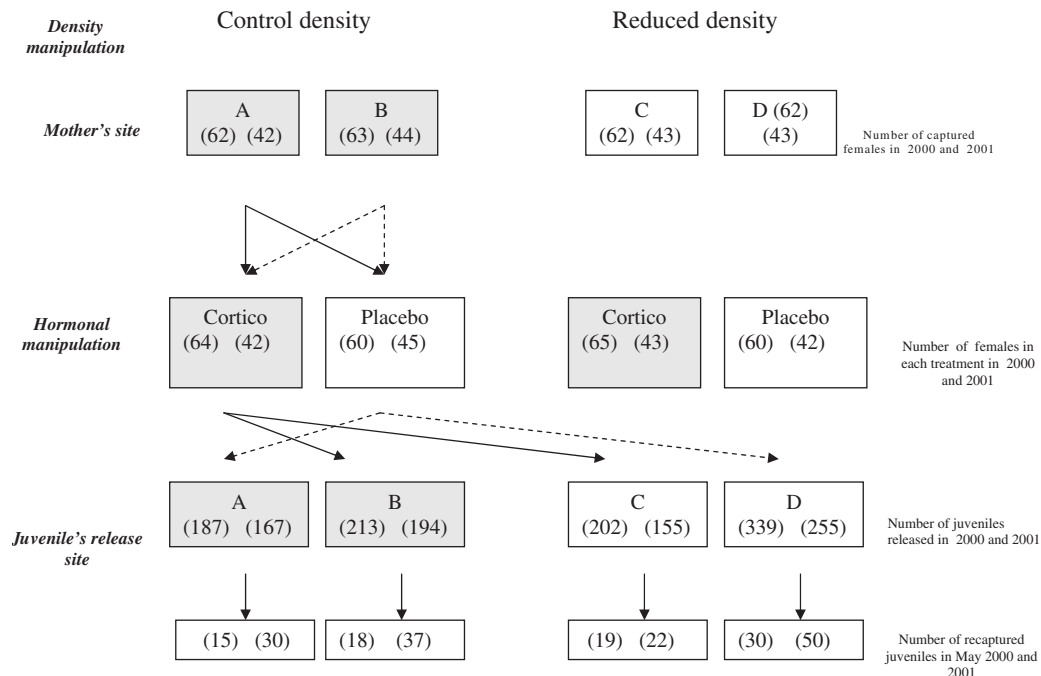


Fig. 1. Experimental design of years 2000 and 2001. We manipulated conditions (density and maternal hormonal level) at different stages of juvenile development (pre- and post-natal). Females treated with corticosterone are indicated as “cortico” vs. placebo. Sample sizes used at different stages are indicated in brackets.

TABLE 1. Timing of experiments of years 2000 and 2001

	Year 2000	Year 2001	Year 2002
Density manipulation	End of May	End of May	
Captures of pregnant females	15–24 June	15–23 June	
Hormonal treatment	28 June–10 August	27 June–11 August	
Dates of parturition	19 July–11 August	18 July–12 August	
<i>Experiments</i>			
Activity at birth	21 July–10 August		
Activity 10 months later		15 May–1 June	
Foraging at birth		20 July–10 August	
Foraging 10 months later			15 May–1 June
Social interaction		15 May–1 June	
Reaction to odor			15 May–1 June

Two weeks after density manipulations (in spring 2000 and 2001), females were temporarily removed from the field and kept in the laboratory until parturition. Then we elevated experimentally the corticosterone level of half of the females. Behavioral assays have been done with juveniles at birth and 10 months later.

Pre-natal density

Pre-natal density manipulation was achieved by removing a quarter of the individuals (in all age classes) in two of the four chosen populations (C and D) at the end of May 2000 and 2001 (see Meylan et al., 2007 for more experimental details). The most distant sites were separated by 4.5 km and the closest sites were separated by 300 m. Previous behavioral experiments (Léna et al., '98) as well as population experiments in semi-natural or natural conditions (Massot et al., '92; Le Galliard et al., 2003; Lecomte et al., 2004) all demonstrate the ability of individuals to perceive small variation in the number or quality of individuals. Moreover, this manipulation proved to have some effects on population demography, in particular on fecundity, female brightness and juvenile dispersal (Meylan et al., 2007).

Maternal corticosterone level

We manipulated the maternal hormonal environment by increasing corticosterone levels in pregnant females, during late gestation. In mid-June 2000 and 2001, we captured respectively 249 and 172 gravid females from the four populations and kept them in the laboratory until parturition (usually at the beginning of August, see Meylan et al., 2007 for details). Circulating levels of corticosterone were manipulated using a non-invasive method for sustained elevation of steroid hormone levels (Knapp and Moore, '97; Meylan et al., 2003). We diluted corticosterone (Sigma C2505, St Louis, MO) in commercial sesame oil (3 µg corticosterone/1 µL sesame oil). Corticosterone was then delivered transdermally to the lizards and was shown to modify juvenile behavior

after birth (Meylan et al., 2002, 2004; Meylan and Clobert, 2005). Within each population, randomly chosen pregnant females ($N = 129$ in 2000 and $N = 85$ in 2001) were given 4.5 µL of the hormone solution dorsally, every day until parturition (15 days on average), whereas control females ($N = 120$ in 2000 and $N = 87$ in 2001) received the same amount of sesame oil (see Fig. 1 for the exact repartition of females in each treatment). Our manipulation does not correspond to pharmacological doses and is in the range of the observed variation in the wild (for more details see Meylan et al., 2003).

Post-natal density

Post-natal density manipulation was achieved by releasing 941 (in 2000) and 771 (in 2001) juveniles (4 days of age) in the two different density conditions. After being sexed (Lecomte et al., '92), measured, weighted, and marked by toe clipping to allow identification, juveniles from a same family were split in two groups (Fig. 1). One group was released in the density control sites (A or B) and the other group in the decreased density sites (C or D). None of the offspring were released in their site of origin to avoid interaction with the mother (Léna et al., '98).

This design allowed to study independently the effect of environmental perturbations at different stages of the juvenile development, therefore enhancing the probability of observing any environmental influences on the production of dispersal-dependent behavioral traits.

Dispersal status—measurement in natural conditions: We assessed dispersal status by recapturing juveniles in September of the year of release and in May of the following year ($n = 409$). A grid

of markers (every 5 m) allowed us to locate recaptures with a 1 m precision. Dispersal was then measured as the distance between the points of release and last recapture. Because kin competition shapes the dispersal decision in *L. vivipara* (Léna et al., '98; Ronce et al., '98), we characterized dispersal status by comparing juvenile movements to the diameter of an adult female home range that we estimated in the study population. Juveniles that moved a distance greater than 20 m (the upper limit of the adult female home range diameter) were considered dispersers, whereas juveniles that moved less than 15 m (average of adult female home range diameter) were considered philopatric individuals (for individuals caught both in September and May, any difference in dispersal status was recorded, see also Massot and Clobert, 2000). Juveniles that moved distances between these two values were not used in the experiment. Previous studies demonstrated that juveniles with natal movements exceeding one female home range never returned to their natal area later on (Massot and Clobert, '95).

Behavioral assays

We selected some behavioral traits that we know to be important for a successful dispersal or settlement in our species (activity, foraging behavior, and social interactions, Clobert et al., '94, 2000). We also selected traits that we could measure at birth (before dispersal) and at 10 months of age (after dispersal, Table 1).

Just after birth, juveniles were kept in a terrarium in a calm part of the laboratory at ambient temperature to avoid any major energetic expenditure. No juvenile was fed before the assay to avoid creating differences in behavior related to different level of satiation. All behavioral assays were conducted in standard conditions of light (a bulb providing light and heat (30°C) for thermoregulation was placed 25 cm above the center of the terrarium) not later than 3 days after birth.

Ten-month-old individuals (born in the laboratory, in July and August) were temporarily removed from the field and kept for a few days (mean 3 days) under isolated conditions (one individual per terrarium, in similar conditions than at birth: neither perturbation nor food) in the laboratory. An individual participated in only one behavioral assay to avoid multiple manipulations and affect their subsequent behavior. Moreover, the tests done at birth and 10 months later were not done on the same individuals because of the low

juvenile survival rate (between 0.26 and 0.52 depending on the year and on the treatments, see Meylan and Clobert, 2005; Meylan et al., 2007) and their medium recapture rate (around 50%, Massot et al., '92).

Activity at birth and 10 months later

The first experiment was designed to investigate the behavior of individuals in an unfamiliar environment. This experiment was performed on juveniles at birth ($n = 409$) and at 10 months of age ($n = 47$). After at least one day of acclimatization in the laboratory, each individual was placed at the center of an empty terrarium ($28 \times 18 \times 12$ cm). After 10 min of acclimatization in the terrarium, we provided in the central part of the terrarium a delimited zone of heat using incandescent illumination. We recorded during 10 min the general activity as in de Fraipont et al. (2000): the time spent walking, the time spent motionless, and the time spent scratching the inner wall. Because the three variables are not independent, we analyzed only the time spent walking and scratching, two behaviors related to the dispersal status of an individual. Because individuals at birth participated in only one behavioral assay, most of the individuals that were captured at 10 months of age had not had their activity measured at birth.

Foraging at birth and 10 months later

To measure the foraging behavior, juveniles were placed alone into a terrarium and given 10 min to acclimate. Three *Apteris drosophila* were then introduced for 10 min, and we recorded the capture of a prey, the time needed for seizing the first prey and the strategy used (chasing or waiting). We performed this experiment on juveniles at birth ($n = 407$) and at 10 months of age ($n = 86$).

Social interactions at 10 months of age

The third experiment aimed to examine the reaction of juveniles to the presence and dispersal status of a conspecific. Because the dispersal status cannot be assessed immediately after birth, these experiments were conducted only on 10-month-old juveniles.

We used the same design used to study activity (i.e. a terrarium with a delimited zone of heat). Two juveniles were introduced at the same time. We recorded the activity (time spent walking and scratching) and the social interactions (attack and

distance between individuals). The experiment lasted 15 min, and individuals experienced only one confrontation. Juveniles in a pair were selected to obtain an equal number of each dispersal status combination (P–P, P–D, D–D, where P is a philopatric individual and D is a disperser), and such that individuals were coming from the same site, but not of the same location within the site. We did not match individuals in a pair for size or sex, but these factors were taken into account in the analyses by including body size of the two individuals in the statistical model. However, to avoid the problem of non-independence between the behaviors of individuals belonging to the same pair, only one individual per pair previously chosen at random was the focus of our observation ($n = 47$), the other one being disregarded in the analyses.

Data Analyses

Corticosterone treatment, density of origin, density of release, and dispersal status were included in all the models (analysis of variance) as independent variables and were considered as class factors. For continuous dependent variables (time spent scratching and walking), we checked for normality (Shapiro–Wilk test, proc univariate, SAS '96) and homoscedasticity (Barlett test). To test for the effects of these variables and all their interactions, we used the procedure GLM of the SAS Institute (SAS '96). Because, we have two sites (replicates) per density treatment, we used nested models with the replicates nested within density treatment. We performed the additional tests h and e that specify, respectively, the error effect and the effect in the preceding model to be used as the correcting variance matrices. With this method, we were able to test for the effect of the density treatment corrected by the potential difference between replicates. We did not introduce a mother effect (as a random factor) because, in most cases, only one single offspring per female was available (regarding the experiments done at birth, of the 408 juveniles used only 42 were siblings, and none for the experiment done at 10 months). For binary dependent variable (foraging behavior), we used the GENMOD procedure of the SAS Institute with a similar model structure as above. We performed a covariance analysis with the different factors (and their interactions) and we simplified the models by backward selection (McCullagh and Nelder, '89). In others words, we dropped the non-significant effects, starting with

the most complex interaction terms. We presented only the non-significant effects corresponding to the experimental manipulations. As in all analyses, the effects of juvenile body size and condition were not significant (all $P > 0.1$) and we did not report these results in the next section.

RESULTS

Dispersal rate was only affected by the density at the release sites (0.31 in control sites vs. 0.42 in manipulated sites, $\chi^2 = 5.64$, $P = 0.01$, see Meylan et al., 2007 for details). In all experiments, the corticosterone treatment, the density at the origin and release site did not interact with the dispersal status to shape behaviors (all $P > 0.05$). In other words, the behavioral traits displayed by dispersing and philopatric individuals were not dependent on the experimental modifications of the environmental conditions before and after birth.

Activity

The time spent walking (at birth: $F_{1, 408} = 2.27$, $P = 0.13$; at 10 months of age: $F_{1, 43} = 0.09$, $P = 0.76$) and the time spent scratching (at birth: $F_{1, 406} = 0.17$, $P = 0.68$; at 10 months of age: $F_{1, 43} = 0.01$, $P = 0.99$) did not differ between dispersing and philopatric individuals. The pre-natal density (walking: $F_{1, 2} = 3.69$, $P = 0.19$; scratching $F_{1, 2} = 8.52$, $P = 0.10$) and the post-natal density (walking: $F_{1, 2} = 0.001$, $P = 0.97$; scratching $F_{1, 2} = 0.87$, $P = 0.52$) did not affect activity at 10 months of age. Moreover, there are no differences between replicates. Only the maternal hormonal treatment influenced the activity of individuals. The time spent active was higher for juveniles born from corticosterone-treated females than for those born from placebo females (scratching at birth $F_{1, 408} = 6.73$, $P = 0.009$, walking at 10 months of age: $F_{1, 58} = 4.64$, $P = 0.03$).

Foraging behavior

At birth, the probability of catching a prey was significantly dependent on the interaction between the dispersal status and the juvenile sex ($F_{1, 406} = 4.52$, $P = 0.03$; Figure 2a). For females, philopatric individual had a higher probability to catch a prey than disperser, whereas there was no difference in males. This interaction also affected foraging strategy (chasing or waiting, $F_{1, 406} = 5.20$, $P = 0.02$; Figure 2b). The influence of the dispersal status on the probability to chase is opposite in females and males. No effect of the

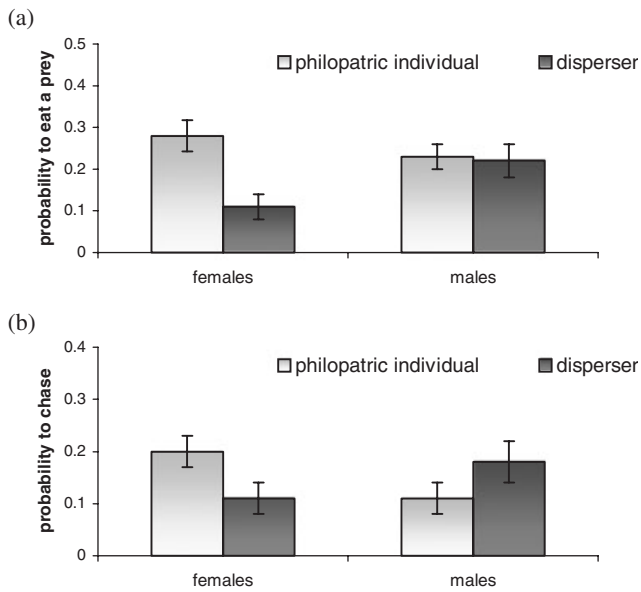


Fig. 2. Difference in (a) the probability of catching prey and (b) the foraging strategy (measured as the probability chasing rather than waiting) at birth between dispersers and philopatric juveniles.

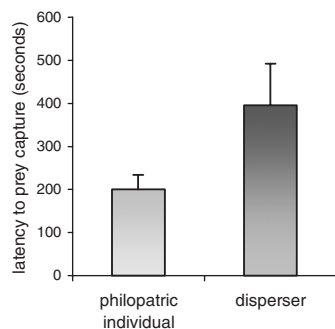


Fig. 3. Influence of yearling dispersal status on the latency to catch a first prey.

hormonal treatment was found on this variable ($df = 130$, $\chi^2 = 0.3$, $P = 0.6$).

At 10 months of age, there was no difference in the probability of catching a prey between dispersing and philopatric individuals ($df = 85$, $\chi^2 = 0.59$, $P = 0.44$). Similarly, foraging behavior (chasing or waiting) did not vary according to dispersal status ($df = 83$, $\chi^2 = 2.78$, $P = 0.09$). Only the time needed to catch a first prey was affected by dispersal status ($F = 5.06$, $df = 1.58$, $P = 0.02$). Dispersers took more time to capture prey than philopatric individuals (Fig. 3). The other variables such as corticosterone, and pre- and post-natal density did not affect foraging behavior (all $P > 0.05$).

TABLE 2. Effects of the dispersal status and of the prenatal and postnatal conditions on the time spent scratching the inner wall of the terrarium when confronted with a conspecific

Independent variables	Df	F value	Pr > F
Density at the release site	1.2	0.08	0.82
Replicate of the populations of release	1.42	3.48	0.07
Density at the site of origin	1.2	0.22	0.68
Replicate of the populations of origin	1.43	0.96	0.39
Dispersal status	1.44	0.48	0.49
Hormonal treatment	1.45	0.89	0.35
Conspecific dispersal status	1.46	10.88	0.002

The time spent scratching the inner wall is higher for an individual facing a conspecific that has dispersed than when facing an individual that has not dispersed. All interactions are non-significant ($P > 0.05$).

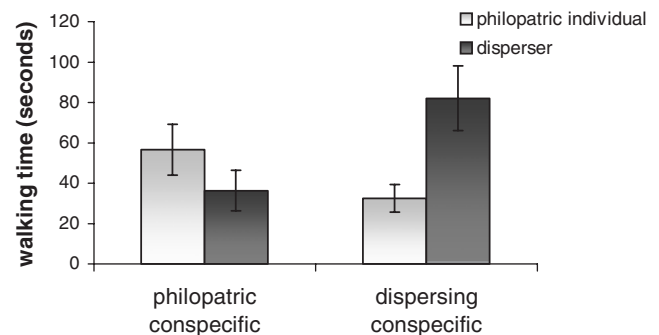


Fig. 4. The time spent walking in relation with dispersal status of both individuals. When a philopatric or a disperser is confronted with a conspecific of the same status, the walking activity is higher than when confronted with a conspecific of different status.

Social interactions

The juvenile behavior when interacting with a conspecific was affected by the dispersal status of the conspecific. The time spent scratching the inner wall is higher for an individual facing a conspecific that has dispersed than when facing an individual that has not (106.74 ± 15.43 sec vs. 51.66 ± 9.58 sec, Table 2). In addition, the time spent walking was dependent on the interaction between the dispersal status of each individual in the pair (Fig. 4 and Table 3). When a philopatric or a disperser is confronted with a conspecific of the same status, the walking activity is higher than when they are confronted with a conspecific of a different status. Corticosterone, post- and pre-natal densities did not influence the juvenile behavior when interacting with a conspecific (Table 3).

The social interactions (attack, distance between individuals) were neither affected by the dispersal status of the individuals in the pair nor by the experimental treatments (Table 4).

TABLE 3. Effects of dispersal status and of prenatal and postnatal conditions on the time spent walking inside a terrarium when confronted with a conspecific

Independent variables	Df	F value	Pr > F
Density at the site of origin	1.2	0.01	0.91
Replicate of the populations of origin	1.41	2.39	0.10
Density at the release site	1.2	0.27	0.69
Replicate of the populations of release	1.42	1.30	0.26
Hormonal treatment	1.43	3.20	0.08
Dispersal status	1.44	1.90	0.17
Conspecific dispersal status	1.44	1.07	0.30
Dispersal status * conspecific dispersal status	1.44	7.10	0.01

TABLE 4. Effects of dispersal status and of prenatal and postnatal conditions on social interactions

Independent variables	Nb of attacks	Nb of escapes	Nb of attractions
Dispersal status	$\chi^2 = 2.27, P = 0.13$	$\chi^2 = 0.29, P = 0.58$	$\chi^2 = 0.06, P = 0.80$
Conspecific dispersal status	$\chi^2 = 0.47, P = 0.49$	$\chi^2 = 0.02, P = 0.87$	$\chi^2 = 0.36, P = 0.54$
Density at the site of origin	$\chi^2 = 0.08, P = 0.76$	$\chi^2 = 0.01, P = 0.90$	$\chi^2 = 0.32, P = 0.56$
Density at the release site	$\chi^2 = 1.73, P = 0.18$	$\chi^2 = 1.45, P = 0.22$	$\chi^2 = 1.18, P = 0.27$
Hormonal treatment	$\chi^2 = 1.14, P = 0.28$	$\chi^2 = 0.04, P = 0.83$	$\chi^2 = 1.71, P = 0.18$

Neither dispersal status nor different environmental manipulations affected attack and distance between individuals. All interactions are non-significant ($P > 0.05$).

DISCUSSION

Individuals that dispersed or stayed have different behavioral traits at birth and 10 months later, a long time after the natal dispersal phase. Although the density and hormonal treatments significantly affected female coloration, clutch size, offspring dispersal, survival and growth (Meylan and Clobert, 2004; Meylan et al., 2007), none of the behavioral characteristics have been found to be treatment-dependent, which suggests that the production of dispersal-dependent behavioral traits is not influenced by pre- or post-natal conditions, at least for the environmental conditions considered.

Stress and dispersal: validity of behavioral assays

Because behavioral assays have been performed under laboratory conditions, we may have induced a stress component in the response and this might complicate the interpretation of our results. In the literature there is indeed some evidence that dispersal activity is linked to an increase in corticosterone (Dufty and Belthoff, 2001), which might in turn promote shyness, aggression or an increase in activity (Dufty et al., 2002). Furthermore, a corticosterone increase during pregnancy produces offspring with a modified behavioral profile (Pollard, '84; Takahashi et al.,

'88) including condition-dependent dispersal (de Fraipont et al., 2000; Meylan et al., 2004; Vercken et al., 2007). Therefore, a differential response to stress might be at the origin of the behavioral differences between dispersing and philopatric individuals. This seems unlikely in our species. First, although we demonstrated that a pre-natal administration of corticosterone modified the perception of the mother's presence at birth (de Fraipont et al., 2000) and promoted philopatry, we did not find here any corticosterone effect on other dispersal-dependent behavioral traits. Furthermore, the application of corticosterone directly on the offspring before dispersal did not modify natal dispersal (Meylan et al., 2002). Secondly, captivity did not affect corticosterone level when measured 2 days after the arrival to the laboratory (Meylan et al., 2003). Thirdly, corticosterone affects activity (de Fraipont et al., 2000, including our experiment), but philopatric individuals did not show higher or lower activity levels than dispersers either before or after the dispersal period when measured under laboratory conditions. It is therefore unlikely that the production of dispersal-dependent behavioral traits is solely owing to stress.

Dispersal status and foraging activity

Inter-individual variation in the ability to access resources in the natal area, and therefore to

compete for establishment, have often been proposed to explain differences in natal dispersal behavior (Nilsson and Smith, '85). Indeed, foraging activity has been found to increase at the onset of dispersal period in some species of birds (Belthoff and Dufty, '98). We also found in this study that foraging activity was different between dispersing and philopatric individuals. At birth, future dispersers were less prompt to catch prey than future philopatric individuals, and, 10 months later, this difference persisted when examining the latency to prey capture. Although it remains difficult to interpret these results, the confrontation with other results in the same species helps to propose a scenario. In natural conditions, dispersers were demonstrated to grow less rapidly than philopatric individuals during their first year of life (Bélichon et al., '96). When observed in semi-natural conditions (field enclosures), dispersers displayed more exploratory behaviors than philopatric individuals (Clobert et al., '94). This suggests that different allocation strategies between activity compartments (food acquisition, exploration, etc.) might constitute the basis for dispersal-dependent foraging characteristics.

Dispersal status and conspecific interactions

Dispersers have been suggested to be either subdominant, solitary or less aggressive individuals (Clobert et al., 2004). For example, Gathereaux ('78) demonstrated that, in birds, dominance rank could be used to predict dispersal distance. Rather than social dominance, social tolerance might be more important in promoting dispersal (Léna et al., '98, Clobert et al., 2004). Indeed, we recently discovered that social tolerance at birth and population density interacted to shape dispersal patterns (Cote and Clobert, 2007a). However, performance in social interactions has rarely been assessed through confrontations, and even less so within and between individuals of the same or different dispersal status. Here we provide evidence that the dispersal status of individuals in a pair affected the outcome of the confrontation. When confronted with conspecifics of the same dispersal status, individuals were more active than when confronted with conspecifics of a different status. This result, along with those of Aragón et al. (2006c) and Cote and Clobert (2007b), strongly suggests that individuals can recognize the dispersal status of same-age conspecifics,

probably directly through their behavioral profile. Indeed, when we used olfactory cues (results not shown), the dispersal status of the odor's donor did not influence the juvenile behavioral response (Aragón et al., 2006a,c). In other words, the physical presence would be required for a behavioral expression of a conspecific dispersal status recognition.

Direct agonistic interactions (bites, chases) were rare and did not depend on dispersal status. Inter-individual distance (a potentially more subtle measure of dominance) was also not dependent on the dispersal status of the individuals in a pair. Only the pattern of activity (walking within the terrarium and trying to escape the terrarium) has been affected but not in the way predicted by the social dominance hypothesis. All individuals, whatever their dispersal status, were increasing their attempts to escape from the terrarium when faced with a disperser.

If the social dominance hypothesis is excluded, why then are individuals affected by the dispersal status of one another? Dispersers or philopatric individuals, besides being individuals displaying different strategies, might also carry some information about their natal and/or current environment (Clobert et al., 2004; Cote and Clobert, 2007b). This information might be of interest to some conspecifics when the latter have to make decisions about their social and/or non-social environment. It might even represent some sort of public information (Valone, '89; Danchin et al., 2004). In this context, natural selection could have promoted a dispersal status-dependent recognition. This scenario has the advantage to match some explanations provided to understand earlier results on dispersal behavior. For example, in a study aimed at understanding the role of connection in the population dynamics of this species, Lecomte et al. (2004) found experimentally that the number of dispersal attempts was positively density-dependent in connected populations, whereas it was not dependent on density in unconnected populations. Furthermore, in unconnected situations, the return of dispersers to their population of origin was followed by a second dispersal peak. This indeed may suggest that the information brought by dispersers has some influence on dispersal decisions made by other individuals. The extent to which the dispersal status of an individual serves as a cue on habitat quality for other individuals (Stamps, '87; Muller, '98, 2001; Danchin et al., 2001) obviously deserves more research (Aragón et al., 2006b).

The origin of a dispersal-dependent behavioral profile

Most of the studies on personalities and behavioral syndromes suggest that there is a considerable amount of genetic variation for personality types (territorial temperament, shy-bold, etc.) and that the behavioral variation is heritable (in birds: Drent et al., 2003; in lizards: Stapley and Keogh, 2004; López et al., 2005). In the same way, it has been recently proposed that personalities that characterize the behavioral strategies of philopatric and dispersing individuals have a strong genetic determinism (Dingemanse et al., 2003). Although we did not study personalities/temperaments or behavioral syndromes per se as we neither use the same individuals at birth and at 10 months of age nor the same individuals for the different behavioral assays (Sih et al., 2004; Groothuis and Carere, 2005), we nevertheless observed that foraging behavior measured at birth was related to dispersal status later on, and that the activity when facing a conspecific and foraging efficiency measured after dispersal were still characterizing individuals that had or had not dispersed. This is somehow in contradiction with the high phenotypic plasticity of dispersal recorded in our species (Massot and Clobert, 2000; Dufty et al., 2002) as in many others species (Ims and Hjernmann, 2001). This can suggest a conservation of dispersal-dependent behavioral traits, which, in turn, militates for some genetic control or some very early determination of these behaviors. However, as these behavioral traits have not been measured on the same individuals, we have to remain cautious about this scenario at this stage.

ACKNOWLEDGMENT

We thank Manuel MASSOT and Jean-François LE GALLIARD for discussion, Borja MILA. We thank everyone who helped to collect data, and the "Office National des Forêts" and the "Parc National des Cévennes" for providing good conditions to work in the field. The CNRS (grant "Environnement vie et société" 98N62/0120) supported this study. This work complied with the current laws of France.

LITERATURE CITED

- Aars J, Johannesen E, Ims RA. 1999. Demographic consequences of movements in subdivided root vole populations. *Oikos* 85:204–217.

- Aragón P, Clobert J, Massot M. 2006a. Individual dispersal status influences space use of conspecific residents. *Behav Ecol Sociobiol* 60:430–438.
- Aragón P, Massot M, Gasparini J, Clobert J. 2006b. Socially acquired information through chemical cues in the common lizard, *Lacerta vivipara*. *Anim Behav* 72:965–974.
- Aragón P, Meylan S, Clobert J. 2006c. Dispersal status-dependent response to the social environment in the Common Lizard, *Lacerta vivipara*. *Funct Ecol* 20:900–907.
- Belthoff JR, Dufty Jr A. 1998. Corticosterone, body condition and locomotor activity: a model for dispersal in screech-owls. *Anim Behav* 55:405–415.
- Bélíchon S, Clobert J, Massot M. 1996. Are the differences in fitness components between philopatric and dispersing individuals. *Acta Oecol* 17:503–517.
- Clobert J, Massot M, Lecomte J, Sorci G, de Fraipont M, Barbault R. 1994. Determinants of dispersal behavior: the common lizard as a case study. In: Vitt L, Pianka R, editors. *Lizard ecology: historical and experimental perspectives*. Princeton: Princeton University Press. p 183–206.
- Clobert J, Oppliger A, Sorci G, Ernande B, Swallow JG, Garland T. 2000. Trade-offs in phenotypic traits: endurance at birth, growth, survival, predation and susceptibility to parasitism in a lizard, *Lacerta vivipara*. *Funct Ecol* 14:675–684.
- Clobert J, Danchin E, Dhondt AA, Nichols JD. 2001. *Dispersal*. Oxford: Oxford University Press.
- Clobert J, Ims R, Rousset F. 2004. Causes, mechanisms and consequences of dispersal. In: Hanski I, Gaggiotti OE, editors. *Metapopulation biology*. San Diego, USA: Elsevier Academic Press; 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.
- Cote J, Clobert J. 2007a. Social personalities influence natal dispersal in a lizard. *Proc R Soc B* 274:383–390.
- Cote J, Clobert J. 2007b. Social information and emigration: lessons from immigrants. *Ecol Lett* 10:411–417.
- Cote J, Dreiss A, Clobert J. 2008. Social personalities and fitness. *Proc R Soc Lond B* 275:2851–2858.
- Danchin E, Heg D, Doligez B. 2001. Public information and breeding habitat selection. In: Clobert J, Danchin E, Dhondt AA, Nichols JD, editors. *Dispersal*. Oxford: Oxford University Press. p 243–258.
- Danchin E, Giraldeau LA, Valone TJ, Wagner RH. 2004. Public information: from nosy neighbors to cultural evolution. *Science* 305:487–490.
- Davis JM, Stamps JA. 2004. The effect of natal experience on habitat preferences. *Trends Ecol Evol* 19:411–416.
- de Fraipont M, Clobert J, John-Alder H, Meylan S. 2000. Increased prenatal maternal corticosterone promotes philopatry of offspring in common lizard (*Lacerta vivipara*). *J Anim Ecol* 69:404–413.
- Denno RF, Peterson MA. 1995. Density-dependent dispersal and its consequences for dynamics. In: Cappuccino N, Price PW, editors. *Population dynamics: new approaches and synthesis*. San Diego, CA: Academic Press. p 113–130.
- Dingemanse NJ, Both C, van Noordwijk AJ, Rutten AL, Drent PJ. 2003. Natal dispersal and personalities in great tits (*Parus major*). *Proc R Soc Lond B* 270:741–747.
- Dixon AFG. 1985. *Aphid ecology*. Glasgow: Blackie.

- Drent PJ, Van Oers K, Van Noordwijk AJ. 2003. Realized heritability of personalities in the great tit (*Parus major*). *Proc R Soc Lond B* 270:45–51.
- Dufty Jr AM, Belthoff JR. 2001. Proximate mechanisms of natal dispersal: the role of body condition and hormones. In: Clobert J, Danchin E, Dhondt AA, Nichols JD, editors. *Dispersal*. Oxford: Oxford University Press. p 223–233.
- Dufty Jr. AM, Clobert J, Moller AP. 2002. Hormones, developmental plasticity and adaptation. *Trends Ecol Evol* 17:190–196.
- Edelaar P, Siepielski AM, Clobert J. 2008. Matching habitat choice causes directed genes flow: a neglected dimension in evolution and ecology. *Evolution* 62:2462–2472.
- Fraser DF, Gilliam JF, Daley MJ, Le AN, Skalski GT. 2001. Explaining leptokurtic movement distributions: intrapopulation variation in boldness and exploration. *Am Nat* 158:124–135.
- Gauthreaux SA Jr. 1978. The ecological significance of behavioral dominance?. In: Bateson PPG, Klopfer PH, editors. *Perspectives in Ethology*, vol. 3. New York: Plenum Press. 177–254.
- Groothuis TGG, Carere C. 2005. Avian personalities: characterization and epigenesis. *Neurosci Biobehav Rev* 29:137–150.
- Ims RA 1990. Determinants of natal dispersal and space use in grey-sided voles, *Clethrionomys rufocanus*: a combined field and laboratory experiment. *Oikos* 57:106–113.
- Ims RA, Hjermann DO. 2001. Condition-dependent dispersal. In: Clobert J, Danchin E, Dhondt AA, Nichols JD, editors. *Dispersal*. Oxford: Oxford University Press. p 203–216.
- Johannesen E, Andreassen H. 1998. Survival and reproduction of resident and immigrant root vole (*Microtus oeconomus*) females. *Can J Zool* 76:763–766.
- Knapp R, Moore MC. 1997. A non-invasive method for sustained elevation of steroid hormone levels in reptiles. *Herpetol Rev* 28:33–36.
- Lecomte J, Clobert J, Massot M. 1992. Sex identification in juveniles of *Lacerta vivipara*. *Amphibia Reptilia* 13:21–25.
- 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.
- Le Galliard, J-F, Ferrière R, Clobert J. 2003. Mother-offspring interactions affect natal dispersal in a lizard. *P Roy Soc Lond B* 270:1163–1169.
- Lemel JY, Belichon S, Clobert J, Hochberg ME. 1997. The evolution of dispersal in a two-patch system: Some consequences of differences between migrants and residents. *Evol Ecol* 11:613–629.
- Léna JP, 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 JP, de Fraipont M, Clobert J. 2000. Affinity towards maternal odour and offspring dispersal in the common lizard. *Ecol Lett* 3:300–308.
- López P, Hawlena D, Polo V, Amo L, Martin J. 2005. Sources of individual shy-bold variations in antipredator behaviour of male Iberian rock lizards. *Anim Behav* 69:1–9.
- Lorenzon P, Clobert J, Oppliger A, John-Alder H. 1999. Effect of water constraint on growth rate, activity and body temperature of yearling common lizard (*Lacerta vivipara*). *Oecologia* 118:423–430.
- Lorenzon P, Clobert, J, Massot M. 2001. The contribution of phenotypic plasticity to adaptation in *Lacerta vivipara*. *Evolution* 55:392–404.
- MacKay PA, Wellington WG. 1977. Maternal age as a source of variation in the ability of an aphid to produce dispersing forms. *Res Popul Ecol* 18:195–209.
- 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, Pilorge T, Lecomte J, Barbault R. 1992. Density dependence in the common lizard: demographic consequences of a density manipulation. *Ecology* 73:1742–1756.
- McCullagh P, Nelder JA. 1989. *Generalized linear models*. New York: Chapman and Hall.
- Meylan S, Clobert J. 2004. Maternal effects on offspring locomotion: influence of density and corticosterone elevation in the lizard *Lacerta vivipara*. *Physiol Biochem Zool* 77:450–458.
- Meylan S, Clobert J. 2005. Is corticosterone-mediated phenotype development adaptive? maternal corticosterone treatment enhances survival in male lizards. *Horm Behav* 48:44–52.
- Meylan S, Belliure J, Clobert J, de Fraipont M. 2002. Stress and body condition as prenatal and postnatal determinants of dispersal in the common lizard (*Lacerta vivipara*). *Horm Behav* 42:319–326.
- Meylan S, Dufty Jr AM, Clobert J. 2003. The effect of transdermal corticosterone application on plasma corticosterone levels in pregnant *Lacerta vivipara*. *Comp Biochem Physiol* 134:497–503.
- 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.
- Meylan S, Clobert J, Sinervo B. 2007. Adaptive significance of maternal induction of density-dependent phenotypes. *Oikos* 116:650–661.
- Muller KL 1998. The role of conspecifics in habitat settlement in a territorial grasshopper. *Anim Behav* 56:479–485.
- Murren CJ, Julliard R, Schlichting CD, Clobert J. 2001. Dispersal, individual phenotype, and phenotypic plasticity. In: Clobert J, Danchin E, Dhondt AA, Nichols JD, editors. *Dispersal*. Oxford: Oxford University Press. p 261–272.
- Nelson EM, DeBault LE. 1978. Transformation in *Tetrahymena pyriformis*: description of an inducible phenotype. *J Protozool* 25:113–119.
- Nilsson JA, Smith HG. 1985. Early fledgling mortality and the timing of juvenile dispersal in the marsh tit *Parus palustris*. *Ornis Scandinavica* 16:293–298.
- Nunes S, Holekamp KE. 1996. Mass and fat influence the timing of natal dispersal in breeding Belding's ground squirrels. *J Mammal* 77:807–817.
- O'Riain MJ, Braude S. 2001. Inbreeding versus outbreeding in captive and wild populations of naked mole-rats. In: Clobert J, Danchin E, Dhondt AA, Nichols JD, editors. *Dispersal*. Oxford: Oxford University Press. p 143–154.
- O'Riain MJ, Jarvis JUM, Faulkes C. 1996. A dispersive morph in the naked mole-rat. *Nature* 380:619–621.
- Pollard I 1984. Effects of stress administered during pregnancy on reproductive capacity and subsequent

- development of the offspring of rats: prolonged effects on the litters of a second pregnancy. *J Endocrinol* 100: 301–306.
- Roff DA, Fairbairn DJ. 2001. The genetic basis of dispersal and migration and its consequences for the evolution of correlated traits. In: Clobert J, Danchin E, Dhondt AA, Nichols JD, editors. *Dispersal*. Oxford: Oxford University Press. p 195–207.
- Ronce O, Clobert J, Massot M. 1998. Natal dispersal and senescence. *Proc Natl Acad Sci USA* 95:600–605.
- SAS 1996. SAS/STAT software changes and enhancements through release 6.11. Cary, NC: SAS Institute.
- Sih A, Bell A, Johnson JC. 2004. Behavioral syndromes: an ecological and evolutionary overview. *Trends Ecol Evol* 19:372–378.
- Sinervo B, Calsbeek R, Comendant T, Both C, Adamopoulou C, Clobert J. 2006. Genetic and maternal determinants of effective dispersal: the effect of sire genotype and size at birth in side-blotched lizards. *Am Nat* 168:88–99.
- Stamps JA 1987. Conspecifics as cues to territory quality: a preference of juvenile lizard (*Anolis aeneus*) for previously used territories. *Am Nat* 129:629–642.
- Stamps JA. 2001. Habitat selection by dispersers: integrating proximate and ultimate approaches. In: Clobert J, Danchin E, Dhondt AA, Nichols JD, editors. *Dispersal*. Oxford: Oxford University Press. p 230–242.
- Stapley J, Keogh JS. 2004. Exploratory and antipredator behaviours differ between territorial and nonterritorial male lizards. *Anim Behav* 68:841–846.
- Takahashi LK, Kalin NH, Barkdale CM, Vanden Burgt JA. 1988. Stressor controllability during pregnancy influences pituitary–adrenal hormone concentrations and analgesic responsiveness in offspring. *Physiol Behav* 42:323–329.
- Valone TJ 1989. Group foraging, public information, and patch estimation. *Oikos* 56:357–363.
- Venable DL, Dyreson E, Pinero D, Beccara JX. 1998. Seed morphometrics and adaptive geographic differentiation. *Evolution* 52:344–354.
- Verbeek MEM, Drent PJ, Wiepkema RP. 1994. Consistent individual differences in early exploratory behaviour of male great tits. *Anim Behav* 48:1113–1121.
- Vercken E, de Fraipont M, Dufty Jr 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.
- Walsh RN, Cummins AR. 1976. The open-field test: a critical review. *Psychol Bull* 83:482–504.
- Woodroffe RB, MacDonald DW, da Silva J. 1993. Dispersal and philopatry in the European badger, *Meles meles*. *J Zool* 237:227–239.