

# Dispersal status-dependent response to the social environment in the Common Lizard, *Lacerta vivipara*

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## Summary

1. Individuals following different strategies such as philopatry or dispersal may also differ in other phenotypic traits, since dispersing individuals have to face novel physical and social environments. There is growing evidence of the use of information obtained from conspecifics in a variety of contexts. It has been demonstrated that before natal dispersal, juveniles of *Lacerta vivipara* use social information through conspecific chemical cues, and that various phenotypes use this information differently. We hypothesized that, after dispersal, the behavioural responses of yearlings to different social environments assessed through conspecific odours depend on the dispersal status.

2. We tested the response of philopatric and dispersing yearlings of *L. vivipara* to different types of social cues, controlling for the prenatal and postnatal environment. Each yearling was faced with environments with no conspecific odours, with scent-marks from one or three yearlings that were held isolated during captivity, and from three socially housed yearlings. Thus, we examined the response to the number of donors and to the social environment experienced by donors. We recorded the time spent walking and attempting to escape as indicators of activity and avoidance response, respectively.

3. Philopatric and dispersing individuals reacted differently to the social environments presented through odour marks. This dispersal status-dependent response was not modulated by the prenatal and postnatal factors examined.

*Key-words:* Behavioural syndromes, chemical communication, dispersal, social information

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## Introduction

Natal dispersal, defined as the complete and permanent departure of an individual from its natal site, is a three-step process (Clobert *et al.* 2001). The first phase consists of the departure of an individual from its natal site. Next comes the transient phase, and finally the individual settles in a new environment. Thus, during the transient and settlement phases, individuals are faced with new social and physical environments.

Theoretical and empirical studies have both shown that the transient and settlement phases may have a negative impact on fitness (Bélíchon, Clobert & Massot 1996; Lemel *et al.* 1997) as a consequence of the costs of unfamiliarity with the new habitat, in terms of exploration, competition, predation, starvation, etc.

(Stamps 2001). There are many examples showing differences in fitness between dispersing and philopatric individuals (Bélíchon *et al.* 1996). However, differences in life-history traits are not always unfavourable to dispersers, since compensations among fitness components has been reported in lizards (Massot *et al.* 1994), birds (Clobert *et al.* 1988; McCleery & Clobert 1990) and mammals (Creel & Waser 1994; Van Vuren & Armitage 1994). Thus, if philopatry and dispersal constitute strategies, we might expect that individuals following these strategies to differ in other phenotypic traits, enabling them to lower the costs of the transient and settlement phases. To predict the consequences of dispersal on the structure of populations, better knowledge of the phenotypic correlates of dispersal is needed (Dingemanse *et al.* 2003; Sih *et al.* 2004). Other than the species in which dispersers show a specialized morphology (e.g. Murren *et al.* 2001), there are only a few examples where more subtle adaptations have

been reported (physiology: Holekamp & Smale 1998; behavioural traits: Pastschniak-Arts & Bendel 1990; Clobert *et al.* 1994; Wilson *et al.* 1994; de Fraipont *et al.* 2000; Fraser *et al.* 2001; Dingemans *et al.* 2003). As can be expected from the theory (Lemel *et al.* 1997), these cases indicate that dispersers are more likely than residents to quickly assess habitat suitability.

Individuals may assess habitat quality through an indirect assessment of the environment, which is less costly than by direct probing (Danchin, Heg & Doligez 2001). The cues involved in an indirect assessment may include the presence of conspecifics (Stamps 1987) or more complex types of social information, such as the performance of conspecifics (Valone & Templeton 2002; Danchin *et al.* 2004). The conspecific attraction hypothesis proposes that dispersers benefit from the presence of conspecifics in either the transient or settlement phases because this may reflect good habitat quality (Stamps 1987, 2001). What is more, there is growing evidence that, besides the presence *per se*, individual attributes are used as cues in many species (Danchin *et al.* 2001), as in any information obtained from observing the behaviour of others (socially acquired information, Giraldeau, Valone & Templeton 2002; Valone & Templeton 2002).

To examine the response after the dispersal departure to the social environment experienced by signalers we conducted an experiment using the Common Lizard, *Lacerta vivipara*, as a model system. The presence of conspecifics as a social cue has already been demonstrated in lizards (Kiestler 1979; Stamps 1987). A previous study on the Common Lizard revealed that hatchlings before natal dispersal react to different types of social information (Aragón *et al.* 2006a) and that there is intraspecific variability in the ability to settle in a new, already occupied, environment (Massot *et al.* 1994).

To test the hypothesis that responses to different social environments depend on the dispersal status, we compared the behaviour of philopatric and dispersing yearlings when faced with scent-marks from isolated or socially housed yearlings. We chose odour cues because: (1) the potential savings in both time and energy are important in species living in dense vegetation (Alberts & Werner 1993) and (2) in reptiles, chemical senses play an important role in intraspecific communication (Halpern 1992; Mason 1992; Cooper 1994), and the available literature indicates that lacertids are capable of finer chemosensory discrimination than was previously recognized (e.g. Léna & de Fraipont 1998; Aragón, López & Martín 2001; Aragón *et al.* 2006a).

To examine the potential role of the prenatal or postnatal environment on the behavioural differences between philopatric and dispersing individuals, we performed experimental manipulations in the laboratory and in four plots of the field study before starting the natal dispersal. More specifically: (1) we decreased the density in two study plots to test the

effect of density experienced by mothers (prenatal effect), (2) we manipulated the circulating levels of corticosterone of pregnant females to test whether there is an effect of the mothers' physiological stress (prenatal effect), (3) after parturition, we released clutches and distributed them equally through the two density levels in the study plots (postnatal effect), and (4) we performed a laboratory experiment in the following season with captured philopatric and dispersing yearlings to examine the behavioural response to different social environments reflected in conspecific scents. Thus, we examined the influence of individual past history (site of origin, density at the site of origin, site of release, density at the site of release and maternal stress during pregnancy) on the response to the social environment.

## Materials and methods

### MODEL ORGANISM

*Lacerta vivipara* is a small, live-bearing lacertid species (50–70 mm adult snout–vent length) inhabiting peat bogs and heath lands. This species is widely distributed across Eurasia, and is found in a large variety of environmental situations, as witnessed by the wide variability of its life-history traits (Sorci, Clobert & Bêlichon 1996). In the four studied sites (Mont Lozère, Cévennes, France, 44°30' N 3°45' E, average elevation 1450 m), mating takes place in May (hibernation is from October to April). After 2 months of gestation, parturition usually begins by mid-July and lasts for 3 weeks. On average, 5 (range 1–13) thin-shelled eggs are laid and usually hatch within 1–2 h after laying.

### EXPERIMENTAL MANIPULATIONS BEFORE NATAL DISPERSAL

We selected four study sites (hereafter A, B, C and D) that were close to one another (range: 450–3350 m) to perform the density manipulation. In early May 2000 and 2001, the density in sites C and D was reduced by 25% by removing individuals from all age classes, whereas sites A and B remained unaltered (see Meylan & Clobert 2004 for more details). In late June 2001, we temporarily removed 172 pregnant females (50 from study site A, 41 from B, 40 from C and 41 from D). Females were housed individually until parturition in plastic terraria (18 × 12 × 12 cm) with about 1 cm of soil and a shelter, and exposed to a natural daylight. In addition, an incandescent lamp was provided for 6 h per day. They were fed with one larva of *Pyralis farinalis* once a week, according to standardized rearing conditions (Massot & Clobert 2000). We increased the circulating level of corticosterone in half these females by applying a solution of sesame oil with diluted corticosterone to their backs. Only sesame oil was applied to other half as a placebo (see Meylan *et al.* 2002; Meylan, Dufty & Clobert 2003 for more details). With this procedure we aimed to examine whether a prenatal

determination of the response to the social environment existed.

At birth, juveniles were individually marked by means of toe-clipping. Natural toe loss has been observed in this species and toe-clipping has been shown to have no effect on the sprint speed or fitness (Dodd 1993; Ott & Scott 1999). Afterwards, we split the juveniles of each clutch in two halves: one half was released in a decreased density site and the other in an unaltered density site. None of the juveniles was released in the mother's site of origin. Thus, with this manipulation we ensured no link between the prenatal and the postnatal environments and, in addition, we avoided mother-offspring postnatal interactions (or with other relative adults). Therefore, this procedure allows the prenatal and postnatal effect on the response to the environment by yearlings to be disentangled.

#### DISPERSAL STATUS

The dispersal of juvenile status was assessed by comparing the release coordinates to the coordinates of the last recapture point (hand recaptures in each study site in May 2002). A grid of markers spaced 5 m apart allowed the location of recapture points to be calculated within 1.5 m. The recapture rate of yearlings born in the laboratory (816 offspring released) was 17.15% (140 yearlings recaptured). We defined those juveniles that moved a distance greater than 20 m (upper 95% confidence limit of the adult female home range diameter) as dispersers, and those that moved less than 15 m (average adult female of the home range diameter) as philopatrics. This definition of dispersal is consistent since individuals classified as dispersers according to this criterion never return to their release site (Clobert *et al.* 1994). Offspring that moved distances between these two values were not used in the laboratory experiment to avoid confounding effects between home range movement and effective dispersal. In addition, these classification thresholds correspond to the interval where the distribution of distances becomes steeper.

#### LABORATORY EXPERIMENT

After the departure phase, which takes place a few days after birth in this species (Clobert *et al.* 1994), 2001-born yearlings were captured in May 2002 and transferred to the laboratory. Responding individuals were then maintained in isolated conditions (only one individual per cage) on different shelves to ensure that no visual or olfactory contact could take place among them. After 2 days of isolation, each individual was placed in a clean new experimental cage where three pieces of blotting paper either with no odour or impregnated with the odour of conspecifics were introduced. For each trial, we recorded two response variables for 10 min: the time that yearlings were walking

around the experimental cage and the time that the lizards were attempting to escape (scratching or trying to climb the walls of the cage). Previous studies showed that the time walking and the time attempting to escape are good indicators of activity and the degree of avoidance of an area, respectively (de Fraipont *et al.* 2000; Aragón, López & Martín 2003, 2006b). The response of yearlings was recorded after 1 min of habituation to the experimental cage to avoid effects of handling.

To obtain odours, absorbent paper was placed so that it covered the entire floor of the captivity cages of donor yearlings held either in isolation or in groups (three yearlings) for 2 days. After the scent-marking process, the paper was cut into pieces by operators wearing rubber gloves. Four sets of experiments were then performed according to the type of odours present on three pieces of blotting paper: (1) all three pieces with no odour as the control (hereafter C); (2) all three pieces with the odour of a single yearling donor (1D); (3) each piece with the odour of a different yearling held in isolation (three donors isolated, 3DI); and (4) all three pieces with the odour of three communally held yearlings (3DC). The last two experiments were meant to analyse the response to the absence or presence of information on social interactions in which responding individuals did not participate. A recent study with this species showed that before dispersal, hatchlings were able to discriminate between scent-marks from isolated and socially housed conspecifics, supporting the claim that chemical cues may reflect the level of social interactions (Aragón *et al.* 2006a). Fifty-eight responding yearlings (representing 46 clutches) of known dispersal status (32 philopatric and 26 dispersers) were used in the trials. Each yearling was tested in all conditions in a repeated measures design and in random order.

#### DATA ANALYSIS

We first used one-way ANOVAS (PROC GLM, SAS Institute 1999) to test for potential differences in morphometric traits between philopatrics and dispersers. In addition, to examine whether there was a relationship between the response variables and morphometric traits we used regression analyses (Procedure REG, SAS Institute 1999).

To measure the difference in response to a novel environment with no social cues, time spent walking and attempting to escape was recorded for all yearlings. In experiment C, when no odour was introduced into the cage, the response of yearlings was assessed according to their dispersal status and controlling for their site of origin, the density at the origin site, the release site, the density at the release site, the hormonal treatment of the mother, and the sex of yearlings as factor effects (PROC GLM, SAS Institute 1999). The effects of the origin and release sites were nested within the density-at-origin and the density-at-release factors,

respectively. Thus, density effects and their interactions were tested specifying the corresponding nested effects as error terms either as main effects or interactions. We started with a general model including all of the main effects and their first-order interactions with the dispersal status. We then selected the most parsimonious model by backward selection (McCullagh & Nelder 1989), dropping all non-significant terms starting with the interactions.

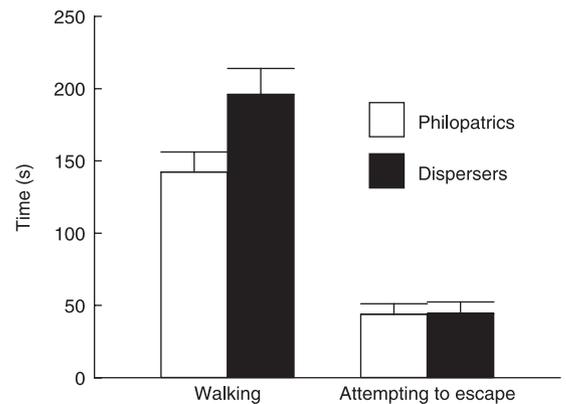
To assess the effect of conspecific chemical cues, we performed the same statistical procedures as above, but the result of the difference between two individual scores obtained from two different treatments was used as a single dependent variable. The first analysis compared, between philopatrics and dispersers, the result of the difference between the time walking (or attempting to escape) in the control experiment (C) and in the single donor experiment (1D) (i.e. C minus 1D). By means of this analysis, we aimed to test whether the response to scents from a conspecific of the same age class is dependent on the dispersal status of responding yearlings. The second analysis compared the result of the differences in the same variables (time walking or attempting to escape) between the experiment with a single donor (1D) and the experiment with odour from three yearlings held isolated (3DI) (1D minus 3DI). Thus, we tested whether yearlings with different dispersal status react differently when the number of donors is increased. Finally, the third analysis compared the result of the difference between the experiment with the odour from three yearlings held isolated (3DI) and the experiment with the odour from three yearlings held communally (3DC) (3DI minus 3DC). Here we tested whether, according to their dispersal status, yearlings respond differently to the social environment experienced by donors.

We used one-way repeated measures analyses (PROC GLM, SAS Institute 1999) to perform local tests in case. We used angular transformation when necessary to meet the assumptions underlying the application of linear models (Sokal & Rohlf 1995). Because families were represented by a maximum of two siblings, regression analyses (Procedure REG, SAS Institute 1999) were used to test whether there was a family effect on the response variables measured for the 11 repeated families. Unadjusted probabilities are reported, but significance was verified using the sequential Bonferroni adjustment for each family of tests (Chandler 1995).

## Results

### INDIVIDUAL MORPHOMETRIC TRAITS

Morphometry did not differ between dispersers and philopatrics (one-way ANOVA; total length:  $F_{1,56} = 0.01$ ,  $P = 0.937$ ; SVL:  $F_{1,56} = 0.37$ ,  $P = 0.547$ ; weight:  $F_{1,56} = 0.01$ ,  $P = 0.929$ ; corpulence:  $F_{1,56} = 1.857$ ,  $P = 0.178$ ) as was shown in a previous study with yearlings



**Fig. 1.** Time spent walking and attempting to escape (mean +1 SE) by philopatric and dispersing yearlings in the experimental cages with no conspecific odours.

of this species (Clobert *et al.* 1994). There were no significant relationships between the response variables and morphometric traits ( $P > 0.05$  in all cases).

### ENVIRONMENT WITHOUT SOCIAL INFORMATION

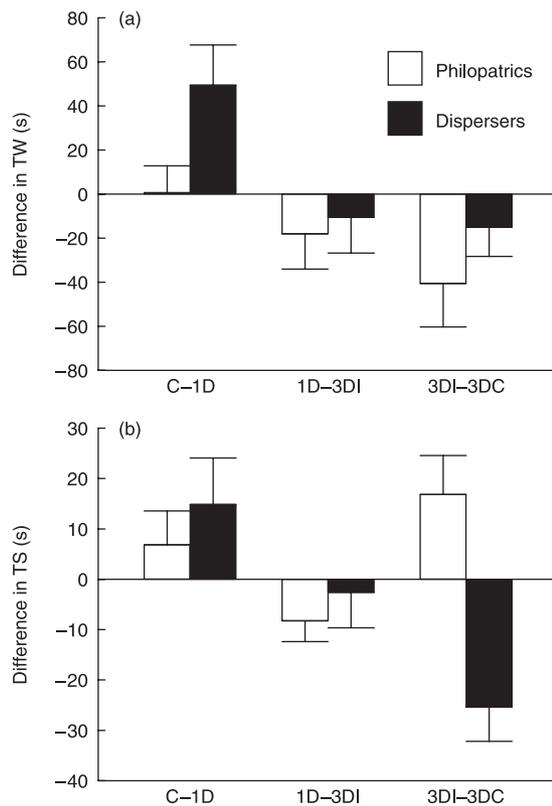
When yearlings were faced with a novel environment with no conspecific odour (C), dispersing individuals spent significantly more time walking than philopatrics ( $F_{1,56} = 10.16$ ,  $P = 0.002$ ; Fig. 1) whereas there were no significant effects of the origin site, the density at the origin site, the release site, the density at the release site, the hormonal treatment of the mother, the sex of yearlings or their interactions ( $P > 0.05$  in all cases). There was no dispersal status-dependent response for the time spent attempting to escape ( $F_{1,55} = 0.15$ ,  $P = 0.70$ ; Fig. 1) or any other effect ( $P > 0.05$  in all cases).

### ENVIRONMENT WITH SOCIAL INFORMATION

The response to the odour of a conspecific (the difference between C and 1D in time walking) was strongly status-dependent ( $F_{1,51} = 7.44$ ,  $P = 0.008$ ; Fig. 2a).

Yearlings that dispersed devoted significantly less time to walking when faced with scents from a conspecific (repeated measures one-way ANOVA;  $F_{1,25} = 5.77$ ,  $P = 0.024$ ; Fig. 2a), whereas philopatrics did not change their behaviour (repeated measures one-way ANOVA;  $F_{1,31} = 0.31$ ,  $P = 0.581$ ; Fig. 2a). In addition, the effect of the site where juveniles were released was significant ( $F_{3,51} = 4.20$ ,  $P = 0.009$ ), though other effects or interactions were not significant (all  $P > 0.05$ ). The time spent attempting to escape was not influenced by any effect included in the analysis ( $P > 0.05$  in all cases).

The increase in the number of donors held isolated (the difference between 1D and 3DI) did not influence the time spent walking or attempting to escape, either directly or depending on the dispersal status (Fig. 2a,b) or other effects (all  $P > 0.05$ ).



**Fig. 2.** Individual score differences between two treatments in time spent by philopatric and dispersing yearlings: (a) walking (TW) (mean + 1 SE) and (b) attempting to escape (scratching or trying to climb the walls of the experimental cages) (TS) (mean + 1 SE) through the experimental cages. C – 1D: response to the control treatment (no odour) minus the response to the conspecific odour from one donor. 1D – 3DI: response to the odour from one donor minus the response to the odour from three donors that were held isolated. 3DI – 3DC: response to the odour from three donors that were held isolated minus the response to the odour from three donors that were held communally.

The social environment experienced by donors influenced the time spent walking (the difference between 3DI and 3DC). Yearlings spent more time walking in 3DC than in 3DI ( $F_{1,57} = 5.47$ ,  $P = 0.022$ ; Fig. 2a), and this response was not dependent on the dispersal status ( $F_{1,56} = 1.05$ ,  $P = 0.309$ ; Fig. 2a) or any other effect (all  $P > 0.05$ ). In contrast, the social environment experienced by donors influenced the time attempting to escape in a status-dependent way ( $F_{1,56} = 17.90$ ,  $P < 0.0001$ ; Fig. 2b). Dispersers spent more time attempting to escape in 3DC than in 3DI (repeated measures one-way ANOVA;  $F_{1,25} = 13.81$ ,  $P = 0.001$ ; Fig. 2b), whereas the opposite was true for yearlings that did not disperse (repeated measures one-way ANOVA;  $F_{1,31} = 5.66$ ,  $P = 0.023$ ; Fig. 2b). Other factors or their interactions had no significant effects ( $P > 0.05$  in all cases).

There were no significant relationships between siblings for any variable measured (regression analyses;  $N = 11$ , all  $P > 0.05$ ).

## Discussion

Yearlings that dispersed and those that remained philopatric differed in their behaviour 8 months after the departure phase. When faced with an environment with no social information, dispersers were more active than philopatrics. The introduction of social information through conspecific chemical cues strongly modified activity patterns in a status-dependent way. In the presence of the scent from a conspecific held isolated, dispersers spent less time walking, while philopatric individuals did not modify their activity patterns significantly. In the presence of scents from conspecifics held communally, dispersers spent more time attempting to escape whereas philopatrics showed an opposite trend. Clearly, the response to social information was dependent on the dispersal status. The differences found here are not related to morphometric differences. Finally, although the site of release in one case had an effect on the time spent walking, this factor did not interact significantly with the dispersal status.

### ENVIRONMENT WITHOUT SOCIAL INFORMATION

When lizards were faced with a novel environment with no conspecific odours, dispersers spent more time walking around the experimental cage than philopatrics. This result agrees with a previous experiment in which dispersing yearlings of *L. vivipara* were more active than philopatric ones in natural conditions (Clobert *et al.* 1994). This confirms that the behaviour recorded in a confined environment reflects that found in more natural conditions. It has been found that individuals of *L. vivipara* with a high activity also had high endurance at birth (Clobert *et al.* 2000), which might be of adaptive value for dispersing individuals to afford the costs of the transient phase. There is growing evidence of activity patterns in a novel environment that differ in the tendency to disperse. For example, a positive correlation has been found between dispersal distance and exploratory behaviour in a bird species (Dingemanse *et al.* 2003), or with boldness in a fish species (Fraser *et al.* 2001). Our result further documents the existence of a link between behavioural syndromes and dispersal (reviewed in Sih *et al.* 2004).

### ENVIRONMENT WITH SOCIAL INFORMATION

The presence of the odour of a conspecific led to a marked decrease in the time dispersers spent walking, whereas this did not affect philopatric individuals. This result was not influenced by an increase in the number of conspecifics when odours were collected from isolated individuals. The presence of a conspecific clearly modifies the activity pattern of dispersers, supporting the hypothesis that the social environment influences dispersing and philopatric individuals differently.

It has been reported in other species that locally recruited individuals and immigrants showed behavioural and/or physiological differences (Woollard & Harris 1990; Holekamp & Smale 1998; Rosenberry, Conner & Lancia 2001). However, none of these studies controlled for the past social environment or the immigrants' population of origin. This study provides the first indication that the different reaction of dispersing and philopatric individuals towards the social information cannot be caused by a population difference or by different maternal histories, since these effects had no significant interactions with the dispersal status.

In a previous study with *L. vivipara* the selection of nocturnal shelters by hatchlings before the dispersal departure phase was dependent on whether scent marks came from isolated or socially housed conspecifics, showing that social information assessed through chemical cues may reflect interactions among donors (Aragón *et al.* 2006a). Results of the present study show that after the departure phase dispersing individuals are more sensitive to novel social environments. They seem to avoid chemical cues from conspecifics that had experienced interactions in which responding yearlings did not participate. In contrast, philopatric individuals showed a tendency to reduce their attempts to escape in the presence of odours from interacting conspecifics. Thus, philopatrics and dispersers use social information in different ways. Although we should be cautious about the specific meaning of these behavioural differences, the behaviour adopted by dispersers may constitute a strategy to avoid conflicts (McShea 1990) with other individuals during transience and settlement while preserving their potential growth, survival and reproduction.

#### POTENTIAL MECHANISMS

Several non-exclusive mechanisms may explain the origin of these differences in the behavioural patterns between dispersers and philopatrics. These behavioural strategies may have a genetic component as has been shown in insects, fish, birds and mammals (Waser & Jones 1989; Korona 1991; Osborne *et al.* 1997; Dingemans *et al.* 2003). We found that the density and the site of origin, the density and the site of release, and the hormonal treatment of the mother did not interact with the dispersal status, showing that the environmental components examined here did not influence the behavioural difference between dispersing and philopatric individuals. However, these manipulations were not weak because density did affect female fecundity and ventral coloration (Meylan & Clobert 2004; S. Meylan, B. Sihervo & Jean Clobert, unpublished data), the maternal hormonal treatment affected offspring sprint speed (Meylan & Clobert 2004), and release population affected yearling activity (present data). Similar invariability in the dispersal status-dependent behavioural pattern, such as the foraging strategy, was obtained in another study with this species (S. Meylan, M. de Fraipont, P. Aragón,

E. Vercken & Jean Clobert, unpublished data). However, it has recurrently been found that a prenatal determination on the propensity to disperse exists in this species (Massot & Clobert 1995; Ronce, Clobert & Massot 1998; de Fraipont *et al.* 2000; Massot & Clobert 2000; Massot *et al.* 2002). There are two potential mechanisms to explain this disconnection with the environmental components examined and the dispersal status-dependent behavioural pattern: (1) there is a connection but with other environmental components not yet tested; and (2) the decision to disperse might occur before the appearance of the behavioural profile measured (through phenotypic plasticity or dispersal-status dependent mortality). Because none of the juveniles was released in the mother's site of origin, there was no link between the prenatal and the postnatal physical environment and therefore individuals could not be preadapted to their novel environment through prenatal determinism. The consequence of this scenario is that the difference between disperser and philopatric behaviours might have been partially achieved through a phenotype-dependent selection, which is compatible with the last mechanism proposed. In fact, previous studies with this species showed that transplanted individuals underwent a higher selection pressure than residents after an experimental introduction (Massot *et al.* 1994) and that individuals forced to disperse had lower survival rates (Boudjemadi, Lecomte & Clobert 1999). In the Root Vole, the social environment has also been shown to affect the survival of translocated resident, transient and colonist individuals differently (Gundersen, Andreassen & Ims 2002). We therefore suggest (see also Doligez, Danchin & Clobert 2002) that social information may have important implications for conservation biology. For instance, the management of reintroduced populations should take into account individual strategies with regard to the social environment since the cost of introduction into a novel environment may be a selective pressure for temperament traits (reviewed in McDougall *et al.* 2006).

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#### References

- Alberts, A.C. & Werner, D.I. (1993) Chemical recognition of unfamiliar conspecifics by green iguanas: functional significance of different signals components. *Animal Behaviour* **46**, 197–199.

- Aragón, P., López, P. & Martín, J. (2001) Chemosensory discrimination of familiar and unfamiliar conspecifics by lizards: implication of field spatial relationships between males. *Behavioral Ecology and Sociobiology* **50**, 128–133.
- Aragón, P., López, P. & Martín, J. (2003) Differential avoidance responses to chemical cues from familiar and unfamiliar conspecifics by male Iberian rock lizards (*Lacerta monticola*). *Journal of Herpetology* **37**, 583–585.
- Aragón, P., Massot, M., Gasparini, J. & Clobert, J. (2006a) Socially acquired information through chemical cues in the common lizard, *Lacerta vivipara*. *Animal Behaviour* in press. DOI: 10.1016/j.anbehav.2005.11.023
- Aragón, P., López, P. & Martín, J. (2006b) Roles of male residence and relative size in the social behavior of Iberian rock lizards, *Lacerta monticola*. *Behavioral Ecology and Sociobiology* **59**, 762–769.
- Bélíchon, S., Clobert, J. & Massot, M. (1996) Are there differences in fitness components between philopatric and dispersing individuals? *Acta Oecologica* **17**, 503–517.
- Boudjemadi, K., Lecomte, J. & Clobert, J. (1999) Influence of connectivity on demography and dispersal in two contrasting habitats: an experimental approach. *Journal of Animal Ecology* **68**, 1207–1224.
- Chandler, R.C. (1995) Practical considerations in the use of simultaneous inference for multiple tests. *Animal Behaviour* **49**, 524–527.
- Clobert, J., Danchin, E., Dhondt, A.A. & Nichols, J.D. (2001) *Dispersal*. Oxford University Press, Oxford.
- Clobert, J., Massot, M., Lecomte, J., Sorci, G., de Fraipont, M. & Barbault, R. (1994) Determinants of dispersal behavior: the common lizard as a case of study. *Lizard Ecology: Historical and Experimental Perspectives, Evolutionary Ecology Part III* (eds L. J. Vitt & E. R. Pianka), pp. 183–206. Princeton University Press, Princeton, NJ.
- Clobert, J., Oppliger, A., Sorci, G., Ernande, B., Swallow, J.G. & Garland, T. Jr (2000) Trade-offs in phenotypic traits: endurance at birth, growth, survival, predation and susceptibility to parasitism in a lizard, *Lacerta vivipara*. *Functional Ecology* **14**, 675–684.
- Clobert, J., Perrins, C.M., McCleery, R.H. & Gosler, A.G. (1988) Survival rate in the great tit *Parus major* in relation to sex, age, and immigration status. *Journal of Animal Ecology* **57**, 287–306.
- Cooper, W.E. Jr (1994) Chemical discrimination by tongue-flicking in lizards: a review with hypotheses on its origin and its ecological and phylogenetic relationships. *Journal of Chemical Ecology* **20**, 439–487.
- Creel, S.R. & Waser, P.M. (1994) Inclusive fitness and reproductive strategies in dwarf mongooses. *Behavioral Ecology* **5**, 539–548.
- Danchin, E., Giraldeau, L.-A., Valone, T.J. & Wagner, R.H. (2004) Public information: from noisy neighbors to cultural evolution. *Science* **305**, 487–491.
- Danchin, E., Heg, D. & Doligez, B. (2001) Public information and breeding habitat selection. *Dispersal* (eds J. Clobert, E. Danchin, A.A. Dhondt & J.D. Nichols), pp. 243–258. Oxford University Press, Oxford.
- Dingemanse, N.J., Both, C., van Noordwijk, A.J., Rutten, A.L. & Drent, P.J. (2003) Natal dispersal and personalities in great tits (*Parus major*). *Proceedings of the Royal Society B* **270**, 741–747.
- Dodd, C.K. (1993) The effects of toe-clipping on sprint performance of the lizard *Cnemidophorus sexlineatus*. *Journal of Herpetology* **27**, 209–213.
- Doligez, B., Danchin, E. & Clobert, J. (2002) Public information and breeding habitat selection a wild bird population. *Science* **297**, 1168–1170.
- de Fraipont, M., Clobert, J., John-Alder, H. & Meylan, S. (2000) Increase pre-natal maternal corticosterone promotes philopatry of offspring in common lizards *Lacerta vivipara*. *Journal of Animal Ecology* **69**, 404–413.
- Fraser, D.F., Gilliam, J.F., Daley, M.J., Le, A.N. & Skalski, G.T. (2001) Explaining leptokurtic movement distributions: intrapopulation variation in boldness and exploration. *American Naturalist* **158**, 124–135.
- Giraldeau, L.-A., Valone, T.J. & Templeton, J.J. (2002) Potential disadvantages of using socially acquired information. *Philosophical Transactions of the Royal Society B* **357**, 1559–1566.
- Gundersen, G., Andreassen, H.P. & Ims, R.A. (2002) Individual and population level determinants of immigration success on local habitat patches: an experimental approach. *Ecology Letters* **5**, 294–301.
- Halpern, M. (1992) Nasal chemical senses in reptiles: structure and function. *Biology of the Reptilia. 18. Brain, Hormones and Behavior* (eds C. Gans & D. Crews), pp. 423–522. University of Chicago Press, Chicago, IL.
- Holekamp, K.E. & Smale, L. (1998) Dispersal status influences hormones and behavior in the male spotted hyena. *Hormones and Behavior* **33**, 205–216.
- Kiester, A.R. (1979) Conspecifics as cues: a mechanism for habitat selection in the Panamanian grass anole (*Anolis aeneus*). *Behavioral Ecology and Sociobiology* **5**, 323–330.
- Korona, R. (1991) Genetic basis of behavioural strategies. Dispersal of female flour beetles, *Tribolium confusum*, in a laboratory system. *Oikos* **62**, 265–270.
- Lemel, J.Y., Belichon, S., Clobert, J. & Hochberg, M.E. (1997) The evolution of dispersal in a two-patch system: some consequences of differences between migrants and residents. *Evolutionary Ecology* **11**, 613–629.
- Léna, J.P. & de Fraipont, M. (1998) Kin recognition in the common lizard. *Behavioral Ecology and Sociobiology* **42**, 341–347.
- Mason, R.T. (1992) Reptilian pheromones. *Biology of the Reptilia. 18. Brain, Hormones and Behavior* (eds C. Gans & D. Crews), pp. 114–228. University of Chicago Press, Chicago, IL.
- Massot, M. & Clobert, J. (1995) Influence of maternal food availability on offspring dispersal. *Behavioral Ecology and Sociobiology* **37**, 413–418.
- Massot, M. & Clobert, J. (2000) Processes at the origin of similarities in dispersal behaviour among siblings. *Journal of Evolutionary Biology* **13**, 707–719.
- Massot, M., Clobert, J., Lecomte, J. & Barbault, R. (1994) Incumbent advantage in the common lizards and their colonizing ability. *Journal of Animal Ecology* **63**, 431–440.
- Massot, M., Clobert, J., Lorenzon, P. & Rossi, J.M. (2002) Condition dependent in dispersal and ontogeny of the dispersal behaviour: an experimental approach. *Journal of Animal Ecology* **71**, 235–261.
- McCleery, R.H. & Clobert, J. (1990) Differences in recruitment of young immigrant and resident great tit in Wytham wood. *Population Biology of Passerine Birds* (eds J. Blondel, A. Gosler, J.-D. Lebreton & R.H. McCleery), pp. 423–439. Springer-Verlag, Berlin.
- McCullagh, P. & Nelder, J.A.S. (1989) *Generalized Linear Models*, 2nd edn. Chapman & Hall, New York.
- McDougall, P.T., Réale, D., Sol, D. & Reader, S.M. (2006) Wildlife conservation and animal temperament: causes and consequences of evolutionary change for captive, reintroduced, and wild populations. *Animal Conservation* **9**, 39–48.
- McShea, W.J. (1990) Social tolerance and proximate mechanisms of dispersal among winter groups of meadow voles, *Microtus pennsylvanicus*. *Animal Behaviour* **39**, 346–351.
- 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*). *Hormones and Behavior* **42**, 319–326.
- Meylan, S. & Clobert, J. (2004) Maternal effects on offspring locomotion: influence of density and corticosterone elevation in the lizard *Lacerta vivipara*. *Physiological and Biochemical Zoology* **77**, 450–458.

- Meylan, S., Dufty, A.M. & Clobert, J. (2003) The effect of transdermal corticosterone application on plasma corticosterone levels in pregnant *Lacerta vivipara*. *Comparative Biochemistry and Physiology A* **134A**, 497–503.
- Murren, C.J., Julliard, R., Schlichting, C.D. & Clobert, J. (2001) Dispersal, individual phenotype, and phenotypic plasticity. *Dispersal* (eds J. Clobert, E. Danchin, A.A. Dhondt & J. D. Nichols), pp. 261–272. Oxford University Press, Oxford.
- Osborne, K.A., Robinson, A., Burgess, E., Butland, S., Shaw, S.A., Coulthard, A., Pereira, H.S., Greenspan, R.J. & Sokolowski, M.B. (1997) Natural behavior polymorphism due to a c GMP-dependent protein kinase of *Drosophila*. *Science* **277**, 834–836.
- Ott, J.A. & Scott, D.E. (1999) The effects of toe clipping and PIT-tagging on growth and survival in metamorphic *Ambystoma opacum*. *Journal of Herpetology* **33**, 344–348.
- Pastschiak-Arts, M. & Bendel, J.F. (1990) Behavioural differences between locally recruiting and dispersing gray squirrels, *Sciurus carolinensis*. *Canadian Journal of Zoology* **68**, 935–941.
- Ronce, O., Clobert, J. & Massot, M. (1998) Natal dispersal and senescence. *Proceedings of the National Academy of Sciences of the USA* **95**, 600–605.
- Rosenberry, C.S., Conner, M.C. & Lancia, R.A. (2001) Behavior and dispersal of white-tailed deer during the breeding season. *Canadian Journal of Zoology* **79**, 171–174.
- SAS Institute (1999) *SAS/STAT User's Guide, Version 8*. SAS Institute, Cary, NC.
- Sih, A., Bell, A.M., Johnson, J.C. & Ziemba, R.E. (2004) Behavioral syndromes: an integrative overview. *The Quarterly Review of Biology* **79**, 241–277.
- Sokal, R.R. & Rohlf, F.J. (1995) *Biometry*, 3rd edn. W H Freeman, New York.
- Sorci, G., Clobert, J. & B elichon, S. (1996) Phenotypic plasticity of growth and survival in the common lizard (*Lacerta vivipara*). *Journal of Animal Ecology* **65**, 781–790.
- Stamps, J. (1987) Conspecific as a cues to territory quality: a preference of juvenile lizards (*Anolis aeneus*) for previously used territories. *American Naturalist* **129**, 629–642.
- Stamps, J. (2001) Habitat selection by dispersers: integrating proximate and ultimate approaches. *Dispersal* (eds J. Clobert, E. Danchin, A.A. Dhondt & J.D. Nichols), pp. 230–242. Oxford University Press, Oxford.
- Valone, T.J. & Templeton, J.J. (2002) Public information for the assessment of quality: a widespread social phenomenon. *Philosophical Transactions of the Royal Society B* **357**, 1549–1557.
- Van Vuren, D. & Armitage, K.B. (1994) Survival of dispersing and philopatric yellow-bellied marmots: what is the cost of dispersal? *Oikos* **69**, 179–181.
- Waser, P.M. & Jones, W.T. (1989) Heritability of dispersal in banner-tailed kangaroo rats, *Dipodomys spectabilis*. *Animal Behavior* **37**, 987–991.
- Wilson, D.S., Clark, A.B., Coleman, K. & Dearstyne, T. (1994) Shyness and boldness in human and other animals. *Trends in Ecology and Evolution* **9**, 442–446.
- Woollard, F. & Harris, S. (1990) A behavioral comparison of dispersing and non-dispersing foxes (*Vulpes vulpes*) and an evaluation of some dispersal hypotheses. *Journal of Animal Ecology* **59**, 709–722.

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