

Mother–offspring interactions affect natal dispersal in a lizard

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Interactions between relatives operate strong selective pressures on dispersal. Recently, a correlative study in the common lizard (*Lacerta vivipara*) suggested that natal dispersal might respond plastically to mother–offspring interactions. Here, we describe a factorial experiment supporting this observation. Two crossed treatments were applied to experimental patches of the common lizard: (i) presence versus absence of the mother, inducing a difference of kinship in offspring neighbourhoods; and (ii) high versus low patch density, resulting in two levels of conspecific abundance and modulating the effect of mother presence on the average kinship within a patch. Dispersal of the same cohort of offspring was observed at the juvenile and yearling stages. We found a sex-dependent response of offspring dispersal to the removal of the mother at the two stages. During the juvenile stage, higher dispersal was found in females in the presence of the mother, with males unaffected. During the yearling stage, the responses of both sexes to the presence of the mother opposed each other. In addition, we found a negative relationship between dispersal and patch density at the juvenile stage. No interaction between density and the presence of the mother was detected, which suggests that behavioural responses to kinship and density are disconnected and that kinship is assessed at a small social scale. We discuss the role of competition and inbreeding avoidance to explain the observed pattern.

Keywords: natal dispersal; kinship; density; common lizard

1. INTRODUCTION

The habitat of many species tends to be fragmented (Hanski 1999). In response to habitat fragmentation, populations may develop local adaptations to local conditions or evolve dispersal adaptations (Thomas *et al.* 1998; Ronce *et al.* 2001). Because offspring dispersal has major consequences on the demography and genetic structure of populations, understanding the selective forces driving the evolution of dispersal strategies has become an important issue at the interface of evolutionary theory, behavioural ecology and population demography.

Hamilton & May (1977) established that interactions between relatives drive the evolution of offspring dispersal in stable and homogeneous habitats. They demonstrated that dispersal can be modelled as a parental manipulation or an offspring strategy evolving under kin selection. Dispersal reduces competition between relatives, which generates some indirect genetic benefits trading against the direct costs of movement following on from Hamilton's rule (Hamilton & May 1977). Despite several developments of the original scenario to more complex spatial and demographic structures (Clobert *et al.* 2001, chapters 5, 9, 11 and 24), almost all these elaborations consider dispersal as a fixed strategy unconditional on local kinship (but see Crespi & Taylor (1990) and Ronce *et al.* (1998)). However, some empirical observations suggest that natal dispersal may actually depend on local relatedness. In some mammals, for example meadow voles, offspring dispersal correlates with the intensity of sib–sib competition

(Bollinger *et al.* 1993), and dispersal of the heaviest female in a litter is a response to stronger sister–sister interactions in red-backed voles (*Clethrionomys rufocanus bedfordiae*; Kawata 1987). In the common lizard, offspring dispersal decreases with lower maternal condition or during mother senescence, hence with a diminishing expected risk of competitive interactions with the mother (Massot & Clobert 1995; Léna *et al.* 1998; Ronce *et al.* 1998).

A further issue is the spatial scale at which the behavioural sensitivity to kinship is expressed, which may expand from the scale of a familial unit (Hamilton & May 1977; Ronce *et al.* 1998) to the scale of a whole patch (Crespi & Taylor 1990; Perrin & Mazalov 2000). If dispersal is a response to the expected relatedness of a patch of habitat, then the potential impact of a kin member may be diluted by the presence of non-relatives. A complete assessment of the effect of a specific relative should, therefore, require control of the abundance of unrelated individuals. We performed such an experiment by constructing replicated populations of the common lizard (*Lacerta vivipara*). We studied the effect of the presence of the mother on offspring dispersal during two successive life-history stages (juvenile and yearling). Local kinship was manipulated by swapping mothers between different populations, while other populations acted as controls (mothers released with their offspring). Local density was manipulated independently by doubling the number of unrelated individuals released into half of the populations. This treatment produced two contrasting levels of patch density and also two levels of patch relatedness when the mother was present, high relatedness at low density and low relatedness at high density. The two treatments were crossed so that we could investigate:

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- (i) whether juvenile dispersal responded to the presence of the mother;
- (ii) whether juvenile dispersal depended upon local crowding; and
- (iii) whether the effect of maternal presence was mediated by the level of local crowding.

2. MATERIAL AND METHODS

(a) *Model organism*

The common lizard, *L. vivipara* (Jacquin 1787), is a viviparous species inhabiting humid habitats across Eurasia. Populations can be structured into three distinct life-history stages: juveniles (year born), yearlings (1 year old) and mature adults. Individuals share overlapping home ranges, as evidenced by the absence of any obvious spatial segregation in natural populations (Clobert *et al.* 1994). Juveniles originate from annual clutches of offspring laid synchronously during June or July. Hatching begins quickly after parturition, juveniles are autonomous at birth and offspring dispersal starts within 10 days of age (Clobert *et al.* 1994). Most dispersal occurs during the first two life-history stages, in both natural and experimental populations (Clobert *et al.* 1994; Boudjemadi *et al.* 1999). Moreover, laboratory trials have demonstrated that offspring discriminate maternal olfactory cues at birth (Léna *et al.* 2000).

(b) *Running of the experiment*

The experiment was conducted on a sample of individually marked lizards collected from their natural habitats in June 1999 and released at our experimental site in July. Offspring dispersal away from the experimental populations was monitored daily until the end of December 2000. This procedure allowed us to estimate dispersal at the juvenile stage during 1999 and at the yearling stage during 2000.

(i) *Collection*

During June 1999, lizards were sampled in a natural habitat on the Mont Lozère (Lozère, France, 44°27' N, 3°44' E) before translocation to the Field Station of Foljuif (Seine-et-Marne, 48°17' N, 2°41' E). Altogether we collected 144 gravid females, 96 adult males and 240 yearlings to establish background populations. Lizards were individually marked, measured for length and weight, and maintained in plastic terraria at the Field Station with food and water provisioned regularly until the laying of gravid females (mid-July). Offspring were individually marked by toe clipping and measured for length and weight. Gender was determined by counting ventral scales (Lecomte *et al.* 1992). We assumed that yearlings and adults were initially unrelated to each other.

(ii) *Experimental system*

Sixteen experimental enclosures were constructed, each with a squared patch (10 m × 10 m) and a one-way, 20 m long corridor (figure 1). Dispersal was defined as the movement out from an initial patch along a one-way corridor. This structure corresponds to both the size of natural home range and the minimum dispersal distance measured in natural populations (Boudjemadi *et al.* 1999). Enclosures were closed to avian predators by nets and to intrusive mammals by daily trapping. However, we were unable to preclude intrusions of greater white-toothed shrews (*Crocidura russula*) in five of our enclosures in 1999 (figure 1).

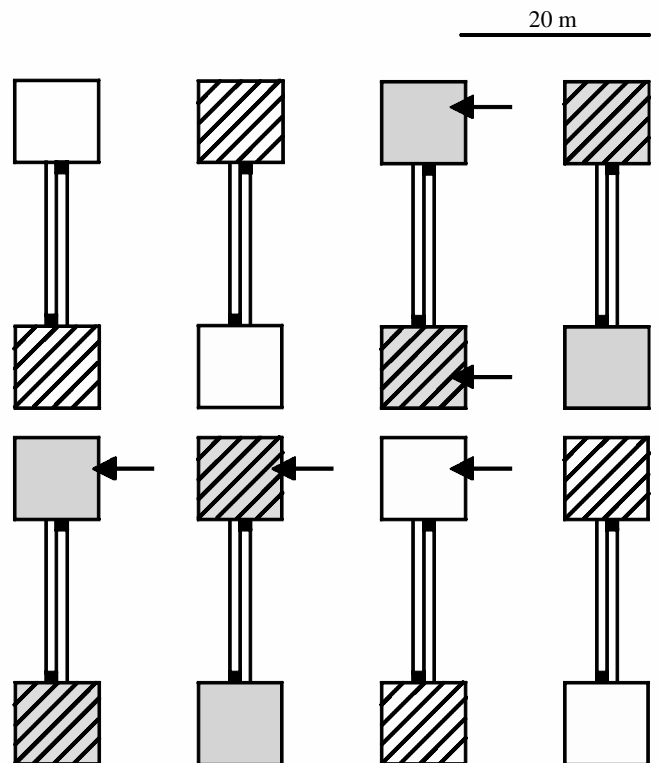


Figure 1. Experimental design. Grey indicates enclosures where the mother of each litter was replaced with an unfamiliar adult female. Otherwise, all offspring were introduced with their mother. Diagonal hatching indicates populations that were initiated at high density. Arrows indicate enclosures affected by predation in 1999, and excluded from the statistical analyses. Pitfall traps at the end of each one-way corridor are represented in black. Scale bar, 20 m.

In 2000, efficient traps (Ugglan, Grahnb, Sweden) were used inside and on the outskirts of the enclosures, so that predation was prevented in all the enclosures.

(iii) *Experimental design*

In July 1999, we initiated our experimental system with a bifactorial design. We manipulated the initial density and crossed this factor with the mother presence-absence (kinship) using enclosure as a replicate (figure 1). We contrasted eight low-density patches (14 yearlings and adult males, six females, 36.5 offspring \pm 2.4 s.e.m.) with eight high-density patches (28 yearlings and adults, 12 females, 71.2 offspring \pm 3.9 s.e.m.). We maintained a similar population age and sex structure in all patches. The starting densities were chosen to frame the estimated carrying capacity of our experimental habitat (J. Lecomte, unpublished data). We applied the kinship treatment by replacing the mother of each litter with an unrelated unfamiliar adult female in half of the experimental populations. This swapping was conducted just before introduction to avoid familiarization. In the remaining half of the populations, offspring were introduced with their mother. The kinship effect was crossed with the density manipulation such that four population replicates were initiated for each combination of the two factors (figure 1).

(iv) *Introduction and monitoring*

Individuals were randomly allocated to the experimental populations. Yearlings and adult males were released during the

same day in July 1999, and siblings were released with their mother or a surrogate female following birth. The randomization procedure used to introduce the lizards was effective at producing an initially homogeneous set (homogeneity tests for population size and individual characteristics among treatments, all $p > 0.4$). Philopatric individuals were monitored by hand recaptures during sessions in August and September 1999, and in April, August and September 2000, with multiple attempts per session (usually three independent days). This robust design allowed very efficient capture (estimated capture probability ranging from 0.80 to 0.98 per session). Dispersers were caught systematically in a trap located at the corridor extremities (checked daily), identified and immediately released in a new enclosure adjacent to the trap (figure 1). This methodology generated a simple metapopulation of two patches mutually coupled by migration.

(c) Data analysis

Dispersers were defined as individuals caught at least once during a year within a corridor pitfall trap. Philopatric individuals were considered as the remaining set of individuals, excluding the non-captured individuals, which were either dead or philopatric (Boudjemadi *et al.* 1999). Two separate analyses were conducted at the two life-history stages using the same cohort of offspring. Indeed, the sample of individuals used to model dispersal was not the same owing to mortality from the juvenile to the yearling stage.

Data were analysed by using generalized linear mixed models (GLMMs) in SAS v. 8.02 (Littell *et al.* 1996). The timing of dispersal was modelled with the MIXED procedure, which amounts to specify a Gaussian error distribution and an identity link function in the GLMM framework. The average per family was used as a response variable. The dispersal status was modelled with the GLIMMIX macro, using a binomial error term, a logit link function and individual dispersal status (philopatry or dispersal) as a response variable (Littell *et al.* 1996). The GLMM approach described the clustering of individual observations, owing to the fact that populations were nested within treatments (figure 1), and accounted for the presence of both fixed treatment effects and random replicate effects (Littell *et al.* 1996). Estimations and test statistics were calculated with a restricted maximum-likelihood approach. Statistical inferences for the fixed part of the model were obtained from type III F statistics and two-tailed tests. The assumptions of those models were investigated by the analysis of residuals. In the case of binomial dispersal data, no significant overdispersion was detected (χ^2 tests, $p > 0.05$).

The body condition was calculated as the residual from a linear regression of body mass against body size. Body condition and body size were not independent of offspring gender (body condition: $F_{1,700} = 141.9$, $p < 0.001$; body size: $F_{1,700} = 16.1$, $p < 0.001$). Males were on average more corpulent at birth than females, whereas females were larger than males. Therefore, we accounted for both covariates in the analysis of offspring dispersal. The fixed part of the models included the two experimental factors, individual covariates (length, body condition, gender) and interactions. The random part of the model included the effects of populations nested within the treatments. Model selection was conducted by backward simplification of the fixed effects. Populations affected by predation were excluded from all analyses, although this did not modify the nature and significance of kinship effects.

3. RESULTS

(a) Effects of the treatments on dispersal chronology

There was no evidence that dispersal chronology was affected by our manipulation during the two first stages of offspring lifetime. The juveniles' dispersal was bimodal with an initial, early dispersal period (age 2–25 days, $n = 23$) and a second more important dispersal period at an older age (30–60 days, $n = 55$). This bimodality was not affected by experimental treatments (logistic regression, density: $\chi^2_1 = 0.001$, $p = 0.97$; kinship: $\chi^2_1 = 0.04$, $p = 0.85$, $n = 78$). Similarly, age at dispersal did not differ between treatments (density: $F_{1,7} = 0.13$, $p = 0.73$; kinship: $F_{1,7} = 0.68$, $p = 0.44$, $n = 78$). Most yearlings' movements occurred before June–July. The chronology of these movements was not influenced by the experimental treatments (density: $F_{1,7} = 0.01$, $p = 0.92$; kinship: $F_{1,7} = 2.57$, $p = 0.15$, $n = 42$).

(b) Effects of the treatments on dispersal status

In 1999, juvenile dispersal was affected by body condition, gender, a marginal interaction between gender and kinship, and density (table 1a). First, dispersal was associated with higher corpulence at birth than philopatry (dispersal: 0.005 ± 0.002 , $n = 65$; philopatry: -0.008 ± 0.009 , $n = 411$), and males disperse more on average than females (odds male: odds female = 1.22). Second, females dispersed more in the presence of their mother than in the presence of a surrogate adult female (female sample, kinship: $F_{1,7} = 6.53$, $p = 0.04$, $n = 236$), whereas male offspring displayed no significant response to the presence of the mother (male sample, kinship: $F_{1,7} = 0.01$, $p = 0.94$, $n = 240$). Together, these two different responses generated the marginal interaction between gender and kinship detected in the selected model (figure 2a). Third, the effect of density on patch dispersal was significant. Contrary to expectations, a lower dispersal was observed in the high-density treatment (figure 2b). There was no indication that density interacted with kinship (table 1a) or with the sex-dependent response (gender \times kinship \times density: $F_{1,460} = 1.17$, $p = 0.28$).

In the following, the study of yearling dispersal showed persistent effects of the kinship treatment modulated by gender and by spring body condition, whereas the effect of density disappeared (table 1b). The interaction between kinship and gender originated from the fact that females displayed a response to the presence of the mother opposite to that of male offspring (figure 2a), albeit both responses were not significant (males, $F_{1,7} = 0.88$, $p = 0.38$, $n = 111$; females, $F_{1,7} = 1.09$, $p = 0.33$, $n = 103$). Males tended to disperse more in the absence of the mother, whereas females tended to disperse more in the presence of the mother. Also, irrespective of gender, the body condition of dispersers was higher than the residents' in the presence of the mother, whereas the reverse was observed when an unrelated female replaced the true mother (table 2). Finally, the effect of density was not significant (figure 2b), and did not interact with kinship (table 1b) or with the sex-dependent response (gender \times kinship \times density: $F_{1,197} = 1.72$, $p = 0.19$).

Table 1. Selected GLMMs describing offspring dispersal at the juvenile stage ((a) 476 observations) and at the yearling stage ((b) 214 observations) depending on offspring body condition, gender, kinship treatment and density manipulation. (The model also included the random effect of patch identity nested within various combinations of kinship and density treatments.)

| | <i>F</i> statistic _{ndf, ddf} | <i>p</i> value |
|--|--|----------------|
| (a) predictor effect of juvenile dispersal | | |
| body condition at birth | 5.32 _{1,462} | 0.02 |
| gender | 5.79 _{1,462} | 0.03 |
| kinship | 2.10 _{1,7} | 0.19 |
| gender × kinship | 3.66 _{1,462} | 0.06 |
| density | 6.09 _{1,7} | 0.04 |
| density × kinship | 0.08 _{1,7} | 0.78 |
| (b) predictor effect of yearling dispersal | | |
| body condition in spring | 0.27 _{1,199} | 0.60 |
| gender | 2.68 _{1,199} | 0.10 |
| kinship | 0.05 _{1,7} | 0.83 |
| gender × kinship | 5.80 _{1,199} | 0.02 |
| body condition × kinship | 9.19 _{1,199} | 0.003 |
| density | 0.93 _{1,7} | 0.37 |
| density × kinship | 0.01 _{1,7} | 0.93 |

4. DISCUSSION

Our experiment demonstrates that maternal presence has a significant effect on sex-biased dispersal from natal patch. During the juvenile stage, higher dispersal was found in female offspring in the presence of the mother, whereas males were unaffected. This result lends experimental explanation to some correlations observed between the intensity of mother–offspring interactions and natal dispersal under natural conditions in the same species. For example, Ronce *et al.* (1998) observed that old females had lower annual survival than young females, which should decrease the likelihood of future mother–offspring interactions for offspring born from older females. This maternal ageing was associated with a stronger female offspring philopatry, whereas male dispersal was not affected (Ronce *et al.* 1998). Other maternal effects, possibly reflecting potential mother–offspring interactions, have been shown to influence offspring dispersal in the same species, including food availability (Massot & Clobert 1995), parasitism (Sorci *et al.* 1994) and hormonal stress (de Fraipont *et al.* 2000; Meylan *et al.* 2002). Such correlations could result from proximal constraints of producing different types of offspring, independently from the ultimate cause involving mother–offspring interactions that we manipulated here. Nevertheless, our experimental suppression of all mother–offspring interactions yields exactly the behavioural response observed in the correlative study of Ronce *et al.* (1998). These concordant results go to prove that female offspring disperse to avoid competitive interactions with the mother in this species. Whether the behaviour documented here results from offspring control on dispersal, or from parental manipulation of offspring behaviour (Hamilton & May 1977; Ronce *et al.* 1998) is difficult to assess. Against the latter hypothesis, we know at least that adult females do not seem to demonstrate any particular behaviour forcing offspring to leave their natal environment (Clobert *et al.* 1994; Léna *et al.* 1998).

The fact that male behaviour was unaffected at the juvenile stage and opposed the female response at the year-

ling stage requires alternative explanations. Despite the fact that offspring have been shown experimentally to suffer from competition with adults (Massot *et al.* 1992), competitive interactions may differ between sexes. For example, females tend to compete for resources, whereas males tend to compete for mates (Pilorge 1987; Massot *et al.* 1992). Thus, young males might suffer less from competition with the mother than young females. Additionally, males may avoid potential mating with their sisters rather than their mother, and therefore adopt a dispersal strategy that is opposite to that of their sisters (Massot & Clobert 2000). Indeed, the likelihood that one brother and one sister of an average clutch (three males and three females) both survive to sexual maturity is high (0.11–0.30, with survival data from Massot *et al.* (1992)), and exceeds the risk of inbreeding with mother (0.07–0.20, with survival data from Ronce *et al.* (1998)). This scenario (female dispersal to avoid competition with mother, and male philopatry to avoid inbreeding with sisters) would match a model of sex-biased dispersal evolving under the joint influences of kin competition and inbreeding avoidance by Perrin & Mazalov (2000).

Dispersers' phenotypes and behaviour are not random. This is particularly evident in some species with dispersing morphotypes, but less extreme differences are also found in many other species (Swingland 1983). Our experiment showed that when dispersal occurred in response to the presence of the mother, dispersers were more corpulent than philopatric individuals, which confirms previous observations (Clobert *et al.* 1994; Léna *et al.* 1998). By contrast, when offspring were released with a surrogate mother, yearling dispersers were leaner than yearling residents. This result supports the view that individuals can differ morphologically depending on their dispersal strategy, but indicates that the actual dispersal decision is made by the offspring in response to proximal cues of potential kin competition.

In species exhibiting intense intraspecific competition, natal dispersal is expected to be positively density dependent (e.g. Aars *et al.* 2000). By contrast, we found that

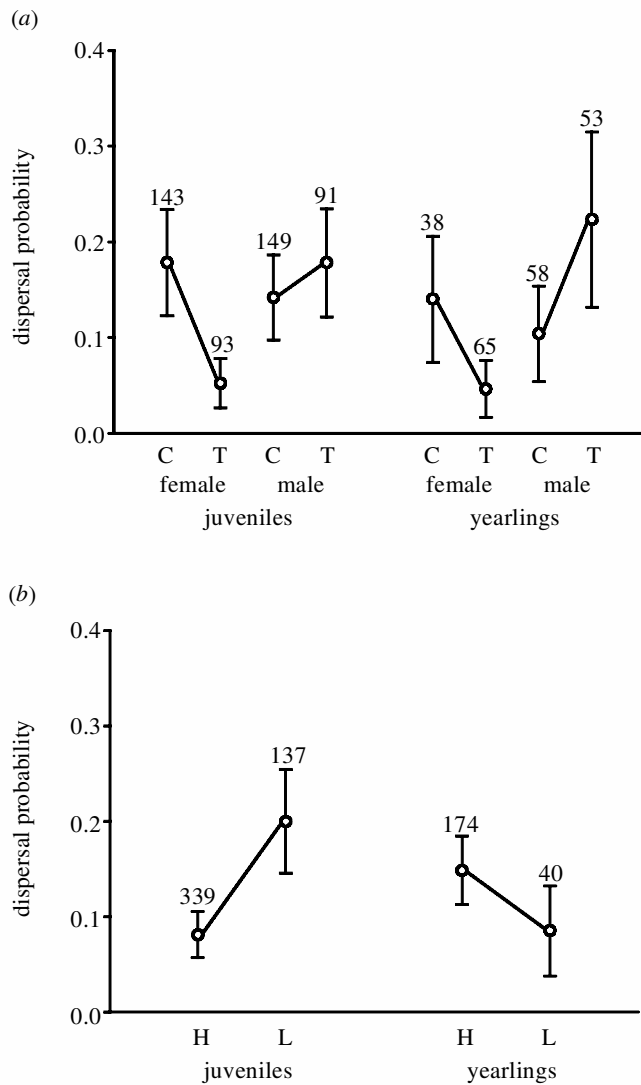


Figure 2. (a) Kinship treatment, offspring gender and dispersal. During the juvenile stage (1999) and the yearling stage (2000), the presence of the mother had a significant effect on the sex-biased patch dispersal. C, control, offspring introduced with their mother; T, mother removal treatment, offspring introduced with a surrogate mother. (b) Patch density and offspring dispersal. Dispersal decreased at high density during the juvenile stage, but was unaffected during the yearling stage. H, high-density patches; L, low-density patches. Values are back-transformed from the GLMM presented in table 1 (least-square means \pm s.e.m.). The numbers indicate the sample sizes.

offspring dispersal was inversely related to local crowding during the juvenile stage. Such a response may indicate constraints of habitat saturation acting on dispersal (see review in Lambin *et al.* (2001)). This would imply that the cost of movement and settlement are higher at high density in natural populations and limit emigration (e.g. Jones *et al.* 1988). A density manipulation in the field has indeed shown that social fences can prevent immigration (Massot *et al.* 1992). Also, it is possible that some individuals choose their habitat based on the presence of conspecifics (conspecific attraction, Stamps (1991)). This hypothesis would apply if the fitness of individuals increases with density (e.g. Allee effect) or if settlement costs are reduced in the presence of conspecifics

Table 2. Body condition according to the dispersal status and the presence of the mother at the yearling stage (offspring dispersing at the juvenile stage were excluded from the analysis). (The first line indicates average value across gender, and data are also illustrated separately for females (F) and males (M) in the next lines. Dispersers were more corpulent than philopatric individuals when the mother was present ($F_{1,7} = 4.94$, $p = 0.03$), but less corpulent when the mother was replaced by a surrogate female ($F_{1,7} = 4.63$, $p = 0.03$). Numbers in parentheses indicate sample sizes. C, Control, offspring introduced with the mother. T, Mother removal treatment, offspring introduced with a surrogate mother. n indicates sample size.)

| | C | T |
|------------|------------------------------------|------------------------------------|
| philopatry | -0.002 ± 0.018 ($n = 82$) | -0.009 ± 0.012 ($n = 99$) |
| F: | -0.036 ± 0.018 | -0.056 ± 0.015 |
| M: | 0.020 ± 0.017 | 0.059 ± 0.017 |
| dispersal | 0.125 ± 0.062 ($n = 14$) | -0.033 ± 0.042 ($n = 19$) |
| F: | 0.053 ± 0.09 | -0.174 ± 0.08 |
| M: | 0.177 ± 0.08 | 0.032 ± 0.04 |

(Greene & Stamps 2001). Finally, our transfer to an unfamiliar environment might have increased the benefits of the public information offered by neighbouring conspecifics as opposed to the individual private information (Valone 1989; Danchin *et al.* 2001). For example, offspring may cue on conspecifics to learn the location of suitable habitats (Stamps 1991). As private and public information built up in the population, one would expect the response to density to vary over time, as was observed here (see also, Clobert *et al.* (2003)). Whether negative density dependence in our experiment reflects information sharing, social attraction or habitat saturation remains to be established.

Local crowding did not influence the response of female and male offspring to the presence of the mother. Therefore, offspring did not react to relatedness at the level of the whole patch but at a smaller scale, such as that of a family unit. This behaviour suggests that assuming a few relatives per patch (Hamilton & May 1977; Ronce *et al.* 1998) is not an unrealistic modelling hypothesis to describe natal dispersal in our species. Alternatively, other lizard species might assess relatedness at different social scales and using different proximate cues. For example, recent evidence gathered in the side-blotched lizard (*Uta stansburiana*) indicates that dispersal promotes the local aggregation of genetically similar individuals irrespective of genealogy (Sinervo *et al.* 2001; B. Sinervo, unpublished data). Thus, identity by state rather than by descent may also influence dispersal behaviour. More generally, the additivity between the effects of crowding and kinship suggests that the evolution of dispersal responses to both factors might have taken place along two independent pathways. This calls for a more detailed investigation of the distinct physiological and behavioural mechanisms involved in both responses (Dufty *et al.* 2002).

5. CONCLUSION

Evolutionary theory has long shown that kin interactions can be important in the evolution of dispersal. Fol-

lowing the parallel made by Hamilton & May (1977) between dispersal and altruism, theoretical studies of the evolution of kin recognition in cooperative species (Agrawal 2001) can be used to predict that kinship-dependent dispersal is likely to evolve. Our experimental results provide evidence for a more complicated scenario of a sex-dependent relationship between mother presence and natal dispersal. The direction of the relationship (here positive in females, negative in males) is likely to depend upon the relative influences of kin competition, inbreeding and kin cooperation (Perrin & Mazalov 2000; Lambin *et al.* 2001). Indeed, whereas the first two effects seem to prevail in our species, studies with some mammals and birds indicate that different responses may actually exist when costs of inbreeding or benefits of kin cooperation dominate (Cockburn *et al.* 1985; Wolff 1992; Lambin *et al.* 2001).

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As this paper exceeds the maximum length normally permitted, the authors have agreed to contribute to production costs.