LETTER

Social information and emigration: lessons from immigrants

J. Cote[1] and J. Clobert[1,2]*

[1]*Laboratoire Fonctionnement et Evolution des Systèmes Ecologiques, Université Pierre et Marie Curie, 7, quai Saint-Bernard, 75005 Paris, France*
[2]*Station d'Ecologie Expérimentale du CNRS à Moulis, Laboratoire Evolution et Diversité Biologique, Moulis, 09200 Saint-Girons, France*
Correspondence: E-mail: jcote@snv.jussieu.fr

Abstract

'Should I stay or should I go?' is a fundamental question facing any candidate for emigration, as emigrating without outside information has major costs. Most studies on this topic have concentrated on risk-reducing strategies (e.g. exploration) developed after leaving the natal habitat. The idea that information might be acquired before leaving has not been investigated. Immigrants carrying information about their origins could provide such information to potential emigrants in their initial habitat. We manipulated the density of common lizard (*Lacerta vivipara*) populations, to investigate whether immigrants originating from these populations transmitted such information to the population they joined. Emigration of the residents of this new population clearly depended on the origin of the immigrant. Immigrants are therefore a source of information, in this case about surrounding population densities, and may have a major effect on dispersal and species persistence in a fragmented habitat.

Keywords

Common lizard, dispersal, immigration, socially acquired information.

Ecology Letters (2007) **10**: 411–417

INTRODUCTION

Emigration without information about the surrounding areas entails a major risk (Clobert *et al.* 2001; Stamps 2001; Dall *et al.* 2005). Indeed, emigration may be unsuccessful, resulting in the death of the emigrant, if the surrounding conditions are unsuitable; this is one of the major costs of dispersal (Clobert *et al.* 2001; Stamps 2001; Dall *et al.* 2005). One way of decreasing the risks and potential costs associated with emigration is to reduce uncertainty about the 'outside world' by gathering information about the surroundings. This approach enables candidate emigrants to make dispersal decisions based on an assessment of their potential success in another population (Valone & Templeton 2002; Doligez *et al.* 2004; Dall *et al.* 2005). Species would therefore be expected to reduce the level of uncertainty about the existence and quality of surrounding populations by gathering appropriate information whenever possible (Danchin *et al.* 1998; Stamps 2001; Dall & Johnstone 2002; Doligez *et al.* 2004; Dall *et al.* 2005).

Various media are used to convey such information in human populations, but it has only recently been demonstrated that non-human species are also adept information gatherers (Valone 1989; Templeton & Giraldeau 1995; Doligez *et al.* 2002; Schjorring 2002; Valone & Templeton

2002; Danchin *et al.* 2004; Dall *et al.* 2005; Aragon *et al.* 2006b). Various parameters of the physical and social environment are potential sources of information for emigrants, providing valuable cues about the state of the future environment (Danchin *et al.* 2004). Individuals can assess environmental quality through socially acquired information, such as the presence or absence of conspecifics, and the activities and performance of these animals (Danchin *et al.* 2004; Doligez *et al.* 2004; Dall *et al.* 2005). For example, individuals settling in a new area assess the quality of that area based on the density (Doligez *et al.* 2004), reproductive success (Doligez *et al.* 2002) or foraging capacities (Templeton & Giraldeau 1995) of residents. At first glance, it would appear that individuals can only obtain such information when visiting new populations (e.g. prospecting) after deciding to leave the natal environment. However, such prospecting is impossible in species with limited exploratory capacities and entails costs in terms of energy, time and predation. However, if visitors to a population can gather information through local individuals, then residents may also be able to obtain information about the outside through visitors. We hypothesized that immigrants might supply residents with information about surrounding populations. This would result in residents having access to information about the quality of several

other patches. Candidate emigrants would then be able to base their dispersal decisions on comparisons between their current population and other populations, without the need for prospecting. For example, the density of conspecifics in new habitats is a key factor for future fitness outcome, and thus in the selection of a new habitat (Stamps 2001). Indeed, fitness and population density are interconnected in several ways (Lidicker 1978; Eckman 1984; Sinclair 1989; Massot et al. 1992). Many fitness-related traits, such as fecundity, behaviour and dispersal, are density-dependent (e.g. Hassel and May 1985; Crespi & Taylor 1990; Massot et al. 1992; Lecomte et al. 1994). For example, high population density is often associated with high levels of aggressiveness and low availability of food and mates (Krebs 1971; Reigh et al. 1982; Stenseth & Lomnicki 1990; Lecomte et al. 1994). Conversely, high-population density is also, at least in part, an indicator of habitat quality. Indeed, many studies have highlighted the key role of density-related information in habitat selection and dispersal decisions (Crespi & Taylor 1990; Lambin et al. 2001; Stamps 2001; Clobert et al. 2004; Doligez et al. 2004).

We used the common lizard (*Lacerta vivipara*) as a model system. We manipulated the density of lizard populations and investigated whether immigrants from these populations conveyed information about population density to the populations they joined. The sensory capacity of the common lizard has been well studied: this species is able to detect relatives (Léna & de Fraipont 1998), to estimate conspecific density (Aragon et al. 2006b), and to recall previous interactions with conspecifics (Aragon et al. 2006b), based on odour cues. Thus, the common lizard frequently makes use of social information when taking behavioural decisions. Furthermore, recent studies have provided evidence that individuals are aware of the existence of other populations (Boudjemadi et al. 1999; Lecomte et al. 2004). Population density affects reproductive success, survival probability, body growth rate and behaviour in this species (Massot et al. 1992; Lecomte et al. 1994; Meylan & Clobert 2004; Le Galliard et al. 2006), and is also a good indicator of habitat quality. We have shown that the probability of emigration may be positively (Massot et al. 1992; Lecomte et al. 2004) or negatively (Le Galliard et al. 2003; Meylan et al. 2007) influenced by density, depending on external conditions. Thus, patterns of dispersal and habitat selection in this species are strongly affected by population density (Massot et al. 1992; Le Galliard et al. 2003; Cote & Clobert 2007). We investigated, experimentally, the possibility that immigrants serve as a source of information, using 16 seminatural populations of common lizards. We manipulated population density in both the original patches of young immigrants and in the patches they migrated to, in a crossed factorial design (see Materials and methods). Pitfall traps were used to identify juveniles

trying to disperse. These dispersers were then released as immigrants in another enclosure, according to our factorial design. This made it possible to assess the effect of the immigrants' origin (high-density or low-density population) and of the interaction of this origin with density in the resident population.

MATERIALS AND METHODS

Release period: experimental system and density manipulation

The experiment was conducted in 2004 at the Foljuif Ecological Research Station (Seine-et-Marne, 48°17′N, 2°41′E). Lizards were captured in the Cevennes (Mont Lozère, South of France, 44°27′N, 3°44′E) in 2000, brought to Foljuif and maintained in enclosed patches (10 × 10 m) containing natural habitats and producing sufficient food and refuges for the maintenance of self-sustaining populations (Lecomte et al. 2004).

At the start of the experiment, in 2004, all lizards (males and females) were collected from the enclosures on two consecutive days. Females were kept in the laboratory until they gave birth and males and yearlings were released into 16 enclosures (eight with high-density populations and eight with low-density populations), 7 days after the last capture. The high-density enclosures contained twice as many animals as the low-density enclosures. The juveniles and their mothers were released into the enclosures 2 days after birth, maintaining the densities assigned to each enclosure (ratio of 1 : 2 individuals between low- and high-density populations). All the offspring of a given female were released, with that female, in the same enclosure. The release of juveniles and females began 3 weeks after capture and continued over a period of 3 weeks, with 85% of the juveniles released within 2 weeks of the start of the hatching period. The difference between density treatments (high vs. low) was maintained throughout the release period, by careful assignment of juveniles and their mothers to particular enclosures. Males, yearlings and families were randomly selected for release into enclosures corresponding to a given density treatment and family characteristics (i.e. mother's body size, number and body size of the offspring) did not differ significantly between density treatments ($P > 0.5$).

At the end of the release period, each high-density population (corresponding to a single enclosure) contained eight adult males, 12 adult females, 20 yearlings (10 males and 10 females) and 34 ± 3.7 SE juveniles. Each low-density population (corresponding to a single enclosure) contained four adult males, six adult females, 10 yearlings (five males and five females) and 17 ± 2.5 SE juveniles. The densities, age and sex structures of these populations

matched those of the natural populations from which the individuals originated (Massot *et al.* 1992). Indeed, Massot *et al.* (1992, and unpublished data) found 10–30 adults 100 m^{-2} in some low-density populations. Some natural populations contain even lower densities of males, but all the individuals used in our experiment originated from populations with high to very high densities (Boudjemadi *et al.* 1999; Lecomte *et al.* 2004). The densities used in this experiment are therefore similar to those found in natural populations. Moreover, the starting densities used were selected such that the highest density corresponded to the estimated carrying capacity of our experimental habitat (J. Lecomte, unpublished data and Le Galliard *et al.* 2003).

The enclosures were of similar size to an adult individual's core home range in natural conditions (Massot *et al.* 1994). Considerable overlap between home ranges is observed in this species, with as many as 30 adult individuals found in an area of similar size in natural conditions (Massot *et al.* 1992; Boudjemadi *et al.* 1999; Lecomte *et al.* 2004). The densities used in this experiment are therefore similar to the densities observed in natural populations (Lecomte & Clobert 1996).

Pairs of enclosures were connected by two one-way corridors (20 m long). These corridors were poorly lit, precluding thermoregulation, and therefore represented a hostile habitat for lizards. We can therefore exclude the possibility of lizards travelling down these corridors as part of their routine daily movements (long corridors of hostile conditions). Lizards travelling down these corridors were caught in a 30 cm deep pitfall trap at the end of the corridor. The lizards captured each day in the pitfall traps are referred to as 'dispersers', whereas those remaining in their starting population are referred to as 'residents'. The length of the dispersal corridors corresponds to the minimal dispersal distance observed in natural populations (Lecomte & Clobert 1996). In our experimental system, the distance between the centres (the point at which juveniles were released) of two connected enclosures was 30 m, and the distance from the centre of the enclosure to the pitfall trap was 25 m. In nature, individuals covering such distances from the site of their birth have been defined as dispersers, because they very rarely return (2% of all movements) (Massot & Clobert 2000). Our experimental measure of dispersal corresponds directly to the distance covered by dispersers in nature. Moreover, the timing of dispersal and dispersal rate in our experimental system were similar to those reported in natural conditions (about 20%; M. Massot *et al.* unpublished manuscript).

Finally, we have used our experimental system for complementary investigations of similar issues in natural populations. Most of the results obtained in our experimental system were consistent with observations in our long-term study and with results obtained for natural populations (effect of the presence of the mother: Le Galliard *et al.* 2003; Meylan *et al.* 2004; positive density-dependent dispersal: Massot *et al.* 1992; Lecomte *et al.* 2004; negative density-dependent dispersal: Le Galliard *et al.* 2003; Meylan *et al.* 2007). Our experimental system therefore seems to mimic the conditions found in natural populations correctly.

Test period: manipulation of the origin of immigrants and field monitoring

Lizards were individually marked by toe-clipping, and both snout-vent length and body mass were measured before release. Body condition was assessed as body mass relative to snout-vent length (i.e. body weight was analysed with snout-vent length as a covariate). Dispersal was monitored daily, from the release of the first family, through hibernation. However, with the exception of a few adult males (no difference between densities, $P > 0.3$) subsequently excluded from the experiment, no attempt at dispersal was observed during the release period. Pitfall traps were checked daily to monitor dispersal. Dispersers were identified, and weighed. Their snout-vent length was measured and they were immediately released into another enclosure. Dispersers were released randomly into an assigned high- or low-density population, taking past releases into account. These dispersers constituted the 'immigrants' in this experiment, and we investigated the possible transfer of population density-related information from these immigrants to the residents of the population to which they were transferred. We manipulated the origin of the immigrants to each population by specifically selecting juveniles originating from a low- or high-density population. Eight of the 16 populations received only immigrants from high-density populations, whereas the other eight received immigrants from low-density populations.

We first released only one immigrant into each enclosure, to determine whether a single juvenile could transfer information to the individuals inhabiting the release enclosure. Following the release of this immigrant, we investigated emigration from the enclosure. On average, emigration from a given enclosure began on average 26 days after the first immigrant was introduced into that enclosure.

We calculated the probability of emigration (i.e. dispersal) from the number of emigrants leaving the enclosures, by dividing the number of emigrants by the total number of juveniles in the enclosure. We then transferred the emigrants to another enclosure, in which they constituted new immigrants. However, these immigrants were not included in counts of the total number of juveniles in the enclosure or in determinations of the total number of emigrants (if the transferred juvenile attempted to emigrate again, as was the case for nine juveniles).

We then tried to separate the effects of the origin of immigrants and the number of immigrants. We controlled the release of immigrants such that different numbers of immigrants were released into different enclosures. We ensured that each enclosure had received at least one immigrant before setting up this gradient in the number of immigrants. At the end of the experiment, each enclosure had received between one and five immigrants. Although density was found to have no effect on the probability of dispersal (see Results), the absolute numbers of juveniles leaving the population were greater for high-density than for low-density populations. As a result, we were able to introduce only one to three immigrants from low-density populations into each enclosure, whereas two to five immigrants from high-density populations were transferred. Although the ranges for the number of immigrants introduced are not identical for both types of immigrant, there is a considerable overlap. Moreover, only one population received five immigrants, the fifth immigrant being introduced at the end of the season (early October). Only six of the 16 populations were at the extreme ends of the range (either 1 or 4–5 immigrants). This made it possible to introduce the number of immigrants a population received into the statistical model as a covariable. However, the number of immigrants did not affect the probability of emigration and similar results were obtained if this covariable was omitted (see Results).

Statistics

The probability of emigration was modelled by mixed-effect logistic regressions, using the GLIMMIX macro in SAS (Littell *et al.* 1996). The initial model included the effects of experimental treatments (arrival patch density and origin of immigrants), the number of immigrants, sex, body size and their interactions as fixed effects, together with the random effects of enclosures nested within treatments and the family effect nested within the population. The final model was obtained by backward elimination, with the stepwise removal of all non-significant effects. Statistical tests are conditional tests for fixed effects. Conditional tests for the significance of a term in the fixed effects specification are given by the usual F-tests based on the usual (REML) conditional estimate of the variance.

RESULTS

Emigration rate depended on the interaction between the population density of the patch of origin of the immigrants, the phenotype of the emigrants and the density of the population receiving the immigrants (immigrant's departure patch density × initial body size of residents × resident patch density: $F_{1,301} = 6.26$, $P = 0.0129$, Fig. 1).
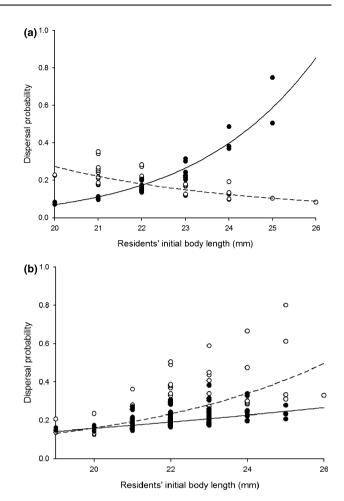

Figure 1 Phenotype- and density-dependant effect of the origin of immigrants on natal dispersal probability. Sensitivity to the origin of immigrants depended on the body size and of population density of residents. Only the resident lizards of low-density patches reacted to immigrants as a function of their population of origin (Table 1). (a) In low-density populations, the probability of residents emigrating was positively correlated with the body size of juveniles in populations receiving immigrants from high-density populations, whereas no correlation was found in populations receiving immigrants from low-density populations. (b) In high-density populations, the probability of emigration was not correlated with body size, regardless of whether immigrants came from low- or high-density populations. Data were back-transformed from the values predicted by logistic regression; each circle corresponds to individual's predicted values for populations with immigrants from high-density populations (closed circle) and for populations with immigrants from low-density populations (open circle). Curves have been fitted to the data for populations with immigrants from high-density populations (solid line) and for populations with immigrants from low-density populations (dashed line).

The effect of the immigrants' origin on emigration rate therefore depended on population density in the residents' patch (Table 1, Fig. 1). Separate analyses for residents'

Table 1 Natal dispersal probability as a function of the origin of immigrants and population density in the residents' patch

	High-density populations	Low-density populations
Initial body size	$F_{1,203} = 1.90; P = 0.1695$	$F_{1,98} = 0.21; P = 0.6507$
Origin of immigrants	$F_{1,5} = 0.00; P = 0.9719$	$F_{1,5} = 13.53; P = 0.0143$
Number of immigrants	$F_{1,203} = 0.05; P = 0.8256$	$F_{1,98} = 1.09; P = 0.2990$
Body size × origin	$F_{1,203} = 0.02; P = 0.8999$	$F_{1,98} = 12.99; P = 0.0005$

Dispersal probability was modelled by mixed effects logistic regression, using the GLIMMIX macro in SAS. The initial model included the effects of experimental treatments (origin of immigrants and number of immigrants), sex and body size at birth as fixed factors and the random effects of enclosure nested within the origin of immigrants and family nested within enclosure. The final model was obtained by backward elimination, with the stepwise elimination of all non-significant effects. Statistical tests are conditional tests for fixed effects.

patches of high and low density revealed that only lizards residing in low-density patches reacted to the immigrants as a function of their population of origin (Table 1). In resident patches with low population densities, the effect of the immigrants' population of origin on the dispersal of residents varied as a function of resident body size. In populations receiving immigrants from high-density populations, there was a positive correlation between the body size of a resident and the probability of that resident emigrating ($F_{1,148} = 4.27$, $P = 0.0405$; Fig. 1a). This relationship was not significant in populations receiving immigrants from low-density populations ($F_{1,156} = 0.01$, $P = 0.97$; Fig. 1b). Emigration rates depended on the origin of the immigrants received, but were entirely independent of the number of immigrants received (all interactions $P > 0.3$).

DISCUSSION

We found that the emigration behaviour of the residents depended on the origin of the immigrants. This suggests that the immigrants supplied information about the status of other populations. Emigration was not significantly affected by the number of immigrants received. Thus, the information transferred was not related to immigration rate; instead it probably concerned the phenotype of the immigrants. At the start of the experiment, individuals were randomly assigned to populations of different densities (see Materials and methods). The manipulation of population density therefore seems to have led to the departure of individuals with particular phenotypes in terms of morphology, physiology or behaviour. It has been shown that different conditions induce the departure of dispersers with different phenotypes (Léna et al. 1998). In our experiment, immigrants displayed no particular morphological features ($P > 0.5$ for body size and body condition). Thus, differences in behaviour or physiology (e.g. odour) between immigrants may provide information about the origin of these individuals.

The reaction to immigrants, in terms of dispersal, was also phenotype-dependent in the residents' patch. This was not entirely unexpected, as dispersal has been shown to be phenotype-dependent in several species, including that studied here (O'Rian et al. 1996; Clobert et al. 2004). Furthermore, the sensitivity of juveniles to the presence and density of conspecifics has also been shown to be phenotype-dependent (Léna et al. 1998). We can thus formulate a verbal model that could potentially account for our results. Large juvenile lizards are highly competitive and dominate in most social interactions. Encountering an immigrant from a high-density population presumably signals to the resident that high population densities are likely to be encountered elsewhere and therefore that only highly competitive residents (i.e. large ones) should attempt to disperse. In contrast, encounters with immigrants from low-density populations may indicate to the residents that the size of emigrants is of no particular concern, resulting in a higher probability of individuals of all phenotypes emigrating to low-density populations.

However, only lizards residing in low-density patches reacted to the immigrants as a function of the immigrants' population of origin. There are several possible reasons for this. First, population density conveys two types of information, concerning the existence of potential competitors and habitat quality (Clobert et al. 2004). The presence of conspecifics has been shown to attract, rather than repel other individuals, and, at population level, emigration has been found to be negatively, rather than positively, related to density in some species, including common lizards, in some situations (Stamps 2001; Le Galliard et al. 2003). It is therefore possible that a high population density is taken as an indicator of a high-quality habitat rather than a crowded habitat. This may explain why the residents of a high-density population (i.e. a high-quality habitat) did not react to the information brought by immigrants, whereas those of a low-density population (i.e. a poor-quality habitat) did. Individuals leaving the high-density population probably did so for reasons other than habitat quality. For example, kin competition (Ronce et al. 1998; Léna et al. 2000) has a density-independent effect on dispersal in this species (Le Galliard et al. 2003).

Another explanation is that individuals immigrating into high-density patches may conceal their behaviour (and

therefore information about their origin) due to the stress resulting from strong competition with residents. This hypothesis is not supported by the results of previous studies investigating the stability of behavioural traits in dispersers. Aragon *et al.* (2006a) and S. Meylan and J. Clobert (unpublished data) have shown that the behavioural traits displayed by dispersers, assessed singly or in pairs, are insensitive to the density of females during the pregnancy, hormonal treatment of the mother and population density at the offspring release site. Similarly, Cote & Clobert (2007) showed that the level of sociality measured at birth, a surrogate measure of the likelihood that the individual will disperse, was similar 1 year later. An immigrant may find it difficult to conceal differences in behaviour, as these differences may still be detectable a few months after dispersal. However, it may be possible for an immigrant to conceal its behaviour if the behavioural patterns associated with its population of origin are more labile or concern more condition-dependent behavioural traits. However, other explanations, such as better transmission of information at low density, or the context-dependent use of information, are also possible. For example, the relative risk of moving from one high-density population to another high-density population might be lower, in terms of intra-specific competition, than the risk of moving from a low-density population to a high-density population. The use of information about the surrounding populations might therefore be more useful to candidate emigrants from low-density populations than to those from high-density populations. Whatever the precise reasons, our results clearly suggest that the use of information from immigrants from surrounding populations is both context- and phenotype-dependent. This plasticity is probably required to optimize an individual's dispersal strategy with respect to the numerous and potentially inconsistent pieces of information that can be gathered about the physical and social environment at meta-population level. Further studies are required to improve our understanding of the precise influence of density and social information on dispersal strategy.

This study is the first to demonstrate the use of information obtained from immigrants for assessing the quality of surrounding populations without visiting them. This form of social information makes it possible for dispersers to reduce the risks of settlement without incurring prospecting costs. This information must be reliable if it is to be of any value. Indeed, it seems likely that immigrants reaching a new population would find it difficult to conceal their origins and would therefore be expected to deliver an 'honest' signal. First, immigrants are subject to imprinting by their population of origin (e.g. food and crowding). Second, most dispersing individuals have a specialist phenotype, which helps to maximize their chances of success as dispersers. We have shown that resident and dispersing juveniles are able to recognize each other 6 months after the dispersal phase

(Aragon *et al.* 2006a). Immigrants are therefore likely to constitute a reliable source of social information about connections in a fragmented habitat. Dispersal decisions based on information brought by immigrants help to strengthen connections between existing populations and to homogenize population sizes, leading to convergence towards an ideal free distribution (Doncaster *et al.* 1997; Hairston *et al.* 2001). This should help to decrease the overall probability of extinction (Hanski & Gaggiotti 2004) and to increase the viability of the fragmented population. Evidence that immigrants provide information about the quality of surrounding populations should lead to profound changes in our views on the evolution, persistence and functioning of meta-populations, and in attitudes to dealing with the conservation of species living in fragmented habitats.

REFERENCES

Aragon, P., Clobert, J. & Massot, M. (2006a). Individual dispersal status influences spacing behavior of conspecific residents. *Behav. Ecol. Sociobiol.*, 60, 430–438.

Aragon, P., Massot, M., Clobert, J. & Gasparini, J. (2006b). Socially acquired information through chemical cues in the common lizard. *Anim. Behav.*, 72, 965–974.

Boudjemadi, K., Lecomte, J. & Clobert, J. (1999). Influence of connectivity on demography and dispersal in two contrasting habitats: an experimental approach. *J. Anim. Eco.*, 68, 1207–1224.

Clobert, J., Danchin, E., Dhondt, A.A. & N., J.D. (2001). *Dispersal.* Oxford University Press, New York.

Clobert, J., Ims, R.A. & Rousset, F. (2004). Causes, mechanisms and consequences of dispersal. In: *Ecology, Genetics and Evolution of Metapopulations* (eds Hanski, I. & Gaggiotti, O.E.). Elsevier Academic Press, Amsterdam, pp. 307–336.

Cote, J. & Clobert, J. (2007). Social personalities influence natal dispersal in a lizard. *Proc. R. Soc. Lond. B*, 274, 383–390.

Crespi, B.J. & Taylor, P.D. (1990). Dispersal rates under variable patch density. *Am. Nat.*, 135, 48–62.

Dall, S.R.X. & Johnstone, R.A. (2002). Managing uncertainty: information and insurance under the risk of starvation. *Proc. R. Soc. Lond. B*, 357, 1519–1526.

Dall, S.R.X., Giraldeau, L.-A., Olsson, O., McNamara, J. & Stephens, D.W. (2005). Information and its use by animals in evolutionary ecology. *Trends Ecol. Evol.*, 20, 187–193.

Danchin, E., Boulinier, T. & Massot, M. (1998). Conspecific reproductive success and breeding habitat selection: implications for the study of coloniality. *Ecology*, 79, 2415–2428.

Danchin, E., Giraldeau, L.-A., Valone, T.J. & Wagner, R.H. (2004). Public information: from nosy neighbors to cultural evolution. *Science*, 305, 487–491.

Doligez, B., Danchin, E. & Clobert, J. (2002). Public information and breeding habitat in a wild bird population. *Science*, 297, 1168–1170.

Doligez, B., Pärt, T., Danchin, E., Clobert, J. & Gustafsson, L. (2004). Availability and use of public information and con-specific density for settlement decisions in the collared fly-catcher. *J. Anim. Eco.*, 73, 75–87.

Doncaster, C.P., Clobert, J., Doligez, B., Gustafsson, L. & Danchin, E. (1997). Balanced dispersal between spatially varying local populations: an alternative to the source-sink model. *Am. Nat.*, 150, 425–445.

Eckman, J. (1984). Density-dependent seasonal mortality and population fluctuations of the temperature zone Willow Tit (*Parus montanus*). *J. Anim. Eco.*, 53, 119–134.

Hairston, N.G., Holtmeier, C.L., Lampert, W., Weider, L.J., Post, D.M., Fischer, J.M. *et al.* (2001). Natural selection for grazer resistance to toxic cyanobacteria: evolution of phenotypic plasticity? *Evolution*, 55, 2203–2214.

Hanski, I. & Gaggiotti, O.E. (2004). *Ecology, Genetics and Evolution of Metapopulations*. Elsevier Academic Press, Amsterdam.

Hassel, M.P. & Nay, R.M. (1985). *From individual behaviour to population dynamics*. Pages 3–32 in R.M. Sibly & R.H. Smith (eds). Behavioural Ecology: Ecological Consequences of Adaptive Behaviour, Blackwell Scientific Publications, Oxford.

Krebs, J.R. (1971). Territory and breeding density in the great fit, *Parus major* L. *Ecology*, 52, 2–22.

Lambin, X., Aars, J. & Piertney, S.B. (2001). Dispersal, intraspecific competition, kin competition and kin facilitation: a review of the emperical evidence. In: *Dispersal* (eds Clobert, J., Danchin, E., Dhondt, A.A. & N, J.D.). Oxford University Press, New York, pp. 110–122.

Le Galliard, J.F., Ferrière, R. & Clobert, J. (2003). Mother-offspring interactions affect natal dispersal in a lizard. *Proc. R. Soc. Lond. B*, 270, 1163–1169.

Le Galliard, J.F., Massot, M., Landys, M.M., Meylan, S. & Clobert, J. (2006). Ontogenic sources of variation in sexual size dimorphism in a viviparous lizard. *J. Evol. Biol.*, 19, 690–704.

Lecomte, J. & Clobert, J. (1996). Dispersal and connectivity in populations of the common lizard *Lacerta vivipara*: an experimental approach. *Acta Oecol.*, 17, 585–598.

Lecomte, J., Clobert, J., Massot, M. & Barbault, R. (1994). Spatial and behavioural consequences of a density manipulation in the common lizard. *Ecoscience*, 1, 300–310.

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. Eco.*, 73, 179–189.

Léna, J.-P. & de Fraipont, M. (1998). Kin recognition in the common lizard. *Behav. Ecol. Sociobiol.*, 42, 341–347.

Léna, J.-P., 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, J.-P., de Fraipont, M. & Clobert, J. (2000). Affinity towards maternel odour and offspring dispersal in the common lizard. *Ecol. Lett.*, 3, 300–308.

Lidicker Jr, W.Z. (1978). Regulation of numbers in small mammal populations – historical reflections and a synthesis. In: *Populations of Small Mammals Under Natural Conditions* (ed. Snyder, D.P.). Pymatuning Symposia in Ecology, Spec. Publ. 5, Linesville, PA, pp. 122–141, 163–166.

Littell, R.C., Miliken, G.A., Stroup, W.W. & Wolfinger, R.D. (1996). *SAS® System for Mixed Models*. SAS Institute, Inc., Cary, NC.

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 dependance in the common lizard: demographic consequences of a density manipulation. *Ecology*, 73, 1742–1756.

Massot, M., Clobert, J., Chambon, A. & Michalakis, Y. (1994). Vertebrate natal dispersal: the problem of non-independence of siblings. *Oikos*, 70, 172–176.

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., 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* (in press).

O'Rian, M.J., Jarvis, J.U.M. & Faulkes, C. (1996). A dispersive morph in the naked mole-rat. *Nature*, 380, 619–621.

Reigh, L.M., Wood, K.M., Rothstein, B.E. & Tamarin, R.H. (1982). Aggressive behaviour of male Microtus brexeri and its demographic implications. *Anim. Behav.*, 30, 117–122.

Ronce, O., Clobert, J. & Massot, M. (1998). Natal dispersal and senescence. *PNAS*, 95, 600–605.

Schjorring, S. (2002). The evolution of informed natal dispersal: inherent versus acquired information. *Evol. Ecol. Res.*, 4, 227–238.

Sinclair, A.R.E. (1989). Population regulation in animals. In: *Ecological Concepts, the Contribution of Ecology to an Understanding of the Natural World* (ed. Cherrets, J.M.). Blackwell Scientific, Oxford, pp. 187–241.

Stamps, J.A. (2001). Habitat selection by dispersers: integrating proximate and ultimate approaches. In: *Dispersal* (eds Clobert, J., Danchin, E., Dhondt, A.A. & N, J.D.). Oxford University Press, New York, pp. 110–122.

Stenseth, N.C. & Lomnicki, A. (1990). On the Charnov–Finerty hypothsesis: the unproblematic transition from docile to aggressive and the problematic transition from aggressive to docile. *Oikos*, 58, 234–238.

Templeton, J.J. & Giraldeau, L.-A. (1995). Patch assessment in foraging flocks of European starlings: evidence for the use of public information. *Behav. Ecol.*, 6, 65–72.

Valone, T.J. (1989). Group foraging, public information, and patch estimation. *Oikos*, 56, 357–363.

Valone, T.J. & Templeton, J.J. (2002). Public information for the assessment of quality: a widespread social phenomenon. *Philos. Trans. R. Soc. Lond. B*, 357, 1549–1557.