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Risky dispersal: avoiding kin competition despite uncertainty

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Abstract. Leaving a population without having information about the surrounding areas is highly risky. Candidates for dispersal may reduce these risks by making decisions based on the level of connectivity between patches, e.g., through immigrants. The benefits of information acquisition may vary within a population according to the dispersal cause and the phenotype of the candidate disperser. For instance, kin-based dispersers should be prepared to accept higher dispersal cost than individuals leaving for competition with congeners, and individuals of better condition should better deal with the costs of dispersing. We investigated whether the use of information obtained from immigrants depended on the reason for dispersal and the phenotype of individuals in common lizards (*Lacerta vivipara*). Dispersal decisions with respect to connection status depended on the cause of dispersal and on body mass. When intraspecific competition was the driving force behind dispersal, the information carried by immigrants allowed candidate dispersers to decrease uncertainty about the success of dispersal. Therefore, larger individuals dispersed when connectivity was low, whereas smaller individuals dispersed when connectivity was high. When kin competition dominated, dispersers did not adjust their dispersal decisions on the basis of information about the existence of surrounding populations, and larger individuals dispersed whatever the connectivity. These results provide support for the hypothesis that kin competition is one of the factors driving colonization.

Key words: common lizards; connection; connectivity; immigration; intraspecific competition; kin competition; Lacerta vivipara; *natal dispersal; risk decisions; social information.*

INTRODUCTION

In a fragmented landscape, the dynamics and evolution of metapopulations depend on the level of connectivity between habitat patches (Hanski and Gaggiotti 2004). Dispersal is a key life history trait underpinning the functioning of metapopulations, but moving from one habitat to another entails major risks and costs to the disperser (Clobert et al. 2001, Stamps 2001). Indeed, dispersal may be unsuccessful because the environment is too hostile, the surrounding areas may be unsuitable habitats, and suitable habitat patches may be too distant (Clobert et al. 2001, Stamps 2001). More generally, a movement between habitats is costly because it requires time and energy that cannot be used for any other activity. Despite that, some individuals decide to disperse. Cost–benefit management has thus become an interesting question in dispersal theory. An individual's dispersal decision would especially depend on three major facts. (1) What does this individual know about the risks of dispersing? (2) How can this individual deal with the costs of dispersing? (3) Why is this individual's motivation to disperse? The interplay between information about the surroundings, the phenotype of dispersers, and the dispersal motivation will then lead to the actual dispersal decision (Clobert et al. 2009).

In the first instance, a candidate disperser may reduce the risks by dispersing only if patches are sufficiently interconnected. Actually, connections between suitable habitats strongly impact the cost of dispersal through the risks associated with travel across hostile environments (Bowler and Benton 2005). Indeed, corridors have been found to increase inter-habitat movements in several species (Aars et al. 1999, Boudjemadi et al. 1999, Coffman et al. 2001). To decrease the risks, candidate dispersers should collect information about the existence and quality of surrounding areas (Danchin et al. 1998, Stamps 2001, Doligez et al. 2004, Dall et al. 2005). It is known that individuals can assess environmental quality through socially acquired information about the presence or absence of conspecifics, their activities, and their performance (Stamps 1991, Danchin et al. 1998, Doligez et al. 2004). In species with limited exploratory capacities, the degree of isolation of a population (i.e., distance to other patches) should impact the cost of dispersal even more in a hostile environment (Bowler and Benton 2005). Then, the use

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of local cues indicating that other populations exist in the vicinity should be favored by natural selection (Conradt et al. 2003, Clobert et al. 2004). Immigrants to a population can be such a cue. Indeed, immigrants may be an important source of information about the existence and quality of surrounding patches either through their number (indicating immigration rate) or through their phenotype. In the common lizard, *Lacerta vivpara*, residents obtain information about surrounding populations from immigrants (Cote and Clobert 2007*a*). In the common lizard, it is known that different conditions induce the departure of dispersers with different phenotypes (Léna et al. 1998, Cote and Clobert 2007*b*, Cote et al. 2007). Differences in morphology, behavior, or physiology (e.g., odor) among immigrants may then provide information about the origin of those individuals. The candidate dispersers therefore might have some available information about the existence and density of other nearby populations (Boudjemadi et al. 1999, Lecomte et al. 2004).

In a second instance, some phenotypic attributes change the costs as well as the benefits of dispersal. Phenotype-dependent dispersal is a widely known process in animal species (Bowler and Benton 2005, Benard and McCauley 2008, Clobert et al. 2009). These phenotypic differences have been found for a variety of physiological, morphological, behavioral, and life history traits (Bowler and Benton 2005, Benard and McCauley 2008, Clobert et al. 2009). Previous studies suggested that dispersers' phenotypic specializations mitigate the costs of dispersal or facilitate settlement, ultimately equalizing lifetime reproductive success between dispersers and residents (with the notable exception of kin competition where equalization involves inclusive fitness). There is good empirical evidence that dispersal involves a variety of costs during transience and at settlement (e.g., Larsen and Boutin 1994, Weisser 2001, Yoder et al. 2004, Bonte et al. 2006, Fjerdingstad et al. 2007), and that selection on some phenotypic traits (e.g., body condition) and behaviors (e.g., boldness, aggressiveness) can act to reduce these costs (O'Rian et al. 1996, Barbraud et al. 2003, Dingemanse and de Goede 2004, Sinervo et al. 2006, Duckworth 2008). Especially, dispersers have been reported to be larger or in better condition than the average resident across a range of taxa including the common lizards (for a review, see Bowler and Benton 2005). Larger individuals may be more inclined to disperse if individuals require a certain amount of reserves before they can undertake costs of dispersal or settlement. Contrary to this, some studies have shown that dispersers are smaller than residents (e.g., Hanski et al. 1991). These results are interpreted as the effects of lower competitive abilities on dispersal motivation or propensity. Thus, body size and body condition modulate the dispersal decision in a complex manner and their effects should depend on the main factor driving dispersal and on the costs and risks of dispersal.

More generally, having access to information about surrounding populations reduces the risk of moving to and selecting another patch, and the phenotype of dispersers reduces the costs of dispersing and interacts with the reasons for dispersal (Clobert et al. 2009). These two aspects therefore should influence the balance between costs and benefits of dispersal. For example, individuals would benefit from information about the potential advantages or disadvantages of dispersing to another area. The necessity of acquiring such information should, however, vary with respect to the potential benefits of dispersing and to the phenotype of dispersers. In particular, the reasons for an individual's departure may strongly influence the usefulness of this information (Clobert et al. 2009). Natal dispersal, the movement between an individual's birth place and its place of first reproduction, is influenced by many different biotic and abiotic factors (Clobert et al. 2001). In particular, intraspecific competition and kin interactions are among the main causes of changes in dispersal patterns (Cockburn 1998, Léna et al. 1998, West et al. 2002, Le Galliard et al. 2003, Sinervo et al. 2006). Theoretically, dispersal that is dependent on intraspecific competition should have evolved such that nondispersers and dispersers are equally fit (Lemel et al. 1997, McPeek et al. 2001, Murren et al. 2001). Individuals of lower quality (e.g., body condition) would be expected to disperse in response to crowding only if they have enough information about the level of competition in surrounding populations in order to enhance their fitness through dispersal. Theoretical predictions concerning kin interactions are different. In a seminal paper, Hamilton and May (1977) showed that kin competition alone was sufficient to promote changes in dispersal, even if dispersal entailed important costs (Ronce et al. 1998, Murren et al. 2001, Perrin and Lehmann 2001). Individuals suffering from kin competition are therefore likely to disperse even if their chances of success cannot be evaluated. Moreover, individuals should use different information depending on their motivation to disperse. Because kin-based dispersers are sensitive to the kin structure of their actual population (Cote et al. 2007), these individuals should base their decisions on information about kin structure in their population rather than on information about the surroundings. Candidate dispersers motivated by kin competition thus might be less sensitive to information about the costs of dispersal and the existence of connections with surrounding populations.

We investigated the influence on natal dispersal decisions of interactions among the presence of kin, the presence of information about surrounding populations, and the phenotype of individuals. We performed a replicated experiment in 16 seminatural populations of *Lacerta vivipara* of fixed density, in which the level of kin competition was manipulated by including or removing the mother. Kin competition may occur between parents and offspring, or between offspring. In the common lizard, strong mother–offspring competition has repeatedly been reported (Léna et al. 1998, Le Galliard et al. 2003, Cote et al. 2007), suggesting that such competition is the major component of kin competition in this species. Offspring were released with their mother or with a surrogate female to manipulate the level of kin competition. When offspring were released with the mother, kin competition occurred through mother–offspring competition. When offspring were released with a surrogate female, the offspring experienced intraspecific competition more than kin competition. In half of the populations, we mimicked the absence of connections between populations by preventing emigration and immigration between populations. This procedure prevented the transmission of information about surrounding populations and provided residents with information about the absence of connection (Boudjemadi et al. 1999, Lecomte et al. 2004). In the other populations, we mimicked information about connections between populations by introducing immigrants and allowing emigration to the other populations. In this case, immigrants transferred information about the existence of surrounding populations (Boudjemadi et al. 1999, Aragon et al. 2006*a*, Cote and Clobert 2007*a*).

This design made it possible to investigate the effects on dispersal of the level of kin competition within a population and information about the presence or absence of connection between populations. Based on theoretical and empirical results, we predicted a lower overall dispersal probability from unconnected populations compared to connected populations (Boudjemadi et al. 1999, Lecomte et al. 2004). This would show that individuals manage uncertainty by way of connectivity-related information carried by immigrants. We also predicted that the propensity to disperse of individuals suffering from kin competition should be less dependent on information about connections with surrounding populations than for individuals suffering from competition with congeners. Finally, we predict that these effects should vary according to the phenotype of individuals. In the common lizard, dispersers differ from residents in their body size and body condition (Léna et al. 1998, Cote et al. 2007). This link between body size and condition and competitive abilities or energy resources leads to a variation in dispersal costs and benefits with body size and body condition that should affect the risk-dependent dispersal decisions.

MATERIALS AND METHODS

Experimental populations

The experiment was conducted in 2005 at the Foljuif Ecological Research Station (Seine-et-Marne, France 48°17′ N, 2°41′ E). Lizards were captured in the Cévennes (Mont Lozère, southern France, 44°27′ N, 3°44′ E) in 2000, and were brought to Foljuif and maintained in large enclosures (10 × 10 m) as self-sustaining populations (Lecomte and Clobert 1996, Lecomte et al. 2004). In June 2005, all lizards were collected from the enclosures over six consecutive days. We then established lizard populations in 16 empty enclosures. Populations were initiated with 6 adult males, 10 adult females, 6 yearlings (3 males and 3 females), and 59.7 ± 13.0 juveniles (mean ± SE; because the number of juveniles/female varies, it was not possible to release exactly the same number of juveniles per population). The densities, age, and sex structures of these populations matched those of the natural populations from which the individuals originated (Massot et al. 1992). These enclosures were of similar size to an adult's core home range under natural conditions (Massot et al. 1992). Considerable overlap between home ranges is observed in this species, with as many as 30 adult individuals being found in an area of similar size under natural conditions (Massot et al. 1992, Boudjemadi et al. 1999, Lecomte et al. 2004). Lizards were individually marked by toe-clipping, and both snout–vent length and body mass were measured before lizards were released.

Enclosures were connected to one-way corridors (20 m long). The corridor walls were high enough to block direct sunlight, thereby preventing thermoregulation in the corridor. Moreover, low direct sunlight prevents the development of vegetation, creating an unfavorable habitat for lizards. Because the corridors were unfavorable habitat for lizards, lizards were not likely to travel down the corridors as part of their routine daily movements. The length of the dispersal corridors corresponded to the minimal dispersal distance observed in natural populations (Lecomte and Clobert 1996). In our experimental system, the distance between the centers (the point at which juveniles were released) of two connected enclosures was 30 m, and the distance from the center 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 and Clobert 2000). Our experimental measure of dispersal corresponds directly to the distance covered by dispersers in nature. Lizards attempting to move across enclosures through these corridors were caught in a 30 cm deep pitfall trap at the end of each corridor. The lizards captured in the pitfall traps are referred to as "dispersers," whereas those remaining in their starting population are referred to as "nondispersers." Dispersal was monitored from the release of the first family until hibernation (from June to September) by checking pitfall traps daily. Dispersers were identified, weighed, measured (snout–vent length), and immediately released in line with the connection treatments outlined below.

Kin competition treatment

We investigated the effect of kin competition on natal dispersal by including or removing the mother. After capture in June 2005, females were kept in the laboratory until they gave birth (Le Galliard et al. 2003). Males were released into empty enclosures a few days after capture. We manipulated kin competition by including or excluding the mother from the enclosure. Kin competition may occur between parents and offspring, or between offspring. In the common lizard, Massot and Clobert (2000) found no evidence for kin competition between offspring in a natural population over 18 years (no correlation between offspring dispersal and clutch size), and they found only weak evidence for same-sex offspring competition (weak correlation between offspring dispersal and sex ratio of the clutch). Nothing is known about father–offspring competition. However, because females may be polyandrous (Laloi et al. 2004) and this species does not engage in parental care, father–offspring competition is not likely to be important. Conversely, strong mother–offspring competition has repeatedly been reported (Léna et al. 1998, Le Galliard et al. 2003, Cote et al. 2007), suggesting that such competition is the major component of kin competition in this species. Two days after birth, all the offspring of a family were released either with their mother or with a surrogate female in order to manipulate kin competition at the individual scale. Families were randomly assigned to treatments and all populations contained the same proportion of families released with their mother or with a surrogate female. Family characteristics (body length of the female, number and body length of offspring) did not differ significantly between the two kin treatments ($P > 0.1$).

Manipulation of population connections

Based on previous studies (Boudjemadi et al. 1999, Aragon et al. 2006*a*, Cote and Clobert 2007*a*), we manipulated information about the existence of surrounding populations by modifying immigration patterns. In half of the populations, we mimicked an absence of information about surrounding populations by stopping emigration to these populations (unconnected populations received no immigrants from other populations). For these eight populations, emigration was also prevented by releasing dispersers back into their population of origin. This release of dispersers back to their original population simulates the behavior of individuals in cases of failed dispersal. Indeed, in such cases, the dispersers generally actively return to their population of origin (Lecomte and Clobert 1996, Boudjemadi et al. 1999). For the other eight populations, we mimicked the presence of information about connections. These eight connected populations received immigrants from other populations and dispersers from these connected populations were released into another enclosure. Unconnected populations therefore received no immigrants, whereas connected populations received immigrants from several enclosures, ensuring information transfer from surrounding populations. Immigrants are likely to constitute a reliable source of social information about connections in a fragmented habitat (Boudjemadi et al. 1999, Aragon et al. 2006*a*, Cote and Clobert 2007*a*). A similar procedure was successfully used previously to simulate a lack of connection between populations (Boudjemadi et al. 1999, Lecomte et al. 2004). This procedure has been shown to provide information about the level of connection of the patch in previous studies; the absence of a connection has been proved to decrease the number of dispersal attempts (Boudjemadi et al. 1999, Lecomte et al. 2004). We used all dispersers (adults, yearlings, and juveniles) to simulate connections between populations. Adult females disperse at an extremely low rate during the summer (4/208 adult females dispersed in total), so the manipulation of mother–offspring competition was not affected by female dispersal. We kept the density of connected populations constant by adjusting the immigration rate as a function of the emigration rate (i.e., an immigrant was released into the population whenever a disperser left).

Statistics

In all the analyses, we used each individual only once. Therefore, dispersal decisions are simply analyzed regarding the initial conditions of release (i.e., presence of the mother); multiple dispersal attempts have been excluded. The probability of natal dispersal was modeled by mixed-effect logistic regression, using the GLIMMIX macro in SAS (Littell et al. 1996). The age of dispersers was modeled using the MIXED procedure in SAS (Littell et al. 1996). The initial model included the effects of experimental treatment (presence of the mother and connection between populations), sex, body size at birth, mass at birth, and all interactions (except that between size and mass) as fixed effects, together with the random effects of enclosures nested within the connectivity treatment and the family effect nested within the enclosure and kin competition treatments. The best model was obtained by backward stepwise elimination of nonsignificant terms ($P > 0.05$). Body condition was modeled by adding body mass and body size to the model as independent variables (Darlington and Smulders 2001, Garcia-Berthou 2001). *F* tests based on the conditional estimate of the variance (REML, restricted maximum likelihood) were used for conditional assessments of the significance of fixed-effect terms. Assumptions of the statistical models were checked in all cases (Quinn and Keough 2002).

RESULTS

Offspring dispersal rate depended on the interaction between the existence of a connection between populations, the phenotype of the juveniles, and the presence of the mother (Table 1, Fig. 1). The effect of connection between populations on dispersal rate also depended directly on whether the mother was present (Table 1, Fig. 1). Separate analyses for offspring released with and without the mother revealed that only lizards released with a surrogate female were influenced by the existence of connections between populations (Table 2). In the absence of the mother, the effect of connections on

TABLE 1. Effects of kin competition and connection between populations of common lizards (*Lacerta vivipara*) on the probability of natal dispersal for offspring.

Factors	Estimates ± SE	*t*	*P*	df	*F*	*P*
Intercept	−3.33 ± 3.09	−1.08	0.02			
Sex (F)	0.61 ± 0.22	2.76	0.01	1, 611	7.62	0.01
Kin competition (M)	0.97 ± 2.99	0.32	0.75	1, 114	1.91	0.17
Connection (C)	5.91 ± 2.56	2.31	0.03	1, 14	1.69	0.21
Connection × kin competition	−6.95 ± 3.64	−1.91	0.05	1, 611	3.70	0.05
Initial body size	−0.12 ± 0.12	−0.98	0.32	1, 611	0.96	0.33
Initial body mass	−17.74 ± 10.92	1.63	0.10	1, 611	3.66	0.05
Body mass × connection	−26.71 ± 12.56	−2.13	0.03	1, 611	0.91	0.34
Body mass × kin competition	−5.66 ± 14.67	−0.39	0.70	1, 611	1.90	0.17
Body mass × connection × kin competition	36.02 ± 17.95	17.96	0.04	1, 611	4.03	0.04
Enclosure(connection)	0.36 ± 0.23				$Z = 1.58$	0.06
Family(enclosure, kin competition)	0.44 ± 0.22				$Z = 2.03$	0.02

Notes: Estimates are given for offspring released with their mother (M), released in connected populations (C), and for female (F) offspring. Random effects are enclosures nested within the connectivity treatment and the family effect nested within the enclosure and kin competition treatments. *Z* tests were used for enclosure, which is a random factor; all other factors are fixed.

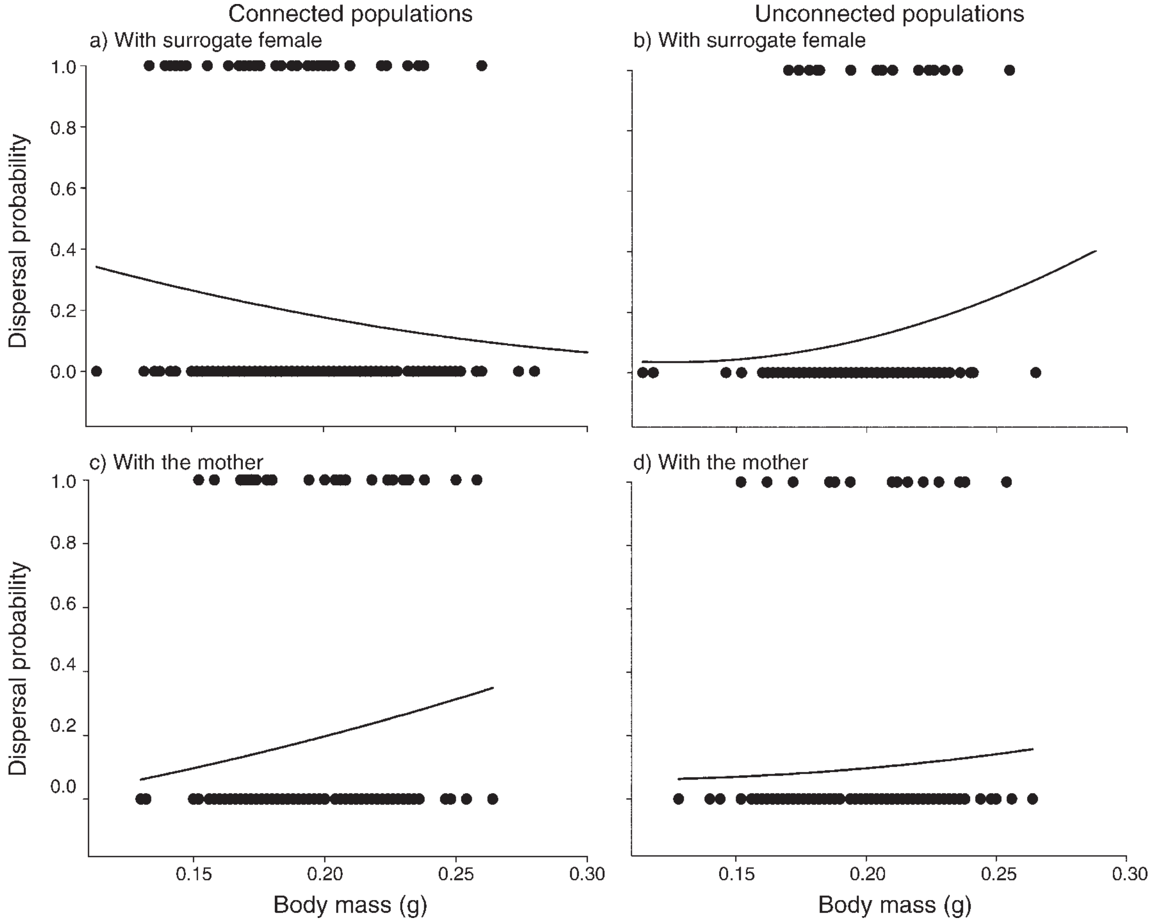

FIG. 1. Phenotype-dependent effect of kin competition and effect of information on the presence–absence of surrounding populations on the probability of natal dispersal. Only common lizards (*Lacerta vivipara*) with no kin competition (i.e., released without their mother) reacted to information about the absence of surrounding populations (see Table 2). The presence or absence of connections between populations was simulated by manipulating emigration and immigration between populations. Unconnected populations were those in which we prevented emigration and immigration. Connected populations were those in which we introduced immigrants and allowed emigration to the other populations. (a) In connected populations, the probability of dispersal was negatively correlated with juvenile body mass, whereas (b) there was a positive correlation between juvenile body mass and the probability of emigrating in unconnected populations. For juveniles in the presence of their mother (c, d), the absence of a connection between populations had no effect on dispersal rate, but the probability of dispersal was positively correlated with body mass. Each solid circle corresponds to the dispersal status of an individual. Curves have been fitted to back-transformed values predicted by logistic regression.

TABLE 2. Effects of connection between populations on the probability of natal dispersal for offspring released with their mother and for offspring released with a surrogate female.

Factors	With mother			With surrogate female		
	df	*F*	*P*	df	*F*	*P*
Sex	1, 294	4.61	0.03	1, 315	3.57	0.06
Body size at birth	1, 294	1.39	0.24	1, 315	0.10	0.76
Body mass at birth	1, 294	8.11	0.005	1, 315	0.12	0.73
Connection	1, 14	0.03	0.87	1, 14	6.46	0.02
Body mass × connection	1, 294	0.24	0.62	1, 315	5.62	0.02
Enclosure(connection)		$Z = 1.27$	0.10		$Z = 1.40$	0.08
Family(enclosure)		$Z = 1.65$	0.05		$Z = 0.59$	0.28

juvenile dispersal also depended on juvenile body mass (Table 2). In unconnected populations, there was a positive correlation between juvenile body mass and the probability of dispersing ($F_{1,152} = 3.98$, $P = 0.048$; Fig. 1b). In populations connected with other populations, a negative relationship was observed between juvenile body mass and the probability of emigrating ($F_{1,163} = 4.23$, $P = 0.04$; Fig. 1a).

For juveniles in the presence of their mother, the rate of dispersal was not affected by the existence of connections between populations (Table 2, Fig. 1c, d). However, dispersal rate was positively correlated with juvenile body mass (Table 2, Fig. 1c, d) and was higher for females than for males ($F_{1,611} = 7.62$, $P = 0.006$), regardless of treatments (all interactions, $P > 0.4$). On average, dispersal rates were lower in unconnected populations than in connected populations: dispersal rates per generation were 0.11 ± 0.02 (mean ± SE) for unconnected populations and 0.19 ± 0.02 for connected populations ($\chi^2_1 = 9.8$, $P = 0.0017$).

Juveniles in connected populations dispersed earlier than those in unconnected populations, but this effect was dependent on juvenile body mass (analyses on dispersers; $n = 111$ juveniles; Table 3). It means that the relationship between juvenile body mass and age at dispersal was different in connected and unconnected populations: it was negative in unconnected populations (n = 40; $F_{1,35}$ = 5.29, P = 0.0276; Fig. 2), but no significant correlation was found in connected populations (n = 71; $F_{1,66}$ = 0.68, P = 0.41; Fig. 2). Age at dispersal was also influenced by the interaction between the mother's presence and the juvenile's sex (Table 3). Juvenile females dispersed earlier when released with their mother (47.0 ± 2.72 days, mean ± SE) than when released with a surrogate female, but without their mother (55.6 ± 2.68 days) (n = 62; $F_{1,57}$ = 5.31, P = 0.0248). In contrast, dispersal age in males was independent of the mother's presence (n = 49; $F_{1,44}$ = 2.62, P = 0.11): 53.26 ± 3.24 days with their mother; 46.20 ± 2.95 days with a surrogate female).

DISCUSSION

Habitat connectivity and phenotype-dependent dispersal

In our study, we mimicked a lack of connection between populations by preventing the arrival of new immigrants and the departure of dispersers. This procedure provides information about the level of connection of the patch in previous studies (Boudjemadi et al. 1999, Lecomte et al. 2004). The absence of a connection has been shown in this study and other to decrease the number of dispersal attempts (Boudjemadi et al. 1999, Lecomte et al. 2004). Immigrants reaching a new population are believed to deliver an "honest" signal about the existence of surrounding populations. Indeed, previous results suggest that, when encountering an unfamiliar individual, a lizard reacts differently according to the intruder's population of origin (Cote and Clobert 2007*a*, Cote et al. 2008). We believe that individuals can distinguish neighbors from foreign lizards for two reasons. First, this species has the

TABLE 3. Effects of kin competition and connection between populations on age at dispersal.

Factors	Estimates ± SE	*t*	*P*	df	*F*	*P*
Intercept	85.29 ± 33.22	2.57	0.02			
Sex (F)	11.52 ± 3.84	3.00	0.005	1, 39	1.30	0.26
Kin competition (M)	7.74 ± 4.57	1.69	0.099	1, 39	0.03	0.86
Connection (C)	−63.60 ± 24.43	−2.60	0.02	1, 14	6.78	0.02
Initial body size	0.03 ± 1.46	0.02	0.98	1, 39	0.00	0.98
Initial body mass	−193.16 ± 104.39	−1.85	0.07	1, 39	0.45	0.51
Body mass × connection	290.01 ± 119.77	2.42	0.02	1, 39	5.86	0.02
Sex × kin competition	−16.70 ± 5.41	−3.08	0.004	1, 39	9.51	0.004
Enclosure(connection)	2.04 ± 18.98				$Z = 0.11$	0.46
Family(enclosure, kin competition)	39.46 ± 2.32				$Z = 2.32$	0.01

Notes: Estimates are given for offspring released with their mother (M), released in connected populations (C), and for female (F) offspring. Random effects are enclosures nested within the connectivity treatment and the family effect nested within the enclosure and kin competition treatments.

capacity for individual recognition through different cues (e.g., olfactory; Léna and de Fraipont 1998, Aragon et al. 2006*b*). Second, in natural populations, lizards rapidly explore an area of a similar size to the enclosure in which we keep them (Lecomte et al. 2004). In our experimental system, it is possible for an individual to rapidly encounter or interact with all the lizards of its population and to detect any change in the composition of its population. In our experiment, immigrants transfer information about the surrounding populations in the connected treatment. In the unconnected treatment, no information about surrounding populations is transferred, or frustrated dispersers transfer information about a low probability of achieving successful dispersal. Residents in unconnected populations thus receive information about some high costs of dispersal, which entails a low rate of dispersal from such populations, as shown in this study and others (Boudjemadi et al. 1999, Lecomte et al. 2004).

Dispersal decisions with respect to connection status were dependent on phenotype (i.e., body mass). The dispersal rate and timing of dispersal varied as a function of juvenile body mass and population connection status. This result was expected because (1) dispersal is most often phenotype dependent (O'Rian et al. 1996, Léna et al. 1998, de Fraipont et al. 2000, Massot and Clobert 2000, Ims and Hjermann 2001, Clobert et al. 2004), and (2) the information carried by immigrants is used differently by individuals of different phenotypes (Cote and Clobert 2007*a*). Actually, individuals in better condition may show a greater dispersal tendency if dispersal requires a certain amount of reserves or if they are more capable of immigrating to a new competitive population.

There is also accumulating evidence across a range of taxa that dispersers are larger or in better condition than residents (Bowler and Benton 2005, Benard and McCauley 2008). Here, juveniles with a low body mass dispersed less frequently and later in unconnected populations than in connected populations. Body mass and size are predictive of competitive ability, reproductive value, and survival in the common lizard (Bauwens and Verheyen 1987, Le Galliard et al. 2004). Thus, individuals in better condition might be better prepared to endure the costs of dispersal (Bowler and Benton 2005, Gyllenberg et al. 2008), e.g., the costs of traveling when no information about surrounding populations is available or when dispersal is less likely to be successful. Finally, the production of a dispersal phenotype is likely to be cause-specific: some phenotypes should be better adapted to deal with some factors and less adapted to others (Clobert et al. 2009). For example, the individual traits involved in dispersal should depend on the source of habitat degradation; sensitivity to competition with congeners may depend on the resource-holding potential (e.g., size, age), whereas sensitivity to shortage of mates is more likely to depend on sex and mating skills (e.g., exploration capacity, attractiveness). In other words, it is quite unlikely that all factors promoting the evolution of dispersal display the same spatial heterogeneity (require the same dispersal distances) and therefore share the same costs to disperse and require the same type of adaptation (Lidicker and Stenseth 1992). As a consequence, information use should depend on both phenotype and cause of dispersal. For example, escaping kin competition is likely to depend on information at a small spatial scale (i.e., the location of related individuals), whereas avoiding intraspecific competition should depend on both small and large spatial scales.

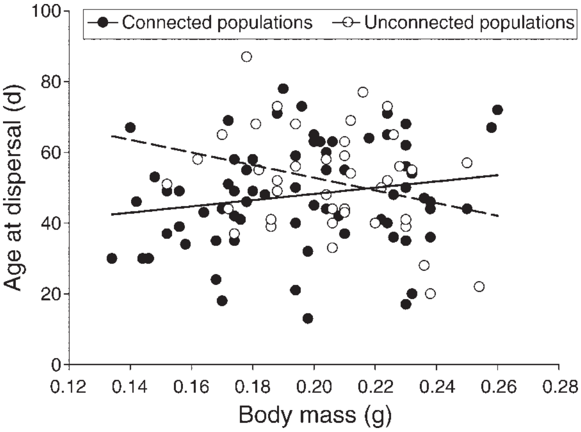

FIG. 2. Phenotype-dependent effect of kin competition and information about the presence–absence of surrounding populations on age at dispersal of common lizards. Juveniles dispersed earlier in connected populations than in unconnected populations, but this effect was dependent on juvenile body mass (Table 3). Regressions indicate that there was a negative relationship ($P = 0.0276$) between juvenile body mass and age at dispersal in unconnected populations, whereas no significant correlation was found in connected populations.

Connectivity, kin competition, and dispersal risk

Unlike juveniles released in the absence of their mother, juveniles released with their mother did not modulate their dispersal decisions as a function of the existence of connections between populations. Kin competition may be so severe in this species that many juveniles decide to disperse even in the absence of information about surrounding habitats or in cases in which dispersal is clearly unlikely to be successful (i.e., they disperse at all costs). The insensitivity to information may result from the dependence of dispersal benefits on dispersal motivations. For kin-based dispersal, the benefit of dispersal should be measured at the family level (inclusive fitness), but the benefit of dispersal caused by conspecific competition should be measured at the individual level. Whenever a mother or offspring lizard can avoid entering into competition with a relative, to maximize the number of gene copies passed to the next generation, it should leave the parent home range even if there is a very great risk of mortality (Hamilton and May 1977, Ronce et al. 1998, Perrin and Goudet 2001). It is therefore not surprising that offspring should be more sensitive to information on the kin structure of their current population (Cote et al. 2007) than to information on surrounding populations. This is not to say that these offspring are totally insensitive to the information brought by immigrants. Indeed, although the kin-based dispersal rate cannot be strongly modulated, dispersal costs may be lower if dispersers leaving the population due to kin-based competition are in better condition.

Previous studies have shown that kin-based dispersal decisions depend on the phenotype of the individual in other species (Moore et al. 2006) as well as in the common lizard (Léna et al. 1998, Le Galliard et al. 2003, Cote et al. 2007). More than other causes of dispersal, kin competition may favor condition-dependent decisions because kin competition-dependent dispersers are predicted to have higher dispersal costs than other dispersers. Any strategy to reduce cost is then expected to evolve to decrease potential costs, such as dispersing in the absence of information, or under conditions in which the probability of success is low. Finally, previous studies have suggested that (1) kin competition partly drives colonization (Cote et al. 2007) and that (2) increasing adult life span selects for increasing juvenile mobility in models allowing for empty sites to be colonized (Olivieri et al. 1995). Kin-based dispersal may then induce the departure of those individuals most likely to be successful at colonization, i.e., those with the best body condition.

Conclusion

This study demonstrates that the use of information obtained from immigrants depends on the individual's reason for dispersal. When intraspecific competition is the dominant cause of dispersal, information about the level of connectivity with other populations allows potential dispersers to decrease the risk of dispersal by reducing the success uncertainty of their movement. When kin competition dominates, dispersers do not adjust their dispersal decisions as a function of information concerning the existence of connections between populations. Juveniles leaving the population for reasons of kin competition disperse independently of the uncertainty about the movement success. Indeed, we previously suggested that kin competition may be one of the factors driving the colonization of empty patches (Cote et al. 2007). The present results are consistent with this hypothesis: kin-based dispersers leave their population of origin even in the absence of information about the existence of other suitable habitats.

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