The importance of a good neighborhood: dispersal decisions in juvenile common lizards are based on social environment

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Within a population, dispersers are likely to differ in their motivation and adaptations to disperse; yet individual heterogeneity in dispersal decisions is still poorly documented. In the common lizard, females can be classified into 3 types of ventral color (yellow, orange, and mixed) that signal alternative strategies in reproduction and behavior. The reproductive success of these alternative strategies depends on the frequency of each color type in their local environment. Therefore, we predicted that adaptive emigration and settlement decisions should differ between color types and respond to the social composition of the environment. To test this prediction, we analyzed juvenile local dispersal decisions in response to an experimental manipulation of the local color type frequencies. Offspring from orange or mixed females showed decreased dispersal rate in populations where the frequency of yellow females was increased, and those who dispersed chose to settle in environments with lower female density but higher frequency of yellow females. Our results demonstrate that the composition of the social environment is used as a direct cue for dispersal decisions that provides information on resource competition and environment quality. The frequency of female color types is thus a key parameter of the social environment that influences habitat choice decisions. However, the pattern of spatial autocorrelation of adult females was not consistent with these color-related dispersal patterns, which suggest that other processes also participate in shaping the distribution of individuals at the population scale.

Key words: color polymorphism, frequency dependence, ideal free distribution, natal dispersal, public information, spatial niche partitioning. [Behav Ecol]
a larger scale, the spatial structure of the populations is also expected to reflect this heterogeneity in habitat choice decisions, with a phenomenon of spatial niche partitioning between strategies (e.g., Sinervo and Clobert 2003; Formica et al. 2004; Formica and Tuttle 2009).

The common lizard *Lacerta vivipara* is a model system that allows us to test such theoretical expectations about the relationship between alternative strategies and dispersal patterns. Previous studies have demonstrated that local dispersal in this species is sensitive to both kin competition and general competition (Léna et al. 1998; Ronce et al. 1998; Le Galliard et al. 2003; Meylan et al. 2007; Cote and Clobert 2010), through a multiplicity of cues (maternal effects: Massot and Clobert 1995, 2000; Massot et al. 2002; Meylan et al. 2004; Vercken, de Fraipont, et al. 2007; relatedness: Léna et al. 1998; de Fraipont et al. 2000; Léna et al. 2000; Le Galliard et al. 2003; density: Léna et al. 1998; Le Galliard et al. 2003; Lecomte et al. 2004; Cote and Clobert 2007b; public information: Aragón, Massot, et al. 2006; Aragón, Meylan, and Clobert 2006; Cote and Clobert 2007a; Cote, Boudsocq, and Clobert 2008). In addition, a recent work documented that individuals dispersing in response to different selective pressures were characterized by different phenotypes (Cote and Clobert 2010). Dispersal is thus a highly plastic adaptive trait in this species that impacts significantly the distribution of individuals at the local population scale.

In addition, female common lizards display variation in ventral color, which can be classified into 3 color types: yellow, orange, and mixed (Vercken, Massot, et al. 2007; Vercken et al. 2008). This color polymorphism was proposed to signal alternative strategies in reproduction (Vercken, Massot, et al. 2007) and behavior (Vercken and Clobert 2009), and female reproductive success was found to depend on the interaction between female color and her social environment (Vercken et al. 2010). More precisely, the frequency of yellow, dominant females affected negatively the reproductive success of all females, with an increased effect on mixed females (Vercken et al. 2010). Therefore, the dispersal patterns of individuals of different colors at the intrapopulation scale are expected to depend on the composition of their social environment, that is, the frequency of color types in a local neighborhood. However, because natal dispersal in common lizards takes place within the first days of life, before individuals express their ventral color, we assumed that the dispersal patterns of juveniles could be predicted by the ventral color of their mother.

But, we predicted that the decision to leave the natal territory should depend on the interaction between maternal phenotype and the relative frequency of color types in the natal environment (i.e., fitness prospects in the natal territory). As female reproductive success was found to be negatively impaired by the frequency of yellow females in the population (Vercken et al. 2010), we predicted that juveniles should disperse more when their mother had a high frequency of yellow neighbors. This effect was expected to be especially strong for offspring from mixed females, who suffered the highest fitness costs from an increased frequency of yellow females (Vercken et al. 2010). Second, we predicted that the determinants of the settlement decision should also depend on maternal phenotype because dispersers of different colors would have left their natal territory for different reasons. Finally, we predicted that the spatial distribution of adult females should be influenced by these habitat choice decisions and reflect some degree of spatial niche partitioning between color types.

In order to test these predictions, we studied juvenile local dispersal patterns in 4 natural populations. To test whether dispersal responded to the composition of the social environment, we experimentally manipulated color type frequency at the local scale in all populations, and we analyzed the effect of the interaction between maternal color and the color of the social environment on dispersal probability. Then, to identify which elements of the social landscape affected settlement decisions in the different color types, we tested how the post-dispersal environment of dispersing juveniles differed from their natal environment. Finally, to test whether dispersal decisions based on the social environment resulted in significant spatial patterns within populations, we analyzed the distribution of females within these populations before the experimental manipulation to reveal potential color-related spatial structure.

**MATERIALS AND METHODS**

**The species**

*Lacerta vivipara* is a small (adult snout–vent length from 50 to 70 mm) live-bearing lacertid lizard, found throughout Europe and Asia. All the study populations are located on Mont Lozère (Southern France, altitude 1420 m). These populations are peatbog or heathland areas surrounded by forest, prairie, or pasture. The distribution of individuals within the populations is relatively homogeneous, with hotspots of density around specific landscape structures like rocks or tree stumps that provide efficient basking spots. As the surrounding habitat is relatively unsuitable for common lizards, the populations are unlikely to experience high levels of emigration or immigration, and we consider them as isolated.

In these populations, adult males emerge from hibernation in mid-April, followed by yearlings, and adult females in mid-May. Mating occurs at female emergence, and gestation lasts for 2 months. Parturition starts in mid-July and lasts for 2 or 3 weeks. Females lay an average clutch of 5 soft-shelled eggs (range 1–12). Offspring hatch within 1 or 2 h after laying and are immediately independent of their mother. The activity season ends in late September, and juveniles are the last to enter hibernation.

In these populations, female ventral color is variable between individuals and ranges from pale yellow to bright orange, whereas males are almost always orange. Juveniles start by being melanic and slowly turn to a pale green ventral coloration when yearlings. Stability of ventral color arises with sexual maturity (usually at 2 years in the Mont Lozère populations). We chose to analyze female color as a discrete variable (yellow, orange, or mixed) because

(i) unlike spectrum components like chroma and hue that vary along the same scale and seem to be open to short-term environmental influences (Cote, Le Galliard, et al. 2008; Vercken et al. 2010), visual classification of females into 3 discrete color classes is stable throughout adult life and inheritable within female lineages (Vercken, Massot, et al. 2007), which makes it more likely to correlate with structural differences between individual’s phenotype or genotype (Vercken et al. 2008) and

(ii) these color classes were found to correlate with differences in life-history (Vercken, Massot, et al. 2007) and behavioral traits (Vercken and Clobert 2008, 2009) and were proposed to reflect alternative strategies, characteristic of a hawk–dove–bully game (Vercken et al. 2010). Ventral color is not actively displayed by individuals, yet it has been shown to affect social interactions between unfamiliar females in an experimental context (Vercken and Clobert 2009). Such differences between color classes are nonlinear (i.e., mixed individuals do not have intermediate profiles between yellow and orange individuals) and thus are better described by a nonordinal variable.

Juvenile dispersal takes place within the first 10 days of life (Léna et al. 1998), before individuals express their definitive ventral color and is definitive (i.e., juveniles will remain as
adults on their natal or their dispersing site). However, ventral color is partly heritable within female lineages (Vercken, Massot, et al. 2007), thus maternal color could be used as a proxy for the future coloration of female juveniles. Moreover, juvenile dispersal is open to many maternal effects (e.g., Ronce et al. 1998; de Fraipont et al. 2000; Massot and Clobert 2000; Vercken, de Fraipont, et al. 2007), and we could expect females to influence the dispersal pattern of their offspring depending on their own strategies.

**Dispersal data**

The 4 populations we studied experimentally are distributed along a linear axis (road), 2 nearby populations being separated by 1.2 km on average (minimum: 800 m, maximum: 2 km).

From 2004 to 2006, 773 females were temporarily removed from the 4 populations (251 females in 2004, 282 in 2005, and 240 in 2006). Forty-eight females were captured at least 2 years and 1 female was captured in each of 3 years. Each year, from the end of June, females were captured and kept in the laboratory until parturition. Females were housed in plastic terraria with damp soil, a shelter and received sprayed water 3 times a day. Females were exposed to natural daylight and were heated 6 h/day with an electric bulb. All animals were treated in accordance with “The National Institutes of Health Guide for Care and Use of Laboratory Animals.”

We obtained 3029 living juveniles over the 3 years of study. At birth, offspring were marked individually by toe clipping and sexed by counting ventral scales (Lecomte et al. 1992). Toe clipping is known to have no influence on probability of recapture (Massot et al. 1992) and maximal sprint speed in the common lizard (Sorci G, personal communication). Offspring and their mother were then released either in their population of origin or transplanted into another population (see Frequency experiment). Recapture sessions in fall and spring allowed us to map the location of juveniles after dispersal. We recaptured 629 juveniles. Juvenile survival is about 40% during the first 2 months of life (Vercken E, unpublished results), and we achieved about 50% recapture rate on juveniles. Dispersers were defined as individuals for whom the distance moved between the release point and the last recapture point was greater than 30 m (upper 95% confidence limit of the home range diameter). Philopatric individuals were defined as individuals that had moved less than 20 m (average home range diameter) (Clobert et al. 1994; Massot and Clobert 2000). Indeed, the distributions of dispersal distances for the 4 study populations, all show a strong mode around 10–15 m, and a second, smaller mode around 30–40 m (Supplementary File 1). In addition, individuals moving more than 30 m were never found to return to their natal territory. Juveniles that had moved between 20 and 30 m were not assigned any dispersal status and were excluded from the analysis. We obtained effective dispersal status for 503 juveniles (80% of recaptured individuals).

**Frequency experiment**

There is little evidence of genetic differences between the 4 populations described above based on the analysis of 6 microsatellite markers (Richard M, unpublished data). As the maximum dispersal distance for a lizard is around 100 m, the study populations cannot be connected through direct migration. Female density and relative frequency of color types have been estimated by mark-recapture analyses. Several recapture sessions occurred in 2004, which allowed us to estimate female density with the Lincoln–Petersen index for closed populations. Density estimates in 2005 and 2006 were based on recaptures between years and were calculated from the Cormack–Jolly–Seber model (“mra” package in R, R Development Core Team 2008; McDonald 2012). At the beginning of the study, the 4 study populations differed in female density and in female color type frequencies (Table 1). We distinguished 2 populations with high frequency of orange females (“high-orange” populations, A and B) from 2 populations with high frequency of yellow females (“high-yellow” populations, C and D).

In 2004 and 2005, yellow females captured in high-yellow populations were released with their offspring in high-orange populations, whereas orange females captured in high-orange populations were released with their offspring in high-yellow populations (for sample sizes, see Table 1). Thus, initially high-yellow populations had the frequency of orange females increased (O+ treatment) and initially high-orange populations had the frequency of yellow females increased (Y+ treatment). Frequency of mixed females and total population densities were not modified. In their new population, immigrant females were released at the capture point of a native female that had been transplanted in order not to modify female density at the local scale. There was no effect of transplantation on female survival or body condition, and transplanted females were found to remain on their release site, which confirms the successful settlement of transplanted females (Vercken et al. 2010).

Because the reciprocal transplants were performed in 2004 and 2005, females experienced an “undisturbed” environment in 2004, a “moderately disturbed” environment in 2005, and a “strongly disturbed” environment in 2006 (for the annual estimations of color type frequency, see Table 1). The dispersal rates observed in 2004 were used as references as they were obtained in undisturbed populations, before any experimental manipulation. We analyzed the difference between the dispersal patterns in 2004 and the following years to estimate the effect of the experimental manipulation (see Statistical analyses), independently of annual effects related to the natural variations of the environment that are expected to be the same for all populations regardless of their experimental treatments. This experimental design has been used in this species with success at several occasions (Lorenzon et al. 2001; Massot et al. 2002; Meylan et al. 2007), and the limited number of experimental replicates is compensated by the large sample sizes within each replicate, maximizing the probability that a significant treatment effect will not result from a population effect. In this type of design, the power for detecting a significant effect is relatively weak because we have a strong power to detect interpopulation differences to the detriment of intertreatment effects. Hence, any significant treatment effect should reflect important experimental differences.

**Statistical analyses**

**Response of dispersal rate to the experimental manipulation**

Statistical tests were conducted using R (R Development Core Team 2009). Dispersal status was considered as a binomial variable (0: philopatric offspring; 1: disperser). Dispersal was analyzed using generalized linear models and generalized linear mixed-effects models with maximum likelihood estimation (package “lme4”; Bates et al. 2011). We tested 2 different random structures to account for differences between populations: 1) random intercept or 2) random intercept and slope of the relationship with year. Fixed effects included juvenile sex and snout-vent length (SVL), ventral color of the mother, year, and frequency treatment in the population of origin and the interactions of year by treatment and year by ventral color. Interactions between ventral color and treatment were not analyzed because of unbalanced design (few yellow females in O+ populations and few orange females in Y+ populations). A significant year effect alone
Spatial distribution of females

Female population size was estimated from the Lincoln–Petersen Index in 2004 and from the Cormack–Jolly–Seber model using "mra" package in R in 2005 and 2006. SE, standard error.

Table 1
Description of the experimental manipulation and its consequences on the social environment

<table>
<thead>
<tr>
<th>Population</th>
<th>A</th>
<th>B</th>
<th>C</th>
<th>D</th>
</tr>
</thead>
<tbody>
<tr>
<td>Adult female population size (SE) in 2004/2005/2006</td>
<td>160(18) / 175(51) / 135(38)</td>
<td>140(9) / 180(61) / 105(40)</td>
<td>175(29) / 165(72) / 140(51)</td>
<td>100(12) / 155(50) / 120(31)</td>
</tr>
<tr>
<td>Orange/yellow female frequency in 2004</td>
<td>0.42/0.36</td>
<td>0.4/0.25</td>
<td>0.2/0.37</td>
<td>0.21/0.42</td>
</tr>
<tr>
<td>Number of transplanted females in 2004</td>
<td>25 orange females and 125 juveniles to population D</td>
<td>26 orange females and 93 juveniles to population C</td>
<td>26 yellow females and 90 juveniles to population B</td>
<td>25 yellow females and 105 juveniles to population A</td>
</tr>
<tr>
<td>Orange/yellow female frequency in 2005</td>
<td>0.54/0.44</td>
<td>0.31/0.34</td>
<td>0.35/0.3</td>
<td>0.27/0.3</td>
</tr>
<tr>
<td>Number of transplanted females in 2005</td>
<td>19 orange females and 78 juveniles to population D</td>
<td>23 orange females and 105 juveniles to population C</td>
<td>23 yellow females and 85 juveniles to population B</td>
<td>19 yellow females and 120 juveniles to population A</td>
</tr>
<tr>
<td>Orange/yellow female frequency in 2006</td>
<td>0.28/0.5</td>
<td>0.25/0.4</td>
<td>0.44/0.19</td>
<td>0.31/0.26</td>
</tr>
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Following Zuur et al. (2009), we selected random structure AIC random labeling, which assumes that the 2 classes of individuals have a random structure within the given spatial range around the mother’s release point (predispersal environment) or the juvenile recapture point (postdispersal environment). We analyzed the composition of the population had been modified by manipulating the composition of the social environment (parents, siblings, or mixed mothers) using a bivariate signed-rank test.

Because the composition of the population had been modified by the experimental treatment at the population level had no effect on the sex ratio of offspring, but all trends were conserved between analyses. The same model comparisons were based on lowest Akaike’s Information Criterion (AIC). The selected model included no main effect of year or treatment, but all models were removed if the difference in AIC was greater than 3.

Many models were removed if the difference in AIC was greater than 3. The best model included the year: treatment interaction, followed by the year: sex interaction and the sex: treatment interaction. All models included the year and the treatment as fixed effects. We used classical generalized linear models, likelihood ratio tests, and type III sum of squares to interpret fixed effects.
Description of the experimental manipulation and its consequences on the social environment

Table 2
Selection of random structure for models of juvenile dispersal response

<table>
<thead>
<tr>
<th>Random structure</th>
<th>Treatment: prenatal environment</th>
<th>Treatment: postnatal environment</th>
</tr>
</thead>
<tbody>
<tr>
<td>Random intercept and slope (year)</td>
<td>AIC 647.3</td>
<td>AIC 649.9</td>
</tr>
<tr>
<td>Random intercept</td>
<td>643.4</td>
<td>646.0</td>
</tr>
<tr>
<td>No random structure</td>
<td>641.1</td>
<td>643.4</td>
</tr>
</tbody>
</table>

Fixed effects: year + color + treatment (prenatal or postnatal environment) + sex + length + year:treatment + year:color.

RESULTS
Response of dispersal rate to the experimental manipulation
Juvenile dispersal was affected by the interactions between year and 1) frequency treatment ($\chi^2_1 = 5.41, P = 0.020$) and 2) maternal color ($\chi^2_2 = 11.72, P = 0.003$). Juveniles from orange or mixed mothers tended to disperse less in Y+ populations in comparison with O+ populations, whereas the opposite pattern was found for juveniles from yellow mothers (Figure 1). Although the same trend was present in 2005, this difference became significant in 2006 only, when the manipulation of color type frequencies was maximal.

Comparison of predispersal and postdispersal environments
The experimental treatment at the population level had no effect on individual settlement decisions: the same results were obtained when analyzing Y+ and O+ populations separately or together, thus we pooled individuals from different populations in the final analysis to increase statistical power.

First, dispersing offspring from females of all color types settled in local environments where there were fewer females than in their prenatal environment (offspring from yellow females: $V = 137.5, P = 0.002, n = 19$; offspring from orange females: $V = 70, P = 0.008, n = 13$; offspring from mixed females: $V = 96, P = 0.003, n = 16$; Figure 2, top). In a heterogeneous environment, such a pattern could result from random distribution of individuals; if individuals tend to leave from most crowded areas, they are likely to settle in less crowded areas just by chance. To rule out this hypothesis, we simulated the random distribution of 10 000 individuals within the populations while eliminating the locally empty areas considered as unsuitable habitat. The 95% CI of the number of female neighbors in these simulations was significantly higher than the number of female neighbors we observed for dispersing individuals, thus indicating active habitat selection by dispersers.

Second, Figure 2, middle, shows that offspring from orange and mixed females tended to settle in environments with higher frequency of yellow females (offspring from orange females: $V = 16, P = 0.039, n = 13$; offspring from mixed females: $V = 12.5, P = 0.007, n = 16$), whereas it was not the case for offspring from yellow females ($V = 55, P = 0.138, n = 19$). Offspring from orange females also tended to settle in environments with lower frequency of orange females ($V = 64, P = 0.027, n = 13$), whereas it was not the case for offspring from yellow ($V = 77, P = 0.500, n = 16$) or mixed females ($V = 44, P = 0.714, n = 19$; Figure 2, bottom).

Spatial distribution of females
Yellow and mixed females showed no pattern of spatial autocorrelation, either positive or negative (Figure 3, top, middle). For orange females, the difference $L_{12} - L_{21}$ was significantly positive for distances between 2 and 4 m (Figure 3, bottom), which indicates positive autocorrelation within this distance, that is, orange females are spatially associated at small spatial scale.

DISCUSSION
By manipulating the composition of the social environment, we demonstrated that its interaction with individual phenotype...
Habitat choice: a trade-off between environment quality and competition intensity?

Female ventral color is thought to indicate dominance status (Vercken and Clobert 2008, 2009), and yellow females were proposed to be the strongest competitors (hawk strategy, Vercken et al. 2010). If weaker competitors like orange and mixed females suffer high costs from competition with yellow females, we would expect offspring from orange or mixed females to avoid environments where yellow females are frequent. However, we observe the opposite pattern, with dispersing offspring from orange and mixed females selecting environments with high frequency of yellow females and low density. A potential explanation for this result is based on the ideal free distribution theory: when individuals differ in their competitive ability in a heterogeneous environment, it is predicted that the best competitors will be more frequent in high-quality habitats (Parker and Sutherland 1986; Sutherland 1996; Doncaster et al. 1997). According to this theory, dominant yellow females are expected to occupy the highest quality territories: in this case, if dispersing offspring from orange or mixed females select high-quality habitats they should settle in environments with high frequency of yellow females. By also choosing low-density habitats, offspring from orange or mixed females might be able to compensate for the increased competitive pressure due to the high frequency of yellow females. Such heterogeneous distribution of unequal competitors according to environment quality was found in several systems with 2 competing species (Pimm et al. 1985; Berec et al. 2006; Franke et al. 2006). At the intraspecific level, several examples exist where continuous variation in a phenotypic trait determines the competitive ability of individuals (e.g., size-dependent habitat choice, Primicerio 2003; Hammond et al. 2007), yet this is one of the first examples that we know of involving a discrete polymorphism of strategies.

**Figure 2**
Average number of neighbors (top) and frequency of yellow (middle) and orange females (bottom) in predispersal (dark bars) and post-dispersal environments (light bars) for offspring from each color type in 2006. Error bars are 95% CIs.

**Figure 3**
Evolution of the difference \( L_{11} - L_{12} \) and its 95% CI for increasing spatial scales for yellow, mixed, and orange females (combined analysis of the 4 populations). A positive difference indicates spatial aggregation.
Public information and dispersal decisions

In addition, it seems that the presence of yellow females is used directly as an indicator of environment quality for juveniles from orange or mixed females (public information, Bell 1991; Danchin et al. 2004). If the presence of yellow females is used as cue for habitat quality, then we expect dispersal rate to decrease in populations where the frequency of yellow females was increased. This is exactly what we observe, which suggests that offspring born in populations where the frequency of yellow females was increased experienced a positive signal of environment quality that affected their dispersal decisions. Public information is recognized as a common way to assess habitat quality at low costs for the individual, yet in most cases, habitat quality is estimated from the reproductive success of neighboring conspecifics (Danchin et al. 1998; Parejo et al. 2007; Boulinier et al. 2008; Galaburda et al. 2008), alone or in combination with environmental predictors (Part et al. 2011; Robinson et al. 2011). In contrast, this study is the first to suggest that heterogeneity in individual phenotypes can be used as an indicator of environment quality, independently of other cues directly related to reproductive success.

The use of public information related to habitat quality for dispersal decisions in our system is further supported by the fact that, although offspring from yellow females are expected to select the highest quality habitats, they were the only ones not to settle in environments with higher frequency of yellow females than their natal environment. On the contrary, if yellow female frequency is to be a reliable indicator of environment quality for orange and mixed females, then yellow females must select actively their habitat using more direct cues, and the dispersal or settlement decisions of offspring from yellow females should not be based on yellow female frequency. In this scenario, offspring from yellow females would be more likely to colonize new, less crowded territories, where they would avoid competition with other dominant individuals (“colonizer strategy”; Cote and Clobert 2007a). On the other hand, offspring from orange or mixed females would follow secondarily the distribution of yellow females (“joiner strategy”; Clobert et al. 2009), thus avoiding the costs of direct exploration of the environment and assessment of its quality. Such alternative colonization behaviors have been suggested in other vertebrate species (Ebenhard 1990), sometimes in association with other behavioral traits (e.g., aggression, Duckworth and Badyaev 2007; boldness, Kuvurs et al. 2010). However, this study provides the first evidence for such colonization behaviors coexisting within populations in association with larger alternative strategies, with potential consequences on population spatial dynamics.

Spatial structure of natural populations

Dispersal distances in common lizards are typically between 30 and 100 m, whereas the areas of the populations we studied range between 5500 and 8000 m² (95–115 m long, 50–70 m wide). Individual dispersal behavior is thus on the same scale as maximal intrapopulation distances and has the potential to affect directly distribution patterns at the population level (Lima and Zollner 1996). However, although we found that dispersal and settlement decisions responded to the composition of the social environment, color-related dispersal patterns are not a direct predictor of the spatial distribution of color morphs in the field. We found that juveniles from orange females tended to settle in environments with a lower frequency of their own color type than their natal environment, which should result in negative spatial autocorrelation for this color morph. Contrary to this expectation, we found a positive spatial autocorrelation of orange females.

A first hypothesis to explain this discrepancy between habitat choice decisions and effective spatial distribution of individuals is that spatial structure is more strongly impacted by philopatry than by dispersal (Solmsen et al. 2011). Indeed, ventral color in the common lizard was found to be maternally heritable (Vercken, Massot, et al. 2007) so that related females are relatively likely to have the same ventral color. In this study, basal juvenile dispersal rate was found to depend on maternal color (color effect on dispersal in 2004 $\chi^2 = 11.91, P = 0.003$). In the first year of the study, before the manipulation of color type frequencies, offspring from yellow females were the most philopatric (average dispersal rate around 20–30%), whereas offspring from mixed or orange females were more likely to disperse (average dispersal rate around 50–60%; Figure 1). Therefore, if spatial autocorrelation resulted mostly from high philopatry, we would rather expect this pattern to occur in yellow females, which was not the case. Alternatively, different dispersal distances between color types (with lower distance for offspring from orange females) could also result in different autocorrelation patterns (Gaufrère et al. 2009).

However, juvenile dispersal distances are independent of maternal color in all study populations ($\chi^2 = 4.54, P = 0.103$), which rules out this potential explanation.

These results imply that dispersal behavior cannot be the only process shaping the distribution of individuals at the population scale. Even if offspring from orange females are not more philopatric than others, orange females could be more closely associated spatially if they produce more offspring on average and/or if their offspring sex ratio is biased toward females. In this study, we found a marginal effect of female color on fecundity ($\chi^2 = 6.47, P = 0.039$) and no effect on clutch sex ratio ($\chi^2 = 1.24, P = 0.538$). Yellow females produced less offspring (3.8 on average) than mixed or orange females (4.2 for both color types). Relatively high offspring philopatry associated with high fecundity in orange females is thus the most likely explanation at present for positive spatial autocorrelation at short distances in this color type. Such a phenomenon would result in fine-scale relatedness structure, which could also be related to the existence of different degrees of kin interactions between color types (Radespiel et al. 2003; Duncan et al. 2010; Davis 2012). Indeed, nonrandom genetic structure between females was reported in other populations of common lizard (Hofmann 2008), but color-related differences were not investigated. Studies to come should focus on elucidating fine-scale genetic spatial structure for the different color types, as a potential component of their alternative strategies.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at http://www.beheco.oxfordjournals.org/.

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