

# Density, social information, and space use in the common lizard (*Lacerta vivipara*)

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Socially acquired information is widespread in the animal kingdom. Many individuals make behavioral decisions based on such social information. In particular, individuals may decide to leave or select their habitat based on social information. Few studies have investigated the role of density-related information, a potential social cue about habitat quality in dispersal. Here, we tested for the possibility that the phenotype of intruder common lizards (*Lacerta vivipara*) may inadvertently carry information about their natal population density. We found that such information use is likely. The behavior of focal lizard was influenced by the natal population density of the intruder it was interacting with. This suggests that individuals may use the behavior of others to acquire appropriate information about surroundings and to base spatial decisions on this information. Density-related information may then affect individual movement decisions and thus metapopulation dynamics. *Key words:* common lizard, dispersal, population density, social information, social interaction. [*Behav Ecol*]

Animals can assess environmental quality through socially acquired information, such as the presence, activities, or performance of conspecifics (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 various cues. Among cues of habitat quality, the density of conspecifics should be a key factor affecting future fitness and thus is expected to influence habitat selection (Stamps 2001). High population density is often associated with high levels of aggression and low availability of food and mates (Krebs 1971; Reigh et al. 1982; Stenseth and Lomnicki 1990; Lecomte et al. 1994). Thereby, high population density may indicate low habitat quality. Conversely, high population density is also, at least in part, an indicator of high habitat quality (Meylan et al. 2007). Many studies have highlighted the key role of density-related information in habitat selection and dispersal decisions (Crespi and Taylor 1990; Stamps and Krishnan 1997; Lambin et al. 2001; Clobert et al. 2004; Doligez et al. 2004; Cote and Clobert 2007a). Potential dispersers are therefore expected to acquire information on densities in their actual population and, whenever possible, in surrounding populations. Although information on the density of one's residence population is usually accessible, gathering information on the densities of surrounding populations requires time and energy. Individuals can obtain such information by visiting new populations (e.g., prospecting), but few species have the biological attributes that permit such visits at low costs (Doligez et al. 2004). Alternatively, resident individuals may obtain such information by using numbers or characteristics of immigrants as a source of density-related information on neighboring populations (Greene 1987; Cote and Clobert 2007a).

Indeed, individuals are imprinted by their population of origin (e.g., food and crowding; Reigh et al. 1982; Stenseth and Lomnicki 1990; Meylan et al. 2007), and density-dependent trait expression exhibited by immigrants might serve as an indirect and/or complementary source of information. Potential emigrants would then be able to base their dispersal decisions on comparisons between information on the habitat characteristics of their current and neighboring populations without visiting them. Only a few studies have investigated the role of density-related information at the population scale (e.g., Doligez et al. 2004; Cote and Clobert 2007a). Direct measurement of density-related information use will help us understanding how individuals are making decisions about moving across populations.

In this study, we looked for the existence of density related phenotypic effects on behavior and morphology and discuss the role of these effects as a vehicle of information across populations. We used the common lizard (*Lacerta vivipara*) as our model system. The sensory capacity of the common lizard has been well studied: this species is able to use olfactory cues to detect relatives (Léna and de Fraipont 1998), to estimate conspecific density (Aragon, Massot, et al. 2006), and to recall previous interactions with conspecifics (Aragon, Massot, et al. 2006). Thus, the common lizard frequently makes use of social information when making behavioral decisions. Population density affects reproductive success, survival probability, body growth rate, and behavior in this species (Massot et al. 1992; Lecomte et al. 1994; Meylan and Clobert 2004; Le Galliard et al. 2006) and is also a good indicator of habitat quality. In this study, we observed the behavioral modification at an individual scale to obtain direct measurements of density related information use. We manipulated the density of lizard populations and then used lizards from these populations as sources of information to other conspecifics. We thus tested 2 different questions: 1) do individuals from populations of different densities have different phenotypic and behavioral profiles that could provide information? 2) do lizards change their activity and their

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space use based on interactions with individuals from populations of different densities? We also discuss whether the behavioral differences among individuals from populations of different densities may be the cue providing information on population densities.

## METHODS

### Species and experimental system

The common lizard (*L. vivipara* Jacquin 1787) is a small lacertidae (adult snout-vent length: males 40–60 mm and females 45–75 mm) inhabiting humid habitats across Eurasia (Avery 1962). Lizards become active between late March and the beginning of April (Massot et al. 1992), and hibernation starts in late September. Females produce offspring once a year, and laying occurs in June–July. Juveniles are independent from their mother immediately after birth, and natal dispersal starts within 10 days of age (Massot et al. 2002). Most dispersal occurs during the juvenile and yearling stages (Clobert et al. 1994; Le Galliard et al. 2003).

The experiment was conducted in 2004–2005 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 habitat and producing sufficient food and shelter for the maintenance of self-sustaining populations (Lecomte et al. 2004). The enclosures were of similar size to an adult individual core home range under natural conditions (Massot et al. 1994). Considerable overlaps between home ranges are observed in this species, with up to 30 adults found in an area of similar size under natural conditions (Massot et al. 1992; Boudjemadi et al. 1999).

### Density manipulation

In May 2004, all lizards (yearlings and adult males and females) were collected from the enclosures on 2 consecutive days. Seven days after the last individual was collected, males and yearlings were released to create 8 high-density populations and 8 low-density ones. The high-density enclosures contained twice as many animals as the low-density enclosures. Pregnant females were kept in the laboratory until parturition. Two days after birth, the juveniles and their mothers were released into the same enclosures according to the density treatments assigned to each enclosure. Lizards were individually marked by toe clipping, and both snout-vent length and body mass were measured before release. Males, yearlings, and families (mother and juveniles) were randomly assigned to enclosures. Body size of females, males, yearlings, and offspring did not differ significantly between density treatments (all  $P > 0.5$ ).

After release, high-density populations contained 8 adult males, 12 adult females, 20 yearlings (10 males and 10 females), and  $34 \pm 3.7$  standard error (SE) juveniles. Low-density populations contained 4 adult males, 6 adult females, 10 yearlings (5 males and 5 females), and  $17 \pm 2.5$  SE juveniles. The densities, age, and sex structure of these populations matched those of natural populations from which the individuals originated (Massot et al. 1992). Indeed, adult sex ratio in natural populations is biased toward females (Le Galliard et al. 2005), and Massot et al. (1992) found 10–30 adults per 100 m<sup>2</sup> in some low-density populations. Moreover, the starting densities used here were calculated such that the highest density corresponds to the estimated carrying capacity of our experimental habitat (Lecomte and Clobert 1996; Le Galliard et al. 2003).

### Interaction experiments

#### *Activity modification after a confrontation*

In April 2005, 64 subadult lizards (i.e., juveniles born in June 2004) were captured during a 4-day session (i.e., 2 subadult males and females per enclosure). Subadults used in this experiment were the individuals that were originally released as juveniles. We conducted our experiment on subadults because these individuals were living in these populations for 10 months since birth and thus were likely to be more imprinted by environmental conditions (i.e., population density). Snout-vent length (nearest mm) and body mass (nearest mg) of these lizards were measured. To provide each individual with the same standardized environment (e.g., food, water, heat, and social interactions), lizards were individually housed in plastic terrariums (25 × 15.5 × 15 cm) containing 3-cm thick litter (Le Galliard et al. 2003). In one corner of the terrarium, a bulb provided light and heat for thermoregulation from 9:00 AM to 12:00 AM, and from 1:00 PM to 5:00 PM. A piece of cardboard and a plastic tube were provided to allow the lizards to hide. The experimental test was conducted the day after capture to avoid potential effects of capture-induced stress. Behavioral measurements were performed in a plastic terrarium of the same dimensions and structure as the rearing terrarium. We first recorded the behavior of a lizard (referred to as “focal lizards” hereafter) alone in the terrarium. During 10 min, we measured the time spent under the shelter, the time spent moving, and the time spent basking using “The Observer” software. Lizards were then transferred into another terrarium at the same time as a second lizard of the same sex and of similar body mass and size. The second lizard (referred to as “intruder” hereafter) came from a high- or a low-density population, lizards being associated two-by-two in a full-crossed design according to population density. The population of this intruder always differed from the population of the focal lizard. Interactions were conducted in a neutral terrarium to avoid “resident” effects and thus “intruder–resident” effects. During 10 min, we recorded the behavior of the focal lizard and the intruder. Lizards were then removed and isolated. After the same procedure detailed above, we observed the behavior of focal lizards alone to test for behavioral modifications induced by the interaction. The same observer, blind to the experimental treatment, performed all the tests without knowing the origin of the lizards. All lizards were then released in their original populations.

#### *Space use after a confrontation*

Forty subadult lizards (i.e., 20 females and 20 males) were captured 10 days after the first experiment (i.e., 2 or 3 yearlings per enclosure). At capture, snout-vent length and body mass were measured. Lizards were individually maintained as described above and experiments started 1 day after capture. Behavioral measurements were performed in a wooden terrarium (50 × 30 × 20 cm) separated into 2 identical parts by a moveable opaque wall. In each part, a piece of cardboard (shelter) was added to the center of the terrarium allowing the lizards to hide and a bulb provided heat for thermoregulation. The distance between the 2 shelters (35 cm) was such that the 2 heat sources produced 2 basking spots that were separated by a neutral zone preventing any basking behavior.

First, a lizard from a high- or a low-density population was introduced in one part of the terrarium (hereafter “focal lizard”), the other part remaining inaccessible to the lizard. The focal lizard was allowed to explore this part of the terrarium for 10 min to induce residency (Aragon, Clobert, et al. 2006). During this time, we did not record the behavior to avoid the

stress of experimental observation. Then, the focal lizard was confronted with an introduced lizard (hereafter “intruder”) matched for sex and body size and originating from a different population than the focal lizard’s. We constructed 2 treatments by specifically selecting subadult intruders originating from a low- or high-density population. The 2 lizards were allowed to interact for 10 min. Then, we removed the intruder as well as the separation wall, rendering the second part of the terrarium accessible. After 10 min of habituation to the new situation, we recorded the thermoregulation spot chosen by the focal lizard (lizards were always under one of the 2 light spots provided). The experiments were performed within 2 days. On the first day, 20 lizards served as focal lizards and the 20 others as intruders. The day after, we repeated the experiments by reversing the role of each lizard (i.e., intruders became focal lizards and vice versa). The same lizards were never used in the same pair. Neither the day of experiment nor the choice of the thermoregulation spot during the first experimental day influenced the results (all  $P > 0.30$ ).

### Statistical analyses

In the first experiment, we estimated the initial activity of each focal lizard before the confrontation using the time spent in the 3 behaviors (hidden, moving, and basking). The duration of these behaviors before the confrontation was analyzed with a general linear model (GLM) procedure in SAS v. 8.02. We also analyzed the body size and condition of the focal lizards used in the 2 experiments with a GLM procedure in SAS v. 8.02. Body condition was assessed as body mass relative to snout-vent length (i.e., body mass was analyzed with snout-vent length as a covariate). Population density of the focal lizards, sex, body size, and body mass were included as fixed effects along with their interactions.

The behavioral modifications induced by the confrontation with an intruder were analyzed using the differences of time spent (after interaction – before interaction) in each of the recorded behaviors. These differences and the focal lizards’ times spent in the 3 behaviors (hidden, moving, and basking) were analyzed with a MIXED procedure in SAS v. 8.02. The linear mixed models accounted for the presence of both fixed effects and random effects. Trial number was set as a random effect and all other factors were fixed effects. For the second experiment, the choice of the thermoregulation spot was coded as 0 or 1 (1 for lizards that moved from the initial spot to the novel spot). This variable was analyzed using the GENMOD procedure in SAS v. 8.02 with a logit link function and a binomial error term.

Population densities, sex, and body size were included as fixed effects along with their interactions. For the analyses of the focal lizards’ activity during the confrontation, we included in the model the time intruders spent moving during the confrontation. All the results obtained were sex independent ( $P > 0.30$  for simple effects and interactions), and we do not report sex effects in the subsequent analyses. The assumptions of these models were verified by examining residuals. Simplification of all models was made using backward elimination of the nonsignificant interactions. Significance level was set at  $P = 0.05$ .

## RESULTS

### Morphological and behavioral traits

In April 2005, the body size of subadults (i.e., juveniles born in June 2004) from low-density populations was significantly greater than from high-density populations (Table 1; low-density population:  $48.65 \text{ mm} \pm 0.51 \text{ SE}$ , high-density popu-

**Table 1**

**Effects of population density on morphology and time spent in different activities for 1-year-old lizards alone**

Dependent variables	Population density treatment	
	Estimates $\pm$ SEs	Test statistics
Body size	$-2.02 \pm 0.71$	$F_{1,102} = 7.63^{**}$
Body condition	$-0.12 \pm 0.06$	$F_{1,101} = 4.12^*$
Time spent moving	$40.17 \pm 11.00$	$F_{1,62} = 13.32^{***}$
Time spent basking	$16.63 \pm 62.79$	$F_{1,62} = 0.07$
Time spent hidden	$5.48 \pm 40.7$	$F_{1,62} = 0.02$

Estimates are given for high-density populations.

\*  $P < 0.05$ , \*\*  $P < 0.01$ , \*\*\*  $P < 0.001$ .

lation:  $46.91 \text{ mm} \pm 0.51 \text{ SE}$ ). Lizards used in the second experiment were longer than those used in the first experiment (experiment:  $F_{1,15} = 6.61$ ,  $P = 0.021$ ); however, the effect of population density on body size was not different between experiments (experiment  $\times$  density:  $F_{1,14} = 2.71$ ,  $P = 0.122$ ). Body condition was negatively affected by density treatments (Table 1; low-density population:  $2.07 \pm 0.07 \text{ SE}$ , high-density population:  $1.95 \pm 0.04 \text{ SE}$ ) but did not vary between experiments (experiment:  $F_{1,15} = 3.91$ ,  $P = 0.07$ ; experiment  $\times$  density:  $F_{1,14} = 0.62$ ,  $P = 0.44$ ).

In the first experiment, we were able to look for relationships between morphological and behavioral traits. Body size and body condition had no effect on the time spent in each behavior for focal lizards (i.e.,  $P > 0.29$  for all). However, population density significantly affected the time that focal lizards spent moving (Table 1). Lizards from high-density populations moved more than lizards from low-density populations (high-density population:  $59.31 \pm 7.96 \text{ s SE}$ , low-density population:  $25.58 \pm 8 \text{ s SE}$ ). Finally, the times that focal lizards spent hidden and spent basking did not depend on population density (Table 1).

### Activity during a confrontation

During a confrontation, the activity of a lizard may depend on the activity of the intruder. Because previous results showed that population densities only affected the time spent moving (see above), we included the time the intruder spent moving into the analyses. The time the focal lizard spent hidden did not depend on the time the intruder spent moving (Table 2). However, the time that the focal lizard spent moving was affected by the time the intruder spent moving in interaction with intruders’ population densities (Table 2). The time the focal lizard spent moving increased with the intruders’ time spent moving for intruders from high-density populations ( $F_{1,7} = 6.49$ ,  $P = 0.038$ ; Figure 1). This relationship did not exist when intruders were from low-density populations ( $F_{1,7} = 0.64$ ,  $P = 0.45$ ; Figure 1). Finally, the time the focal lizard spent basking was negatively influenced by the time the intruder spent moving (Table 2). The time spent in the different activities did not depend on the population densities of both the focal lizard and the intruder alone.

### Activity modification after a confrontation

Focal lizards significantly changed the time spent hidden after a confrontation with respect to intruder’s population density (Table 3). Focal lizards increased the time spent hidden after a confrontation with lizards from high-density populations (Table 3; change =  $82.58 \pm 40.46 \text{ s SE}$ ,  $P = 0.05$ ; Figure 2)

Table 2

Effects of population density and the activity of the intruder on the time the focal lizard spent hidden, moving, and basking during a confrontation

Factors	Time the focal lizard spent hidden		Time the focal lizard spent moving		Time the focal lizard spent basking	
	Estimates $\pm$ SEs	Test statistics	Estimates $\pm$ SEs	Test statistics	Estimates $\pm$ SEs	Test statistics
Time the intruder spent moving	0.43 $\pm$ 0.55	$F_{1,29} = 0.10$	-0.16 $\pm$ 0.17	$F_{1,29} = 0.92$	-1.18 $\pm$ 0.84	$F_{1,29} = 4.44^*$
Population density of the intruder	22.39 $\pm$ 52.7	$F_{1,29} = 0.18$	-16.8 $\pm$ 16.8	$F_{1,29} = 1.00$	46.94 $\pm$ 79.7	$F_{1,29} = 0.35$
Interaction	-0.61 $\pm$ 0.76	$F_{1,29} = 0.64$	0.55 $\pm$ 0.25	$F_{1,29} = 4.94^*$	-0.13 $\pm$ 1.16	$F_{1,29} = 0.01$

Estimates are given for high-density populations.

\*  $P < 0.05$ .

irrespective of their own population density (Table 3). No change was observed when the intruder originated from a low-density population (change =  $-36.78 \pm 40.46$  s SE,  $P = 0.37$ ; Figure 2). The time spent active (i.e., out of the shelter) is divided in time spent basking and in time spent moving. Although the time spent active is modified after a confrontation (see the results above), both the change in time spent basking and the change in time spent moving did not depend on the population densities of either the focal lizard or the intruder ( $P > 0.40$  for all). Body size and body condition did not affect behavioral modifications ( $P > 0.68$  for the 3 behaviors observed), and the main effects described above remain unchanged when we added these covariates.

### Space use after a confrontation

After the intruder was removed, lizards did not choose a basking spot according to their population density of origin (population density of the focal lizard:  $\chi^2_1 = 0.70$ ,  $P = 0.40$ ), but their choice was significantly affected by the population density of the intruder (population density of the intruder:  $\chi^2_1 = 5.18$ ,  $P = 0.006$ ; Figure 3). The interaction among the population densities of the focal lizards and intruders was not significant ( $\chi^2_1 = 0.01$ ,  $P = 0.92$ ). Focal lizards changed basking spots more frequently when facing an intruder from high-

than from low-density populations (high density:  $0.5 \pm 0.11$ ; low density:  $0.3 \pm 0.10$ ). The probability of change was also positively affected by focal lizards' body size ( $\chi^2_1 = 6.60$ ,  $P = 0.01$ ). Body condition did not affect the choice of basking spots ( $P > 0.32$  for simple effects and interactions).

### DISCUSSION

Our results showed that the behavior of a lizard was influenced by the natal population density of the intruder it was interacting with. As individuals from high-density populations were more active than individuals from low-density populations, our results suggested that the activity level of intruder constitutes the cue for intruder's population density.

### Conspecifics as a cue about the quality of surrounding habitats

Conspecifics are sources of information for many behavioral decisions, including mate choice, foraging activities, and habitat selection (reviewed in Valone and Templeton 2002; Danchin et al. 2004). A recent experiment demonstrated that immigrants can serve as source of information about surrounding population densities (Cote and Clobert 2007a). However, the mechanisms by which this information transfer operates were largely unknown. The present results suggest that, when encountering a nonfamiliar individual (from a different enclosure), a lizard reacts differently according to the intruder's population density of origin. After interacting with lizards from high-density populations, individuals spent more time hidden and usually left their original basking spot when the option to leave the place of the interaction exists. This result indicates that differences in phenotypic traits

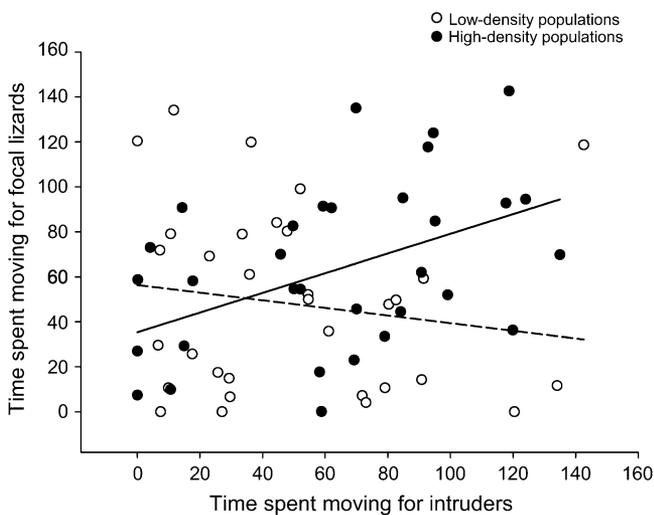


Figure 1

Time the focal lizard spent moving during a confrontation (seconds) as a consequence of the activity and the population density of the encounter. Plotted is the least square regression line (dashed line: low-density populations; solid line: high-density populations).

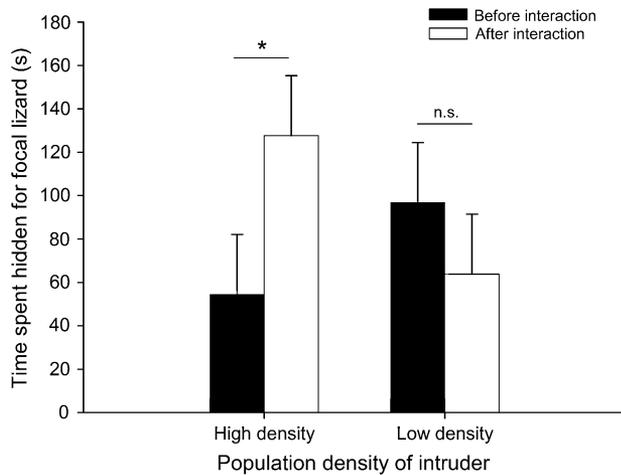
Table 3

Effects of population density on the change in time that focal lizards spent hidden after a confrontation with an intruder

Factors	Change in time the focal lizard spent hidden	
	Estimates $\pm$ SEs	Test statistics
Population density of the focal lizard	-83.5 $\pm$ 56.7	$F_{1,31} = 2.17$
Population density of the intruder	119.4 $\pm$ 57.2	$F_{1,31} = 4.35^*$
Interaction	92.3 $\pm$ 113.7	$F_{1,31} = 0.66$

Estimates are given for high-density populations.

\*  $P < 0.05$ .

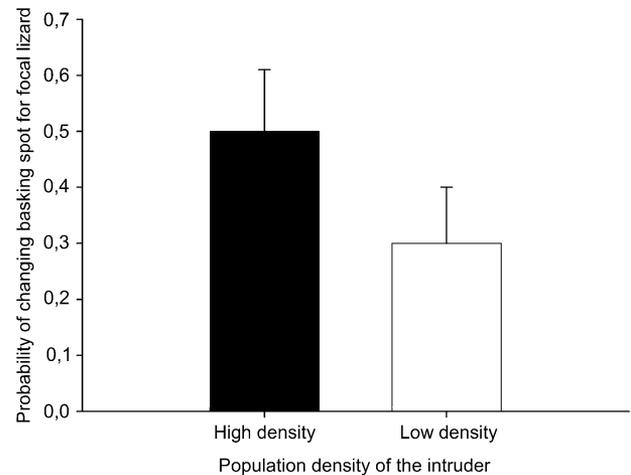


**Figure 2**  
Time the focal lizard spent hidden (seconds  $\pm$  SEs) depending on the population density of the lizard that was interacting with the focal lizard.

(i.e., morphological, physiological, and/or behavioral traits) among individuals from different population densities may provide information about the origin of those individuals. Indeed, immigrants are imprinted by their population of origin (e.g., food and crowding). Therefore, an immigrant carries density-related information that can be used by a focal lizard to make behavioral decisions related to the immigrants' population density. High competition for food and space usually acts as stressors, and individuals living in dense population should have developed particular behavioral, morphological, or physiological traits (Cote and Clobert 2007b; Meylan et al. 2007). Individuals from high-density populations were smaller, leaner, and were more active. Phenotypic traits might then act as cues to other individuals about the level of social and nutritional stress displayed by the individual bearing these traits. Although the exact significance of the behaviors displayed in our experiments are certainly open to alternative interpretations, our results clearly illustrate that the nature of the conspecific encountered, and especially the density of its population of origin, has some important effect on an individual space use even when the stressor has been removed.

Nevertheless, the use of this information requires that individuals can tell neighbors from foreign lizards. We believe that lizards can recognize foreign conspecifics from their neighbors for 2 reasons. First, this species has the necessary capacity for individual recognition through different cues (e.g., olfactory cues; Léna and de Fraipont 1998; Aragon, Massot, et al. 2006). Second, in natural populations, lizards rapidly explore an area of similar size to the enclosure in which we kept them (Lecomte et al. 2004). Thus, in our experimental system, an individual has the possibility to encounter and/or interact with all lizards of its population. However, even if lizards are able to distinguish between strangers and neighbors, candidate dispersers do not necessarily know from which direction immigrants come. In a hostile environment (i.e., fragmented habitat), one major cost of dispersal relates to the uncertainty about the existence of suitable surrounding populations. Information carried by strangers therefore provides benefits even if the direction from which strangers come is unknown.

Our study illustrates that some transfer of density-related information occurs, but it seems necessary to explore the intruders' phenotypic traits that might be used as cues about habitat quality.



**Figure 3**  
The choice of a basking spot as a consequence of density-dependent interaction. The probability of changing basking spots after a confrontation depending on the population density of the lizard that was interacting with the focal lizard.

### Conspecific activity as cues about habitat quality?

Any particular trait of an individual can potentially serve as a cue about the environment as well as about the biological state of that individual. In our study, density treatments affect both body condition and body size. However, body size and body condition were not found to influence the outcome of interactions among individuals. Morphological traits do not therefore appear to be good candidates for such types of information transfer in this species. Density-dependent activity constitutes the best candidate as a source of information. In several species, including the common lizard, high density increases activity levels. Our results confirmed the increased activity levels for lizards from high-density populations. Thus, increased activity might be a cue by which other individuals assess the density of an immigrants' population of origin. During the confrontation, the activity levels of lizards depended on the activity of the intruder. Focal lizards modified the time spent in the different activities more when the individuals they encountered were moving more. Increased locomotor activity is believed to be a current reaction to harsh conditions (i.e., stress response). For example, corticosterone, a stress hormone, induces an increase in many types of activities (e.g., thermoregulation activity; Moore et al. 1984; Dufty and Belthoff 1997; Breuner et al. 1998; Cote et al. 2006). When encountering a conspecific, the activity intensity may thus constitute a source of stress-related information. Focal lizards from high-density populations were more active. We can thus predict that all individuals from high-density populations (focal lizards and intruders) were more active. As intruders from high-density populations were more active and as the activity of intruders modified the behavior of focal lizards during the confrontation, we can hypothesize that density-related activity is a cue of density-related information carried by intruders. However, we cannot exclude other cues, for example, olfactory cues, as a source of information. Indeed, olfactory cues are used as a source of social information in the common lizard (Léna et al. 2000; Aragon, Massot, et al. 2006b), and corticosterone can potentially modify the odor's profile (Labra Lillo A, Cote J, Meylan S, Le Galliard J-F, unpublished data). Further experiments will be necessary to determine the exact vehicle of density-related information.

In conclusion, our study illustrates that density-related activity may be a cue used by common lizard to assess surrounding

environments as it has been found for other phenotypic traits (Aragon, Clobert, et al. 2006). This density-related source of information is likely to influence space use and dispersal (Cote and Clobert 2007a), and it might then have profound consequences on habitat selection theory.

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