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ARTICLES

Socially acquired information from chemical cues in the common lizard, *Lacerta vivipara*

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The use of information from chemical cues about the presence of conspecifics and their social interactions may be advantageous because it allows individuals to assess the social environment in the absence of the signallers. We tested experimentally whether the selection of nocturnal shelters by juveniles of the common lizard was influenced by the scent marks from three isolated or three socially housed adult males or females, keeping constant the number of donors for all treatments. We gave each juvenile a choice between a shelter containing odours from adults and a shelter with no odour and we compared the response to odours from three adults housed singly with that to odours from three adults that had the opportunity to interact. The shelter site selection of juveniles was influenced by the odour of socially housed adult males, but not by that of isolated males, and partly depended on the mother's site of origin and the juvenile's body condition. This study shows that juveniles use social information from conspecific chemical cues and that various phenotypes may use this information in different ways.

Costs associated with intraspecific competition have led to the evolution of competition avoidance mechanisms such as spatial, temporal or dietary segregation (Schoener 1974; Huntingford & Turner 1987) and dispersal (Herzig 1995). However, prior occupation of an area by conspecifics may indicate that the habitat is suitable for immigrants (in terms of availability of resources, reproductive success, predator protection, etc.; Danchin et al. 2001) and there are examples of individuals being attracted to conspecifics even in territorial species (Stamps 1988; Muller et al. 1997; Doligez et al. 2002). Thus, depending on the species, environment and individual characteristics, individuals might avoid or be attracted to occupied areas (Clobert et al. 2004).

Information on the social environment or on patch quality can be acquired by sampling directly, which may be costly in terms of, for example, time, risk of injuries and predation (Danchin et al. 2001). One way to avoid such costs is by acquiring information from the social network (McGregor et al. 2000). There is growing evidence of socially acquired information (any information obtained from observing the behaviour of others; Giraldeau et al. 2002; Valone & Templeton 2002), used in a variety of contexts from foraging behaviour (Galef & Giraldeau 2001) to mate choice (Gibson & Höglund 1992).

Studies on social information have primarily examined the role of visual (Valone & Templeton 2002) and acoustic cues (Grafe 2005; Naguib 2005). However, for many species, acquiring social information visually may be costly, whereas focusing on chemical cues may allow individuals to assess the social environment in the absence of the signallers. For instance, chemical cues provide social information for the assessment of predation risk (Chivers et al. 2001) and competitive ability of signallers (Johnston et al. 1997; Rich & Hurst 1999), and for socially transmitted food preferences (Galef & Giraldeau 2001). However, to our knowledge, there are no examples of using

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chemical cues to acquire information on conspecific interactions in which the receivers themselves did not participate.

To study the use of this type of information, we selected *Lacerta vivipara* as a model. In reptiles, chemical senses are important for intraspecific communication (Halpern 1992; Mason 1992; Cooper 1994), and the presence and relative concentrations of chemical compounds vary between the sexes and between individuals (Alberts 1990; 1993). This variation may serve a variety of functions (Cooper 2004; López & Martín 2004). *Lacerta vivipara* inhabits dense vegetation where relying on chemical cues might save time and energy (Stamps 1977; Alberts & Werner 1993). We chose juveniles as receivers and adults as donors of the chemical signals because: (1) juveniles of this species discriminate the chemical signals of both adult sexes (Léna & de Fraipont 1998); (2) juvenile dispersal takes place shortly after birth (Clobert et al. 1994), so, because of their lack of experience, juveniles should rely more heavily on social information than adults (Danchin et al. 2001); (3) juvenile survival rates are lower when adult density is increased suggesting that juveniles suffer asymmetric competition or interference from adults (Massot et al. 1992); and (4) natal dispersal correlates either positively (Léna et al. 1998; Boudjemadi et al. 1999) or negatively (Léna et al. 1998; Le Galliard et al. 2003) with adult density, depending on the sex of the adults and the population history. The studies cited above suggest that the presence of conspecific adults may modulate dispersal decisions in different ways depending on other factors, in addition to density per se, such as competition or patch quality.

Given this background, a further step would be to test whether juveniles assess intraspecific competition or patch quality through the social environment experienced by adults. To address this question, we carried out experiments where each juvenile was offered the choice between a nocturnal shelter with no odour (reflecting an empty site) and a shelter with different types of conspecific odours (reflecting an occupied site). We aimed to present juveniles with a trade-off between a site that reflected good patch quality but with high competition (patch with odour) and a site that reflected poor patch quality but with no competition (patch with no odour). To examine whether there was a response to social interactions among donors, we compared the responses of juveniles to odours coming from three isolated or three communally held adult males or females. We used nocturnal site selection because variability in retreat site selection in the laboratory is associated with dispersal decisions in the field (Léna et al. 2000).

If dispersal decisions depend at least partly on social information (Clobert et al. 2004), then the response of juveniles should depend on their sex and body condition (residuals of the regression of weight on size) and sex of the adults since these traits modulate natal dispersal in this species (Massot et al. 1994a; Sorci et al. 1996; Léna et al. 1998; Sorci & Clobert 1999; Massot & Clobert 2000). Accordingly, various phenotypes may use social information in different ways (Doligez et al. 1999).

To be valuable, social information should be reliable (conspecifics cannot afford to hide their performance; Danchin et al. 2001). Therefore, if juveniles assess intraspecific competition and/or patch quality through the social environment experienced by adults, then juveniles should discriminate between scents from three grouped and three isolated adults. According to the conspecific attraction hypothesis, individuals should be attracted to patches with odours from adults, whereas the opposite trend is expected from the competition hypothesis. On the other hand, there is growing evidence that individuals may rely not only on the presence of conspecifics (Stamps 1988) but also on their performance (Danchin et al. 2004). Thus, if social interactions reflect both intraspecific competition and a patch of high quality (Kennedy & Gray 1994), a trade-off between a patch with no odour and a patch with odour should occur only when scents come from socially housed donors. We thus predicted that when juveniles are presented with a choice between shelters with no odour and shelters with odour from three interacting donors, they should take different positions along a phenotypic trade-off depending on sex and body condition. In contrast, no trend should be found when the scents come from three isolated donors since both sites (with and without odour) should reflect similar patch quality.

METHODS

Species and Study Sites

Lacerta vivipara is a small, live-bearing lacertid that inhabits peat bogs and heath lands. In our study population, males emerge from hibernation in April, followed by yearlings and adult females in early May. Parturition occurs 2 months later. Females lay on average five soft-shelled eggs. Neonates (average snout–vent length = 21.7 mm; range 18.5–24.5 mm) are autonomous and natal dispersal occurs within the first 10 days of birth (Clobert et al. 1994). The activity season ends in late September and juveniles are the last to enter hibernation. A more complete description of the life history can be found in Avery (1975), Pilorge (1987) and Clobert et al. (1994).

We captured gravid females in two study sites (500 m apart) at Mont Lozère in the Cevennes National Park (44°30′N, 3°45′E), Massif Central, France, at an elevation of 1420 m. The study sites, A and B (9000 m^2 and 3500 m^2, respectively), are moors mainly covered with grass, heath, trees and rocks, and are similar in their physical and biological characteristics except for exposure, humidity and percentage of the area covered by trees (Massot et al. 1992). We selected two sites because local conditions can influence behaviour. For example, humidity and temperature during gestation affect offspring dispersal at birth (Massot et al. 2002).

The research was conducted with the approval of the Parc National des Cévennes and the European Commission.

General Design

We captured 132 (83 from A and 49 from B) and 90 (58 from A and 32 from B) gravid females by hand in early July

2001 and 2003, respectively. In the field, each lizard was kept individually in a cage (18 × 12 cm and 12 cm high) and then transported to the laboratory (16 km from the study sites). Gravid females were housed individually in plastic terraria (18 × 12 cm and 12 cm high) with about 2 cm of soil and a shelter. Fresh water was provided daily. In addition to natural daylight (0630–2130 hours), we provided an incandescent lamp as a heat source for 6 h per day (0900–1200 and 1400–1700 hours) to facilitate thermoregulation. Average room temperature was 26°C. Gravid females from site B were fed every week with one meal moth larva, *Pyralis farinalis* (average live weight ± SE = 0.189 ± 0.051 g, $N = 30$; average dry weight ± SE = 0.075 ± 0.025 g, $N = 30$) according to standardized rearing conditions (Sorci et al. 1994; Massot & Clobert 2000). Half of the females from site A were fed with one larva every week and the other half every 2 weeks during rearing periods (July–August) for a long-term study beginning in 1986 (Massot & Clobert 2000). The differential feeding rate to mothers from site A did not affect the selection of nocturnal shelters by juveniles, either as a main effect (logistic model; procedure GENMOD; SAS Institute 1996; $\chi^2_1 = 1.28$, $N = 140$, $P = 0.257$) or in interaction with juvenile sex ($\chi^2_1 = 0.03$, $P = 0.852$), juvenile body condition index (see Statistical Analyses; $\chi^2_1 = 0.13$, $P = 0.714$), donor sex ($\chi^2_1 = 0.38$, $P = 0.539$) or social environment experienced by donors ($\chi^2_1 = 0.20$, $P = 0.657$). Furthermore, juveniles from mothers with different feeding rates were randomized through the treatments and also controlled statistically. At birth, juveniles were measured, weighed and sexed by counting ventral scales (Lecomte et al. 1992). All mothers and their litters were released after the experiments at the mother's last capture point. We used 270 hatchlings of both sexes in the experiments.

As scent donors, we selected 81 adult males and 121 adult females from various populations between sites A and B. We used this procedure because juveniles might react differently to scents from donors from the same site because of familiarity or some prenatal determination. We kept donors in the laboratory in similar conditions as gravid females, except during the scent-marking process when we put absorbent paper on the floor instead of soil.

To measure the sensitivity of juveniles to the odours offered, we conducted a choice experiment in which we manipulated the odours present in nocturnal shelters. For each trial, juveniles were offered the choice of spending the night in one of two shelters, one containing odours from three conspecifics and the other containing no odour. We thus ensured independence of the data by comparing treatments (different types of odour). Juveniles were tested in transparent plastic cages (25 × 25 cm and 17 cm high) with the two shelters placed 10 cm apart on each side of the experimental cage. Water was not provided, as juveniles become inactive once they enter a shelter.

On days 2–4 after birth, each juvenile was placed in the middle of the experimental cage at 1900 hours. Light bulbs (25 W) were aligned perpendicularly 25 cm over the experimental cages at an equidistant point between the two shelters. Lights were immediately switched on for 1 h (from 1900 to 2000 hours). This allowed juveniles to explore the experimental cage under standardized conditions of temperature and light. The room was exposed to daylight from 0630 to 2130 hours and the average ambient temperature was 22°C. We noted the location of the juveniles at 2400 hours as (1) inside the odourless shelter, (2) inside the shelter containing the odour or (3) outside both shelters. Individuals that were outside the shelters (18.8% of the total) were not included in the analyses. All juveniles were in the same location on the morning of the following day (0900 hours). Each juvenile was used in only one trial.

Odour Collection

To obtain odours, we placed absorbent paper in each adult cage covering the entire floor. Donors were allowed to scent-mark for at least 2 days depending on the treatment (see below). After the scent-marking process, and while wearing rubber gloves, we cut the paper, with scissors, into three equal pieces (with or without odour) which we then placed inside each shelter covering the walls. We randomized both the side of the cage on which shelters with odour and no odour were placed and the donor's site of origin.

Experimental Design

We carried out three experiments to examine the response of juveniles to social interactions among donors. In all experiments, we used two main procedures to present odours to juveniles depending on the captivity conditions of donors during the scent-marking process. (1) When different groups of three donors were held together during the scent-marking process, we placed three pieces of paper from the same cage inside the shelters; and (2) when donors were isolated during the scent-marking process, we placed three pieces of paper, each with a scent from a different donor, inside the shelters (i.e. scents from a total of three donors from three different cages). With this procedure, we were able to test the effect of social interactions on site selection independently of group size since all shelters with odours had three donors. Donors that had the opportunity to interact were not used for the isolation treatment. All different trios differed in at least two donors. In experiment 1 (July 2001) we used, in separate trials, males and females as either receivers (juveniles) or scent donors (adults). The results of experiment 1 revealed a treatment effect only when odours of adult males were presented, and that the significance of this effect was more evident in the case of juvenile males. Thus, to investigate the mechanism underlying the results obtained in experiment 1, we used only males for experiments 2 and 3 (carried out in July 2003).

During the first hour of the 2-day period, we monitored the activity of the lizards. Agonistic interactions among grouped males were observed only during the first 15 min or so, probably because then the lizards become familiar with each other, which reduces the frequency of agonistic interactions in lacertids (López & Martín 2001). Agonistic interactions consisted mainly of threat postures (arched neck and raised posture) or submissive responses (foot shaking). They never came to the point of persistent chases and did not lead to sustained attempts to escape. All the animals were healthy throughout the experiments. After the treatment, lizards were fed with one larva of *P. farinalis* and then released at their capture point.

Experiment 1: social interactions

Depending on the treatment, donor lizards were housed singly or communally. Communally housed donors (three males or three females) were kept in the same cage for 2 days. In the choice test, juveniles could choose between a shelter with no odour and a shelter with the odour from one of these groups. We compared this response to that of juveniles that chose between a shelter with odours from three adults that were housed singly and a shelter with no odour. To correct for the density of scent marks left on the absorbent paper, we kept isolated lizards in smaller cages (18 × 12 cm and 12 cm high) than the lizards held in threes (25 × 15 cm and 17 cm high).

Of 135 juveniles, 110 responded to 46 different trios of donors: 18 males and eight females in trials with scents from isolated adult males; 10 males and six females in trials with scents from socially housed adult males; 15 males and 20 females in trials with scents from isolated adult females; and 18 males and 15 females in trials with scents from socially housed adult females.

Experiment 2: Time lag and marking duration

In experiment 1, the size of the scent-marking cages was associated with the social environment, and, therefore, donor lizards might not move randomly with respect to the treatment, which might lead to different distributions and/or densities of scent marks between treatments. Experiment 2 presents an alternative way of correcting for this potential effect. To obtain a similar quantity of scent marks in both isolated and socially housed treatments, we collected the scents of three interacting individuals for a shorter period (2-day treatment; Fig. 1) than for isolated individuals (6-day treatment) in cages of the same size (18 × 12 cm and 12 cm high; i.e. the scent-marking time for single isolated donors was three times that of three socially housed donors). Because the chemical signal of scent marks from isolated adults might change during the 6-day treatment, which might lead to a difference from the 2-day treatment that is not necessarily associated with the social environment experienced by the donors, we added the following three treatments to examine the response to the age of scents. For lizards held together, we added one treatment in which conditions were the same as in the 2-day treatment, except that we delayed the use of odours for 4 days after the scent-marking process (2-nonrecent-day treatment; Fig. 1). In the other two treatments, we used scent collected from individuals isolated for 3 days, either directly after collection or 3 days after their collection (3-day and 3-nonrecent-day treatments; Fig. 1). Scent marks in the nonrecent day treatments were allowed to age at room temperature (22 °C) in their original cages. Comparisons between the 2-day and 2-nonrecent-day treatments and between the 3-day and 3-nonrecent-day treatments might indicate whether the age of the scents affected the response. We also compared treatments of socially housed donors with those of isolated donors.

Of 85 juvenile males 68 responded to 27 different trios of donors: 15 in the 2-day treatment, 11 in the 2-nonrecent-day treatment, 13 in the 6-day treatment, 14 in the 3-day treatment and 15 in the 3-nonrecent-day treatment.

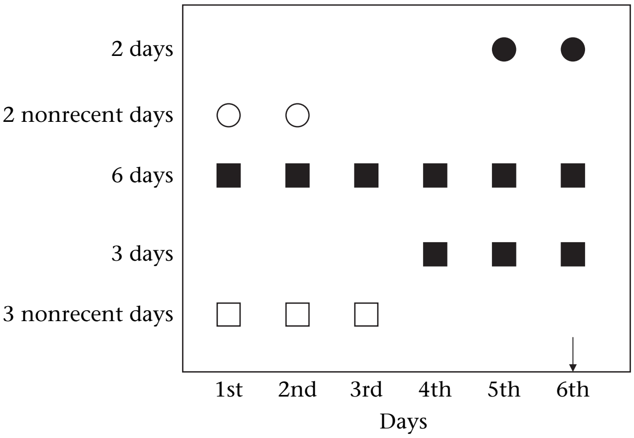

Figure 1. Schematic calendar used to obtain scent marks for the different treatments of experiment 2. ○, ●: Treatments in which donor male *Lacerta vivipara* were held together during the scent-marking process; □, ■: treatments in which donors were isolated; ●, ■: treatments in which recent odours were used in the trials (just after the scent-marking process); ○, □: treatments in which nonrecent odours were used. The arrow shows the day of the trials.

Experiment 3: alternated encounters

Individuals that leave scent marks in a shelter are not necessarily involved in direct interactions inside the shelter. Nevertheless, individuals might have interacted with conspecifics throughout the day outside the shelters, and then deposited scents carrying that information inside the shelters. In this experiment, therefore, we decoupled the scent-marking process from social encounters.

Three males were kept together in the same terrarium and three single males were kept isolated in individual terraria (18 × 12 cm and 12 cm high) for 2 h (0900–1100 hours). All individuals were then removed and each one kept isolated in a terrarium devoted to the scent-marking process for the rest of the day. We repeated the procedure the next day with the same males in clear terraria for the first 2 h, but for the scent-marking process each male was put in the same terrarium that it had been in on the first day. Thus, in contrast to experiments 1 and 2, socially housed donors were in groups of three for 4 h (2 h per day), but were isolated during the scent-marking process in the same way as those donors that did not interact. For the trials with juveniles, we put three pieces of papers inside each shelter, each piece from a different donor. Using this protocol, we corrected for the quantity and distribution of scents, and avoided a potential bias from the age of the scent. As in the other experiments, we compared the response to odours from three interacting donors with that to odours from three donors that did not interact, when the other choice was a shelter with no odour.

Of 50 juvenile males 41 responded to 18 different trios of donors: 20 to isolated donors and 21 to donors that had the opportunity to interact.

Statistical Analyses

To evaluate the significance of each effect, we fitted logistic models by using likelihood tests, and compared them by likelihood ratio tests (procedure GENMOD; SAS Institute 1996). In the models, we included the sex of the adult donors and the juveniles, the juveniles' body condition, the study site and the treatment. We estimated the body condition index (BCI) by taking the residual score of the linear regression of body weight on the snout–vent length (SVL). These residuals are a size-specific measure of body shape that better represents potential growth differences between individuals (Calsbeek & Sinervo 2002). The model also included the site of origin because differences between the two study sites (exposure, humidity and percentage of trees) may influence behavioural traits (Massot & Clobert 2000).

We started with a model with all the effects and their interactions, and gradually dropped the nonsignificant terms. We examined the interaction terms first, and when a significant interaction was found, the main effects that were part of this interaction term were kept in the final model (backward selection procedure, McCullagh & Nelder 1989). Significance levels are two tailed, except when there was a clear a priori prediction obtained from the results of the first year, where the directed test was used. This type of test is more conservative than the one-tailed test because it accounts for a potential unexpected direction of the results by specifying a pair of asymmetrical rejection regions in terms of *P* values (i.e. a smaller critical region to reject the null hypothesis when the trend is in the unexpected direction; Rice & Gaines 1994).

Siblings could not be assumed as independent statistical units a priori (Massot et al. 1994b; Massot & Clobert 2000). Similarly, source of scents might not be independent since we used more juveniles than different trios of donors. To account for this, we used the DSCALE option of the GENMOD procedure (SAS Institute 1996), developed for the application of generalized linear models (McCullagh & Nelder 1989). The DSCALE option allows the overdispersion factor, ^c, to be calculated (caused, for example, by a nonindependence between individuals or source of scents), and corrects the model selection by dividing the chi-square values by this factor (for details see McCullagh & Nelder 1989). The success of this procedure on correcting for overdispersion has been confirmed by previous studies (e.g. Lebreton et al. 1992; Anderson et al. 1994; Massot et al. 2003).

RESULTS

Experiment 1: Social Interactions

The choice of a shelter was influenced by the treatment experienced by adult donors (isolated versus three held in a group) in interaction with the sex of the juveniles and adults ($\chi^2_1 = 5.38$, $N = 110$, $P = 0.02$). This response was also dependent on juvenile BCI in interaction with the treatment and the sex of the adults ($\chi^2_1 = 5.84$, $N = 110$, $P = 0.015$), and in interaction with the site of origin and the sex of the juveniles ($\chi^2_1 = 7.40$, $N = 110$, $P = 0.006$). In contrast, we found no effect of SVL when it was included in the model (main effect and its interactions, all effects NS).

The choice of a shelter by juvenile males or females was unaffected by the treatment experienced by adult female donors. However, we found an interaction between juvenile BCI and site of origin, which was significant for juvenile females and marginally significant for juvenile males (Table 1).

The choice of a shelter by juvenile males and females was influenced by the treatment experienced by adult male donors both as a main effect and in interaction with juvenile BCI (Table 1). The BCI of juvenile males influenced their response to the adult male treatment (Fig. 2). Juvenile males with a high BCI avoided the shelter with odours from interacting males whereas lean juveniles selected it. Juvenile males and females differed in the way they responded with respect to the site of origin. In contrast to juvenile females, juvenile males were unaffected

Table 1. Effect of the body condition index of juveniles (BCI), treatment (T) and the site of origin (S) on the probability of selecting nocturnal shelters with odours from adults versus shelters with no odours in experiment 1

	Adult donor males				Adult donor females			
	Juvenile males		Juvenile females		Juvenile males		Juvenile females	
Effects	χ^2_1	*P*	χ^2_1	*P*	χ^2_1	*P*	χ^2_1	*P*
BCI	14.25	<0.001	2.25	0.133	0.39	0.532	2.65	0.103
T	7.55	0.006	3.63	0.056	2.26	0.132	0.30	0.585
S	0.29	0.59	5.07	0.024	0.04	0.839	0.18	0.671
BCI*T	9.13	0.002	4.05	0.044	0.69	0.405	1.35	0.224
S*T	<0.01	0.995	6.59	0.010	0.08	0.772	2.04	0.152
S*BCI	<0.01	0.948	6.14	0.013	3.40	0.065	6.05	0.013

The treatment factor was exposure to the scent marks of three donors that were held either singly or together.

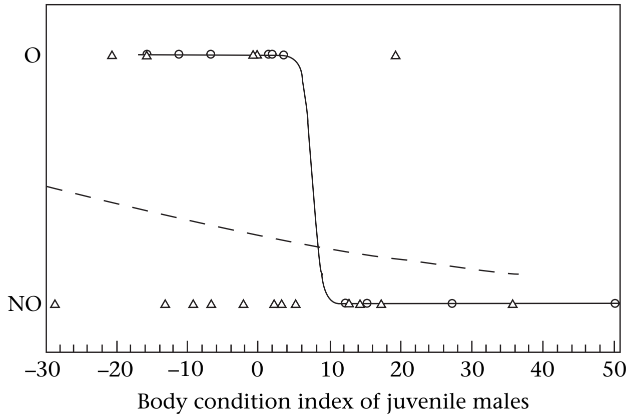

Figure 2. Selection of nocturnal shelters by juvenile male *Lacerta vivipara* in experiment 1. Each juvenile had a choice between a shelter that contained pieces of paper with odours from three adult males (O) and a shelter that contained pieces of paper with no odour (NO). Lines are logistic regressions in relation to body condition index. ○, — : Trials in which odours came from three adult males housed together; △, ‒‒‒: trials in which odours came from three adult males housed singly.

by the site of origin (Table 1). Juvenile females from site A were more attracted (50%) towards the odour of males that had interacted than those from site B.

In summary, the odours of adult males that had interacted influenced the choice of a shelter by juveniles of both sexes. This response depended on juvenile sex, BCI and site of origin.

Experiment 2: Time Lag and Marking Duration

The odour of isolated adult males did not influence the shelter choice of juvenile males (Table 2), regardless of the time lag and the duration of scent collection (comparison of 6-day, 3-day and 3-nonrecent-day treatments; Fig. 1).

Table 2. Effect of the body condition index of juvenile males (BCI), treatment (T) and the site of origin (S) on the probability of selecting nocturnal shelters with odours from adult males versus shelters with no odours in experiment 2

	Donor males together		Donor males isolated	
Effects	χ^2_1	*P*	χ^2_1	*P*
BCI	0.96	0.327	0.90	0.342
T	9.07	0.002	2.59*	0.274
S	9.53	0.002	0.01	0.927
BCI*T	12.34	<0.001	1.38*	0.502
S*T	<0.01	0.993	2.24*	0.326
S*BCI	12.21	<0.001	0.78	0.378

For scent marks coming from isolated donors, the treatments were scents deposited for 3 and 6 days. Scents deposited for 3 days could be recent (used just after the scent-marking process) or old (used 3 days after the scent-marking process; Fig. 1). For donors that were held together, the treatments were scents deposited for 2 days and were either recent scent marks (used directly after the scent-marking process) or old scent marks (used after 4 days).
*$df = 2$.

In contrast, the time lag in scent collection, in interaction with juvenile male BCI (2-day versus 2-nonrecent-day treatments; Fig. 1), influenced the shelter choice when adult donor males were held together (Table 2). With recent odours, we found the same result as in experiment 1 (selection of shelters in relation to juvenile BCI; Fig. 3). In contrast, old scents did not influence the choice of shelter (logistic regression only for the 2-nonrecent-day treatment: $\chi^2_1 = 0.22$, $N = 11$, $P = 0.641$; Fig. 3).

Finally, since there were no significant differences between them, we pooled all treatment conditions of isolated donors to compare them with the treatment conditions of grouped donors (2-nonrecent-day or 2-day treatments versus all treatments of isolation pooled). The response of juvenile males towards old scents of interacting adult donor males (2-nonrecent-day treatment) was similar to that towards scents from isolated males (all treatments of isolation pooled; interaction between juvenile BCI and treatments: $\chi^2_1 = 0.01$, $N = 53$, $P = 0.93$). In contrast, the response towards recent scents of interacting males (2-recent-day treatment) was significantly different from that towards scents of isolated males (all treatments of isolation pooled; $\chi^2_1 = 8.46$, $N = 57$, $P = 0.003$). Finally, there was a significant interaction between juvenile male BCI and site of origin (Table 2).

Experiment 3: Alternated Encounters

In experiment 3, we found a marginally significant interaction between treatment and the BCI of juvenile males ($\chi^2_1 = 3.30$, $N = 41$, $P = 0.067$; Fig. 4), whereas none of the other main effects and their interactions were significant (NS effects in all cases). Juvenile males with a lower BCI were attracted to the odour of adult males that had interacted, whereas juveniles with higher BCI behaved in the opposite way (logistic regression only on juveniles in contact with the odours of interacting males:

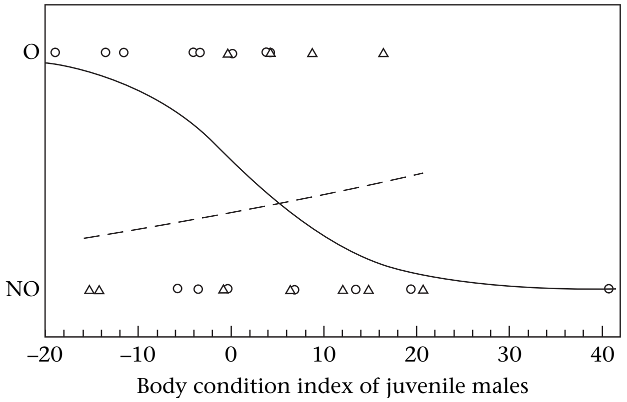

Figure 3. Selection of nocturnal shelters by juvenile male *Lacerta vivipara* in experiment 2. Each juvenile had a choice between a shelter that contained pieces of paper with odours from three adult males that were held together (O) and a shelter that contained pieces of paper with no odour (NO). Lines are logistic regressions in relation to the body condition index of juveniles. ○, —: Trials in which recent odours were used (2-day treatment; Fig. 1); △, ‒‒‒: trials in which nonrecent odours were used (2-nonrecent-day treatment).

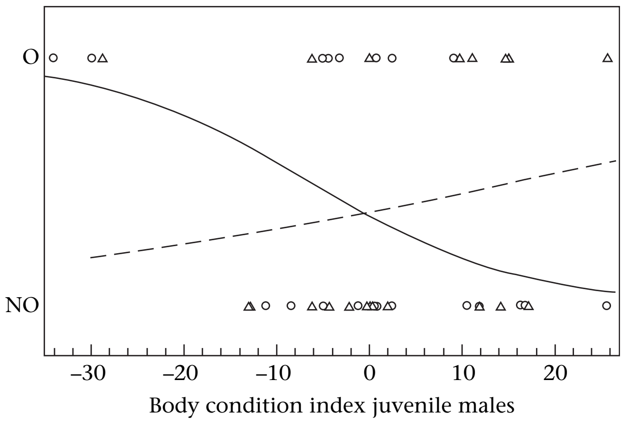

Figure 4. Selection of nocturnal shelters by juvenile male *Lacerta vivipara* in experiment 3. Each juvenile had a choice between a shelter that contained pieces of paper with odours from three adult males (O) and a shelter that contained pieces of paper with no odour (NO). Lines are logistic regressions in relation to the body condition index of juveniles. ○, —: Trials in which odours came from three adult males that had been in contact but were isolated during the scent-marking process; △, ———: trials in which odours came from three adult males housed singly.

$\chi^2_1 = 3.84$, $N = 21$, $P = 0.031$; directed test; Fig. 4). These results point in the same direction as those in experiments 1 and 2 for juvenile males.

DISCUSSION

Depending on the treatment, three pieces of paper from three socially housed donors or three pieces of paper from three isolated donors were put inside the shelters. All our results, therefore, are independent of group size of donors since we balanced the number of grouped and isolated donors by artificially pooling odours from three different individuals when they were kept isolated. In all of the experiments, when the odours were collected from adult males held communally, juvenile males with lower BCI than the average selected the shelter with odour. Juveniles did not react to adult female interactions (experiment 1). We also found that old scents from males held communally did not influence the choice of a shelter (experiment 2). Finally, the mother's site of origin influenced shelter choice.

Information Specificity and Potential Mechanisms

Many environmental factors can modify the condition or behaviour of an individual (e.g. Romero & Wikelski 2001; Breuner & Hahn 2003). For example, organisms in stressful situations may release specific chemical signals which can then be used as a source of information by other individuals (Stowe et al. 1995). Predation, parasitism or social dominance may induce physiological and/or behavioural modifications that may be perceived by conspecifics without necessarily giving any information about the factor inducing this change. This situation is unlikely in our case. We found that juvenile males, depending on their BCI, responded differently towards the odour of socially housed adult males but not towards that of socially housed adult females. Therefore, there was a specific response associated with male–male interactions.

According to the challenge hypothesis (Wingfield et al. 1990; Oliveira et al. 2001; Ros et al. 2002), it is likely that social interactions with other males affected males' androgen production. Pheromonal activity in lizards is based on skin, precloacal and femoral gland secretions (Simon 1983; Cooper & Vitt 1984; Alberts 1989; Mason & Gutzke 1990; Aragón et al. 2001). Femoral glands are well developed in males and are regulated by androgens (Mason 1992); therefore, males' social interactions could be reflected in scents by this mechanism. Whatever the type of signal involved, it reflects recent male–male interactions, since old scents did not influence juvenile choice. There is therefore a strong covariation between the chemical information and the current social environment. This enhances the value of the information with regard to its potential link to fitness (Danchin et al. 2001).

The juveniles' response had, in part, a prenatal determination since it also depended on the mother's site of origin. This was not due to a genetic difference, since the two sites are not genetically differentiated (M. Richard, unpublished data), or to the direct effect of the study area (postnatal effects) because juveniles were born in the laboratory. Previous studies have shown that natal dispersal in this species depends on maternal conditions during gestation (Sorci et al. 1994; Massot & Clobert 1995, 2000; Ronce et al. 1998; de Fraipont et al. 2000; Massot et al. 2002).

Information Content

We found that the selection of shelters by juveniles depended on their sex and BCI, traits that have been recurrently found to affect dispersal decisions in this species (Léna et al. 1998; Massot & Clobert 2000; Meylan et al. 2002; Le Galliard et al. 2003). Furthermore, the variation between juveniles in their ability to discriminate between different types of conspecific chemical cues is associated with the variation in juvenile dispersal propensity in both artificial (de Fraipont et al. 2000) and natural (Léna et al. 2000) conditions. In our study, juvenile males with a lower BCI selected the odour of interacting males whereas those with a higher BCI avoided it. Although adult males are the most dominant individuals in this species (Massot et al. 1992), juveniles tend to be more attracted to patches where males are at higher density (Léna et al. 1998). Our results are also compatible with studies in which juveniles of lower BCI remained in seminatural enclosures together with other conspecifics, including adult males, whereas those of higher BCI avoided conspecifics (Le Galliard et al. 2003; 2005).

In our experiments, juveniles had to choose between a shelter with no odour (reflecting an empty patch) and one with conspecific odour (reflecting an occupied patch).

The available literature suggests that there is a trade-off between selecting an empty patch and one that is already occupied, since both possibilities may entail costs as well as benefits. Habitat selection theory has proposed that the presence of conspecifics may be used as a cue to assess habitat quality (e.g. food availability; Stamps 1988). Furthermore, public information theory proposes that not only the presence but also the performance of individuals might serve as a cue for habitat assessment (Danchin et al. 2001, 2004; Valone & Templeton 2002). More specifically, Kennedy & Gray (1994) proposed that individuals may perceive agonistic interactions of conspecifics as a cue of good patch quality. The presence of interacting males might therefore be perceived as a sign of habitat quality. However, agonistic interactions might lead to energetic costs (Marler & Moore 1988), such that the balance between the costs and benefits of selecting an already occupied habitat is expected to depend on individual characteristics (Doligez et al. 1999; Danchin et al. 2001). In this context, the cost of selecting an empty patch would be lower habitat quality, but the benefit would be lower competition, whereas the opposite would be true for an occupied patch. Therefore, different phenotypes might adopt different tactics when faced with this trade-off. Thus, juvenile males in good conditions (higher BCI) might be able to afford to stay in empty, low-quality patches as a means of avoiding competition. In contrast, lean juveniles might not be able to afford costs such as starvation in low-quality patches, and should avoid them even when the alternative entails higher competition. As responses of males depended on BCI, it is likely that different phenotypes follow different strategies of site selection. Morphological traits of juveniles are correlated with performance abilities (Meylan & Clobert 2004). Initial endurance (running time to exhaustion measured at birth) increases with juvenile BCI, and juvenile annual survival probability increases with initial endurance under dietary restriction of juveniles but not under a full feeding treatment 1 month after birth (Le Gaillard et al. 2004) These results suggest that natural selection on initial endurance is stronger in low-food locations (Le Galliard et al. 2004). Our results support this hypothesis, as juvenile males of lower BCI avoided empty patches (shelters with no odour) that reflected poor-quality locations. Further studies are needed to test whether juvenile males with differing BCI also differ in other strategies such as hunting, thermoregulation and competition or predator avoidance.

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