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Responses to conspecific scent marks and the ontogeny of territorial marking in immature terrestrial salamanders

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Abstract We investigated the ontogeny of responses to scent marks in immature terrestrial salamanders (*Salamandra lanzai*) that inhabit the southwest Alps. In this species, sexual maturity is usually reached at about 8 years, and adults exhibit territoriality. One should expect territoriality to take place largely before the acquisition of sexual maturity if sexual competition is not the main force driving territoriality. However, both the difficulties for inexperienced animals to find a suitable territory and size-related competition may delay the acquisition of territoriality in juveniles. We performed choice tests with juveniles belonging to two age groups (1±1 years old versus 4±1 years old). Each focal animal was offered, in random order, the choice between two shelters, one without scent and the other containing one of the following scents: own, same-aged animal, a juvenile belonging to the other age group, or adult female. We also performed choice tests with adult females for which the scents of two juveniles belonging to a different age group were successively offered in a random order. Older juveniles were strongly attracted toward their own shelter and mostly avoided the shelters that contained the scent of juveniles of about the same age and of adult females. Adult females avoided the scents of older juveniles but not younger juveniles. These results therefore suggest that older juveniles use territorial marking. Conversely, young juveniles behaved randomly with respect to their own scents and to those of a same-aged juvenile, and they were

significantly attracted towards the odor of an older animal, especially adult females. Both older juveniles and adult females displayed a random behavior toward the scents of young juveniles. Our results suggest that young juveniles do not defend territories but use spaces occupied by older individuals.

Keywords Ontogeny · Juvenile territoriality · Scent marking · Ontogenic shift · *Salamandra lanzai*

Introduction

Territoriality, as evidenced by both aggressiveness towards intruders and signals of ownership, is thought to arise when critical resources such as food, refuges or mates, are both limited and defensible (Noble 1939; Stamps 1977; Wolff 1993; Powell 2000). In many terrestrial or aquatic species, ownership is signaled by using scent marks (Brashares and Arcese 1999; Powell 2000). In this situation, territorial animals usually display both an aversion to scent marks deposited by competitors and an attraction towards their own scent marks (reviewed in Gosling and Roberts 2001) or towards the scents of other group members in the case of species living in a group (e.g., Bel et al. 1995; Sun and Müller-Schwarze 1998). Juveniles of some species are territorial (e.g., lizards, Stamps 1988, 1991.), although several environmental constraints, social or not, can seriously disadvantage juvenile territoriality. Attraction to adults may help juveniles to locate suitable habitats or safe refuges in species without parental care (e.g., snakes, Graves et al. 1986) even when juveniles are territorial (Stamps 1988, 1991). Moreover, characters associated with competitive ability, such as size, may compromise the territorial success of younger animals (e.g., salamanders, Mathis et al. 1995). Thus, one may expect a switch in social affinity to occur during the ontogeny of juvenile territoriality, but the ontogeny of territoriality has not been studied well for most species.

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Terrestrial salamanders have a large range of life-history traits and social organization (Duelman and Trueb 1986; Griffiths 1995). Both scent marking and territorial defense are well documented in adult salamanders that are exclusively terrestrial and show direct development, such as certain Plethodontidae in North America and Salamandridae in Europe (reviewed in Mathis et al. 1995). These behaviors allow access to suitable territories and related resources (food and refuge) and are expressed as strong shelter fidelity (Joly 1963, 1968; Jaeger 1984, 1986; Gunzburger and Guyer 1998) and a restricted home range (Jaeger et al. 1982; Verrell 1986; Mathis 1990a, 1990b; Simons et al. 1997). However, overlapping home ranges between adults and juveniles have been observed in some of these species despite occurrence of food competition between immature animals and adults (Jaeger et al. 1995; Faragher and Jaeger 1997). The difficulty of finding a suitable territory (especially a safe shelter) for inexperienced animals could explain these results if kin selection compensates for the cost of resource sharing (Jaeger et al. 1995; Faragher and Jaeger 1997). Absence of sexual competition between adults and juveniles could also favor a greater tolerance of adults for immature animals than for other adults of the same sex in their territories. Species with delayed sexual maturity may help to disentangle food/territory and sexual competitions: the later the maturity, the easier it becomes to examine the territoriality of experienced and inexperienced animals out of the sexual context.

The aim of our work was to study the ontogeny of territorial marking in immature terrestrial salamanders, *Salamandra lanzai*, a long-lived species which inhabits grass and woodland areas in high-mountains (Gasc et al. 1997; Miaud et al. 2001). We specifically tested (1) whether immature salamanders discriminate between their own scent marks and scent marks of conspecifics of the same age, (2) whether this discriminatory behavior is related to their age, and, if so, (3) whether this variation is related to a switch in their spatial affinity towards the scents of adults.

In Alpine populations situated above 2,000 m a.s.l., such as the Lanza salamanders in the southern Alps, both dryness and low temperatures restrict activity, and the salamanders are often underground (Nascetti et al. 1988). A strong shelter fidelity and a reduced home range around the shelter have been reported in this species (Andreone et al. 1999b; Ribéron and Miaud 2000). Adults of both sexes defend a territory and use scent marking to prevent intrusion (Andreone 1992; Gautier and Miaud 1999, 2003). They reach the age of maturity at about 8 years (Miaud et al. 2001; Andreone et al. 2003), which allows us to compare the territorial status of juveniles of different ages. Younger immature animals (<2 years old) are unlikely to compete for resources with adult salamanders in this species because they eat different sizes and types of prey (Andreone et al. 1999a). The size of immature animals is highly correlated with age (Miaud et al. 2001), and food competition between adults and juveniles should increase as juveniles become older and begin to consume

the same prey as adults. Consequently, older immature animals (>3 years old) may exhibit more territorial behavior than younger juveniles and should be likely to avoid adults.

Methods

Study site and species

The Lanza salamander (*Salamandra lanzai*) is a viviparous species endemic to Mount Viso in the southwest Alps (Gasc et al. 1997). This species is listed in Annexe II of the CEE and is protected by the French Law on Wild Species. Sexual maturity is reached at an age of 8 years, depending on the population origin (Miaud et al. 2001). Females give birth to terrestrial fully developed neonates after 3 or 4 years of gestation (Miaud et al. 2001). The studied population is situated on the French side of Mount Viso at 2,300 m (44°42'N, 7°03'E). In this population, the activity period is mainly restricted to the summer (Ribéron et al. 1996).

All experiments were performed during the summer of 1999. Given the endemic status of this species, we planned a repeated-measurement design in order to reduce the number of animals needed to perform the experiments (see the general design below). A total of 30 animals were caught by hand in late June (Licence no. 96/180 from the French Ministry of Environment to C.M.) in order to obtain 10 animals within the three following age groups: younger juveniles (<2 years old), older juveniles (3–5 years old), and adults (>7 years old). Age was estimated from body size, as skeletochronology in this population shows a strong correlation between age and size during the juvenile stages (Miaud et al. 2001). Younger juveniles (1±1 years old) showed a snout-vent length (SVL) of <47 mm (mean ± SD = 42.2±3.2 mm, range: 33.6–46.8, n=10). Older juveniles (4±1 years old) had an SVL between 50 and 60 mm (mean ± SD = 55.4±4 mm, range: 50.8–59.4, n=10). Both the minimum size for adults (SVL >70 mm) and the presence of external sexual characteristics (shape of the vent) were used to select adult females (mean ± SD = 77.7±6.0 mm, range: 71–84.4, n=10).

Salamanders were housed in individual terraria (opaque cubic plastic l×b×h = 250×120×120 mm) with soil, moss, and a stone as refuge. They were fed weekly with live crickets and earthworms. All animals were released at the place of capture just after the experiments, i.e., early September.

General design and experimental apparatus

The affinity for scent cues was examined using an unforced choice test: in each test, one focal animal was offered the choice between two shelters, one containing a scent, the other scent-free ("blank"). All juveniles of the two age groups were exposed in random order to the following scents: own, same-age juvenile, different-age juvenile, and adult female. The adult females were offered the scents of both younger and older juveniles in random order. The females' response to their own scent and to the scent of other adults has been tested previously (Gautier and Miaud 1999, 2003).

We also performed control trials to check the effect of our experimental apparatus on the animals' behavior. For this purpose, six juveniles from each age group were used in a control test, during which they were offered the choice between two shelters without any scent.

All tests were performed as follows: in the evening (2000 hours), the focal animal was placed in the middle of an opaque plastic terrarium (l×b×h = 800×600×210 mm) containing only two shelters (plastic pipes, l=200 mm, diameter = 50 mm), which were randomly placed at opposite-ends of the terrarium. The scent was obtained by housing the source animal in the shelter for 18 h before the test; "blanks" were clean pipes. The terrarium was covered with an opaque lid. The position of the salamander was recorded on

three occasions (2200 hours, 2400 hours, and 0200 hours). On each occasion, we noted whether the salamander was inside a shelter and if so, which shelter it had chosen. After each recording session, the shelters were randomly relocated at the opposite side of the terrarium and the salamander was replaced in the middle of the terrarium. After each trial, all the material used was rinsed with water containing a detergent in order to eliminate any residual chemical traces. All tests were successively repeated 4 times (i.e., repeated with the same focal animal and the same scent donor), so that each animal had a total of 12 behavioral measurements for every scent tested.

Data analysis

We tested the effects of the scent offered on the behavioral response of focal animals while taking into account their social status (i.e., sexual maturity and age in the case of immature animals). Responses were recorded as the two following binary variables: (1) whether the animal entered one of the two shelters (i.e., the propensity to enter the shelters) and, if so, (2) whether the animal chose the shelter containing the scent or the shelter containing no scent (i.e., the shelter choice). To test whether a scent affected the propensity to enter the shelters, we compared the probability of entering a shelter in the experimental trial to that in the control trials. To examine whether a scent affected the shelter choice, we compared the shelter choice observed in the scent treatment to a random expectation (i.e., 0.5).

We used the generalized estimating equations (Liang and Zeger 1986; Carey et al. 1993), implemented in the GENMOD procedure of the statistical package SAS v8.2 (SAS 2001) to model the effects of explanatory covariates on repeated binary measurements. These models embed a correlation matrix in the covariance function to account for the different dependency levels between the different responses observed (Liang and Zeger 1986; Carey et al. 1993; Kuss 2002). In our case, each focal animal was offered all scents, and its response was measured several times for each of the scents. We therefore specified two dependency levels within the measurements performed on one particular animal (i.e., within a same cluster): between the different scent types (i.e., between sub-clusters) and within one scent type (i.e., within sub-clusters). However, it was not always possible to include the two dependency levels when analyzing the choice of the shelter: in some cases the number of animals entering a shelter was too small to allow it. In this case, we reduced the correlation matrix to one parameter estimating the dependency between the responses belonging to the same animal. We first constructed a global model to test whether the effects of the scent treatments on the behavioral response varied according to the age of the focal juvenile. Partial analyses were thereafter performed to examine the effect of the scent treatments on the responses of the focal animal within each juvenile age group. Contrast analyses were also performed to compare either the responses to the different scent treatments within each juvenile age group or the behavioral responses between the juveniles of the two focal age groups according to the scent cues offered. The responses of the adult females to the scent of the juveniles from both age groups were examined using the same procedure. All tests were performed using the generalized score tests for type III contrasts and were based on the empirical correlation matrix in order to minimize bias due to a misspecification of the correlation matrix (SAS 2001).

Results

Did young and older juveniles differ in their response to scent cues?

We first examined whether the propensity to enter shelters and the choice of shelter varied according to both age of

the focal animal and scent offered. These analyses showed that both propensity to enter the shelters and shelter choice differed significantly according to the age of the focal animal and the scent offered (age of focal animal*scent treatment effect on the propensity to enter the shelters: $n_{\text{rep}}=1,104$, $\chi^2_{4df}=17.62$, $P=0.0015$; age of focal animal*scent treatment effect on the shelter choice: $n_{\text{rep}}=515$, $\chi^2_{3df}=17.14$, $P<0.001$). Contrast tests between the two juvenile age groups on the scent offered confirmed that young and older juveniles responded differently to shelters with their own scent and to shelters with the scent of a juvenile of the same age. However, this difference was significant only for the shelter choice (age of focal animal*scent treatment effect on the propensity to enter shelters: $n_{\text{rep}}=480$, $\chi^2_{1df}=0.32$, $P=0.35$; age of focal animal*scent treatment effect on the shelter choice: $n_{\text{rep}}=248$, $\chi^2_{1df}=10.99$, $P<0.001$). Young juveniles entered the shelters more often than older juveniles when the scent of an adult female was present (age of focal animal on the shelter choice: $n_{\text{rep}}=240$, $\chi^2_{1df}=16.36$, $P<0.001$). Moreover, young juveniles were also more attracted than older juveniles to the shelter with the scent of an adult female (age of focal animal on the shelter choice: $n_{\text{rep}}=143$, $\chi^2_{1df}=11.66$, $P<0.001$).

Influence of scent cues on the behavior of young juveniles

Did the scent treatments affect the propensity to enter the shelters?

The scent treatments had a significant influence on the juveniles' propensity to enter shelters ($n_{\text{rep}}=552$, $\chi^2_{4df}=9.81$, $P=0.044$; Fig. 1). Juveniles did not enter the shelters more often when their own scent was offered than when the shelter offered the scent of a juvenile of the same age or of an older juvenile (contrasts: young juvenile versus self, $n_{\text{rep}}=240$, $\chi^2_{1df}=0.40$, $P=0.53$; older juvenile versus self, $n_{\text{rep}}=240$, $\chi^2_{1df}=0.40$, $P=0.53$). In contrast, the probability that the young juvenile would enter the shelters was significantly higher when the scent of an adult female was present than when their own scent was present (contrasts: adult female versus self, $n_{\text{rep}}=240$, $\chi^2_{1df}=8.56$, $P=0.003$).

The effect of the scent of an adult female was also significant when compared to the control experiment, which was not the case for the other scents (contrasts: self versus control, $n_{\text{rep}}=144$, $\chi^2_{1df}=0.18$, $P=0.67$; young juvenile versus control, $n_{\text{rep}}=240$, $\chi^2_{1df}=0.01$, $P=0.92$; older juvenile versus control, $n_{\text{rep}}=144$, $\chi^2_{1df}=1.06$, $P=0.30$; adult female versus control, $n_{\text{rep}}=144$, $\chi^2_{1df}=8.15$, $P=0.004$).

Did the scent treatment affect the propensity to select the shelter containing scent cues?

The scent treatments significantly affected the juveniles' propensity to select the shelter containing the scent cues

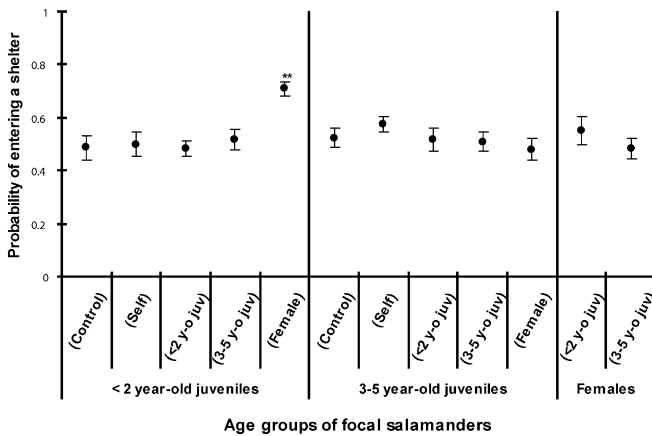


Fig. 1 Influence of scent treatments on propensity to enter a shelter. The probability (estimated with GEE analysis, SAS 2001) that focal individuals in three age groups [i.e., young individuals (<2 years old), older juveniles (3–5 years old), and females] of *Salamandra lanzai* entered one of two shelters, versus no entered shelter, according to the scent treatment. In experimental trials, the focal animal was faced with a choice between two shelters, one without scent and one with a conspecific scent (scent donor in parentheses). In control trials, the focal salamander also had a choice of two shelters, but both shelters were without scent. Sample sizes were 10 animals in each treatment within each tested age group. The bars indicate the 95% confidence interval of the estimated probabilities. For each juvenile age group, a significant difference in the probability to enter one of the two shelters in the experiment with odor versus the control experiment without odor is noted as follows: ** $P < 0.01$

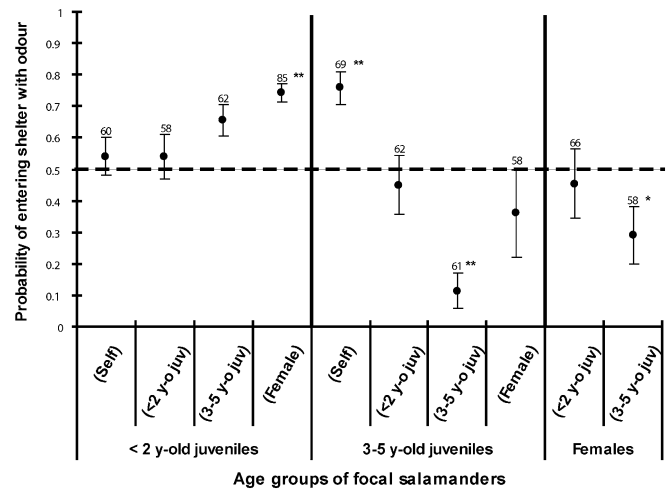


Fig. 2 Influence of scent treatments on propensity to select the shelter with scent clues. The probability (estimated with GEE analysis, SAS 2001) that focal individuals from the three age groups [i.e., young individuals (<2 years old), older juveniles (3–5 years old), and females] of *S. lanzai* entered the shelter containing conspecific scent rather than the shelter without scent according to the scent offered (scent donor in parentheses). Sample sizes were 10 animals in each treatment within each tested age group. The numbers under the bars indicate the total number of times the animals entered one of the two shelters (i.e., n_{rep} in Results). The bars indicate the 95% confidence interval of the estimated probabilities. The horizontal dotted line represents the expected value under a random binomial distribution. A significant deviation from this value is noted as follows: * $P < 0.05$; ** $P < 0.01$

($n_{rep}=265$, $\chi^2_{3df}=8.54$, $P=0.036$, Fig. 2). Separate analyses within the different scent treatments showed that the presence of their own scent, the scent of a juvenile of the same age or the scent of an older juvenile did not significantly affect the choice of shelter (self: $n_{rep}=60$, $\chi^2_{1df}=1.24$, $P=0.26$; juveniles of the same age: $n_{rep}=58$, $\chi^2_{1df}=1.43$, $P=0.23$; older juvenile: $n_{rep}=62$, $\chi^2_{1df}=3.28$, $P=0.07$). However, young juveniles were attracted to the shelter containing the scent of adult females (adult female: $n_{rep}=85$, $\chi^2_{1df}=9.17$, $P=0.0025$).

The young juveniles did not show a significant preference for the shelter with their own scent as compared to the scent of a juvenile of the same age (contrast: juvenile of the same age versus self, $n_{rep}=118$, $\chi^2_{1df}=0.07$, $P=0.79$). However, the probability that the focal animal would select the shelter with the scent cues was significantly higher when the shelter contained the scent of an older juvenile or of an adult female than when it contained its own scent (contrasts: older juvenile versus self, $n_{rep}=122$, $\chi^2_{1df}=4.91$, $P=0.026$; adult female versus self, $n_{rep}=145$, $\chi^2_{1df}=7.68$, $P=0.006$). They also significantly preferred the scent of adult females to the scent of older juveniles (contrasts: adult female versus older juvenile, $n_{rep}=147$, $\chi^2_{1df}=4.40$, $P=0.036$), and they significantly preferred the scent of an older juvenile to the scent of a same-aged juvenile (contrasts: older versus young juvenile, $n_{rep}=120$, $\chi^2_{1df}=5.55$, $P=0.018$).

Influence of scent cues on the behavior of older juveniles

Did the scent treatments affect their propensity to enter the shelters?

We did not detect a general effect of the scent treatments on the older juveniles' propensity to enter shelters ($n_{rep}=552$, $\chi^2_{4df}=6.24$, $P=0.18$; Fig. 1).

Did the scent treatment affect the propensity to select the shelter containing scent cues?

The scent treatments significantly affected the juveniles' shelter selection ($n_{rep}=250$, $\chi^2_{3df}=9.76$, $P=0.021$, Fig. 2). Separate analyses for each scent treatment showed that the older juveniles significantly preferred the shelter with their own scent ($n_{rep}=69$, $\chi^2_{1df}=8.22$, $P=0.004$). However, they significantly avoided the shelter containing the scent of a juvenile of the same age and tended to avoid the scent of an adult female (juvenile of the same age: $n_{rep}=61$, $\chi^2_{1df}=9.07$, $P=0.003$; adult female: $n_{rep}=58$, $\chi^2_{1df}=3.24$, $P=0.072$). The scent of a young juvenile did not have a significant effect on their choice ($n_{rep}=62$, $\chi^2_{1df}=0.99$, $P=0.32$).

Contrast analyses showed that the older juveniles preferred the shelter with their own scent to the shelter of any other social partner (contrasts: juvenile of the same age versus self, $n_{rep}=130$, $\chi^2_{1df}=9.51$, $P=0.002$; young

juvenile versus self, $n_{\text{rep}}=131$, $\chi^2_{1df}=6.28$, $P=0.012$; adult female versus self, $n_{\text{rep}}=127$, $\chi^2_{1df}=7.63$, $P=0.006$). However, they significantly avoided the shelter containing the scent of a juvenile of the same age more often than the shelter with the scent of an adult female (contrast: juvenile of the same age versus adult female, $n_{\text{rep}}=119$, $\chi^2_{1df}=4.76$, $P=0.029$).

Did the affinity of adult females for juveniles vary with age of the juveniles?

Adult females entered one of the two shelters more frequently when one of them contained the scent of a young juvenile than when it contained the scent of an older juvenile ($n_{\text{rep}}=240$, $\chi^2_{1df}=5.33$, $P=0.021$; Fig. 1). However, they did not significantly prefer the shelter that contained the scent of young versus older juveniles ($n_{\text{rep}}=124$, $\chi^2_{1df}=2.12$, $P=0.14$).

Nevertheless, separate analyses within each scent treatment showed that the shelter containing the scent of an older juvenile was significantly avoided, but the shelter containing the scent of a young juvenile was not (older juvenile: $n_{\text{rep}}=58$, $\chi^2_{1df}=6.46$, $P=0.011$; young juvenile: $n_{\text{rep}}=66$, $\chi^2_{1df}=0.64$, $P=0.42$; Fig. 2).

Discussion

The age of juveniles significantly affected their relative affinity towards their own scent, the scent of older juveniles, and the scent of adults. Young juveniles were attracted to the shelters containing the scent of older juveniles or of adult females. Older juveniles, on the other hand, significantly avoided shelters containing the scent of juveniles of the same age or of adult females. These results indicate that the relative affinity towards conspecific cues is radically opposed for young and older juveniles in this long-lived species.

Attraction towards conspecific scents can sometimes be artificially induced by laboratory conditions (Stamps 1988). In our study, however, this cannot explain why the affinity towards the scents of older juveniles and of adult females is different for young and older juveniles. Moreover, the salamanders spent a relatively large portion of time outside the shelters even when neither shelter contained a scent (see Fig. 1). This is not surprising: a high level of moisture was maintained in our experimental apparatus to avoid detrimental conditions for the salamanders as it favors the animals' activity in the field (Andreone et al. 1999b). Nevertheless, since the number of times that an animal was found outside the shelters was not negligible, one may ask whether shelter selection actually indicates the relative affinity towards the scent offered (Léna and De Fraipont 1998; Léna et al. 2000). Indeed, in this situation, inferring the relative affinity towards a scent from the shelter selection could be misleading if the scent's effect on the shelter choice is not consistent with its effect on the entrance rate. But this was

not the case in our study since the only scent treatment that had a significant influence on the propensity to enter the shelters also altered the shelter selection consistently. Finally, one may ask whether our analyses do not suffer from a lack of power to detect the significance of a scent effect because of the small number of animals used in this study. However, this is unlikely to have occurred: within the global model, the correlation parameters estimated both between and within the scent treatments on the responses observed on the same focal animal were weak (on the propensity to enter the shelters, the within and between correlation estimates were respectively -0.311 and -0.0006 , while on the shelter choice they were respectively -0.494 and -0.02). As there was a large number of repeated measurements made on each focal animal within each scent treatment, this suggests that the contribution of the focal animal's identity on the response observed was weak and is therefore unlikely to hide a scent effect from detection. All of the above findings lead us to interpret shelter selection as a relative spatial affinity towards the scent offered.

Juvenile spatial affinity for conspecific scents

In young juveniles, we did not detect significant effects of the scent of a young juvenile on the behavior of any focal animals, regardless of their age and even if the scent was its own. This may be because young juveniles do not produce scent marks or because their scent cues do not influence spacing behavior of conspecifics. Young juveniles were attracted towards the scents of older animals (i.e., older juveniles and adult females), even if the latter were neither related nor familiar to the young juveniles. Conclusively, younger *Salamandra lanzai* juveniles are able to identify conspecific scents, as has been shown for several other amphibians (Belden et al. 2000). As with Plethodontidae (e.g., Jaeger et al. 1995), young juvenile *Lanza* salamanders might use the scent cues of older animals to locate suitable habitats and/or safe shelters. Young juveniles do not compete with adults for food because adult salamanders mostly prey on adult arthropods that are too large for young immatures (Andreone et al. 1999a).

Young juveniles were also significantly more attracted to the scent of an adult female than to the scent of an older juvenile. Several hypotheses could explain this result. Adult scents may be easier to track than the scents of immature animals. It could be beneficial for younger juveniles to be in the same burrows as adults because adults eat potential predators of the smaller juveniles (see Jaeger and Forester 1993). Territoriality favors the ownership of better habitats by adults. However, the diet of younger juveniles is unlikely to overlap with that of an adult, while it can, at least partly, overlap with the diet of the older juveniles because of their intermediate size (Andreone et al. 1999a).

Territoriality in salamanders (e.g., salamandrids; Andreone 1992; Gautier and Miaud 1999, 2003; Ribéron and

Miaud 2000; this study; and plethodontids, Jaeger and Forester 1993; Jaeger et al. 1995; Faragher and Jaeger 1997; reviewed in Bruce et al. 2000) indicates that young juveniles strongly depend on the availability of resources that are defended by older animals. In *Plethodon cinereus*, immature animals were both attracted towards the scents of adults and spatially associated with adults in the field (Jaeger et al. 1995). In *S. lanzai*, gestation is particularly long (up to 4 years, Miaud et al. 2001) and is associated with feeding on intrauterine maternal secretions during the latter stage of gestation (Guex and Greven 1994; Greven and Guex 1994). These characteristics could allow a particular link (such as olfactory imprinting) leading to a possible preferential spatial association in the field between mothers and their offspring. In this context, and in the absence of sexual competition, kin selection is a possible hypothesis to explain our results. Recognition of the mother may be implicated in juvenile dispersal and/or settlement facilitation in several species of viviparous lizards (Main and Bull 1996; Bull and Baghurst 1998; Léna and De Fraipont 1998; Léna et al. 1998, 2000). Both the spatial distribution of salamanders in the field and the potential implication of maternal recognition in this process are currently being studied (Gautier 2003).

Reversal of spatial affinity for conspecific scents and territorial acquisition

Older juveniles were attracted to shelters with their own scent, which is consistent with territorial behavior. Furthermore, they were repelled by the scent of juveniles of the same age.

The older juveniles were less than 6 years old, while the minimum age of sexually mature animals is 8 years old in this population (Miaud et al. 2001). Our results therefore strongly suggest that territorial behavior does not coincide with the acquisition of sexual maturity. In some members of the family Plethodontidae, such as *P. cinereus*, the age of maturity is reached at 3 years old (Saylor 1966), and experiments did not indicate any territorial behavior in juvenile stages (Jaeger et al. 1995). However, some species show territorial behavior before reaching sexual maturity (Stamps 1988; Walls 1991). In *S. lanzai*, we hypothesize that the territorial behavior of older juveniles resulted from competition for resources such as food that are associated with refuges. Competition for food should be greatest for similarly sized individuals, and older juveniles more often avoided the scent of juveniles of the same age than of adult females. Similarly, older juveniles could be excluded from more suitable habitats that are already monopolized by adults.

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