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Kin recognition in the common lizard

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Abstract The ability to recognize parents has never been reported in species in which parents do not provide care to their young; in such species, only sibling recognition has been found. However, there may be several advantages of parent recognition, even in the absence of parental care. We investigated the ability of neonates to recognize olfactory cues from both their mother and siblings in the common lizard, *Lacerta vivipara*, a species without parental care. Juveniles from 264 gravid females were reared for 2 days either with their mother, with another female, or separated from all other adults. Juveniles from some families were split into two or three groups so that each juvenile was unfamiliar with a subset of its siblings. After 2 days, we offered the juveniles a choice of two nocturnal shelters: one containing a lizard odor and the other without odor. The response to the odor of an unrelated and unfamiliar adult was influenced by both the sex of the adult and the sex of the juvenile. Juveniles of both sexes recognized the odor of their mother whether they were familiar with her or not (pre-natal determinism). Juveniles recognized familiar but not unfamiliar siblings (post-natal determinism). In the wild, spatial association with kin declines shortly after birth. Thus, recognition of the mother is likely to have biological relevance. Recognition of the mother may reduce competition and/or enhance juvenile establishment.

Key words *Lacerta vivipara* · Mother recognition · Sibling recognition · Olfaction · Common lizard

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Introduction

Kin recognition is commonly explained by kin selection (Hamilton 1964 a,b) and inbreeding avoidance (Bateson 1978, 1983). In the particular case of parent-offspring recognition, studies correctly focused on the importance of parental care. In dense populations, parents have to recognize their offspring to avoid misdirected parental care, and juveniles have to recognize their parents to avoid aggressive rejection by unrelated adults (Evans 1980; Elwood 1991; Porter 1986; Waldman 1988). There are other advantages of parent-offspring recognition. Many species show infanticide; for instance, males may attempt to provoke estrus in females by killing the offspring they are nursing (Elwood 1991, 1992; Fitzgerald and Whoriskey 1992; de Fraipont et al. 1992). Infanticide can also reduce competition (Holmes and Sherman 1982; Elwood 1992). In these situations, it will disadvantage parents if they misidentify their own offspring and cannibalize or kill them (Elwood 1991, 1992). Parent-offspring recognition may also decrease kin competition by reducing aggressiveness (Halpin 1981; Hurst and Barnard 1991), or by promoting helping (Kurland 1980; Holmes and Sherman 1982). Finally, parent-offspring recognition may contribute to optimization of mate choice (Bateson 1983; Hayashi and Kimura 1983).

However, advantages of parent-offspring recognition have only been reported in species with parental care (Wilson 1987; Waldman 1988; Byers and Bekoff 1991; Ferkin et al. 1992). Furthermore, parental care may also provide the opportunity to recognize parents or offspring on the basis of familiarity (Ferkin et al. 1992). Thus, it is still not clear if parent-offspring recognition remains advantageous when there is no parental care.

The few studies of kin recognition in species without parental care (Fletcher and Michener 1987) have only reported sibling recognition (Blaustein et al. 1987a,b; Werner et al. 1987; Simmons 1989; Blaustein and Waldman 1992; Brown and Brown 1993; Pfennig et al. 1993), though maternal factors may serve as cues for sibling recognition in some of these species (Hepper and Waldman 1992; Blaustein and Waldman 1992). Parent-offspring recognition may not have evolved because parents usually abandon their offspring soon after laying, whereas siblings remain grouped. Studies are needed using species where parents and offspring may encounter each other after birth (overlapping home ranges), to determine whether parent-offspring recognition occurs in the absence of parental care.

We report a study of kin discrimination in the lizard *Lacerta vivipara*, which does not provide parental care, but in which parents and offspring have overlapping home ranges (Clobert et al. 1994). Kin recognition has rarely been reported in reptiles (Blaustein et al. 1987b; Hepper 1991; Main and Bull 1996). One study has found evidence for sibling recognition in a lizard by means of chemical cues (Werner et al. 1987). Nasal chemical receptors are well developed in lacertid lizards (Halpern 1992). The common lizard can discriminate predator's odor (Thoen et al. 1986; Van Damme et al. 1990). This species lives in dense vegetation, where odor cues are more efficient than visual cues (Stamps 1977; Singer et al. 1980; Alberts and Werner 1993). Many lacertid lizards have nocturnal burrows (Stamps 1977), and may leave odor to indicate recent burrow use. Therefore avoidance of or attraction towards an individual can be simulated by the response to a shelter containing lizard odor.

In this study we tested the response of juveniles of both sexes to scent cues contained in a shelter, according to the sex, the age, and the relatedness of the scent donor. We also investigated the influence of familiarity with kin.

The aim of this study was not to attribute a function to this recognition, but to provide an example of kin recognition in a species lacking parental care.

Methods

Study species and site

The common lizard, *Lacerta vivipara*, is a small (average adult size: 60 mm snout–vent length, SVL) viviparous, lacertid lizard that inhabits peatbogs and heathlands. Mating occurs in May, immediately after female emergence. Parturition begins 2 months later, and females lay on average five eggs which hatch as they are laid. Neonates (20 mm SVL) are autonomous just after hatching and may disperse from their natal site within a few days of birth (40–80% of juveniles disperse at high population density, Clobert et al. 1994). The study site is on Mont Lozère in the Cevennes National Park (Massif Central, France) at 1420 m altitude (Pilorge et al. 1987; Clobert et al. 1994). Since 1986, gravid females have been captured by hand in early July and kept in the laboratory for a few weeks until parturition. In 1993 and 1996, 264 females, 528 of their offspring and 45 adult males were housed with food and water ad libitum in individual terraria (18 × 12 × 12 cm), which were heated for 6 h per day under a regime of natural daylight. All lizards were released immediately after the experiment at their last capture point. We sexed juveniles by counting ventral scales (Lecomte et al. 1992).

General design

This study tested the discrimination of hatchlings of both sexes for odors of adults and juveniles contained in a shelter.

In most tests of kin discrimination, subject animals are offered a choice between kin and non-kin cues. However, this method does not discriminate between attraction to kin cues and avoidance of non-kin cues. Furthermore, laboratory conditions and the odor treatments used can result in a juvenile refusing to enter a shelter. We therefore preferred to use unforced choice experiments. This involved a choice between cue and no cue, to measure the response (attraction or avoidance) to both kin and non-kin cues, and to test the potential interaction of each odor treatment with laboratory conditions. We offered juveniles a choice between two nocturnal shelters, one containing an odor and the other without odor. In 62 control experiments neither shelter contained an odor. This measured any bias resulting from laboratory conditions. Finally, we performed a set of forced choice experiments to test the preference of the juvenile between its own odor and the odor of its mother.

We collected odors by placing blotting paper pieces in contact with an individual for two days. All experiments were performed in equal sized terraria (25 × 15 × 17 cm). Two shelters (plastic half-cylinders, L × R:50 × 16 mm) were randomly placed at opposite sides of an empty terrarium. Blotting paper pieces (with or without odor) were put into each shelter with tweezers.

In each experiment one 2-day-old juvenile was placed in the middle of a terrarium at 1700 hours. The terrarium was placed randomly in a room exposed to daylight and ambient temperature (21 °C), and left for 13 h including 9.5 h of total darkness (2130–0600 hours). We recorded the position of the juvenile with a flashlight three times, at 1800, 2400, and 0600 hours, noting whether the lizard was outside or inside the shelters, and in the latter case, which shelter was chosen. The observer did not know which shelter contained an odor. After each experiment, the terrarium and shelters were rinsed with water containing detergent to eliminate residual chemical traces. Each juvenile was used in only one experiment.

Odor treatments

We tested the response of juveniles to the following odors (sample sizes used in each odor treatment according to the rearing condition are summarized in Table 1).

Unrelated and unfamiliar adult males or females

We offered 53 juveniles the choice between a shelter with the odor of an unrelated male and a shelter with no odor. We offered 52 juveniles the choice between a shelter with the odor of an unrelated unfamiliar adult female. We investigated the influence of the sex of 70 juveniles in these experiments.

Unrelated unfamiliar juveniles

We offered 60 juveniles the choice between a shelter with the odor of an unrelated juvenile and a shelter with no odor.

Mothers

A total of 123 juveniles were used, of which 81 were sexed. Just after hatching, juveniles were subdivided into three groups: for 2 days, 55 were housed with their mother, 35 were isolated from adult conspecifics, and 33 were housed with an unrelated postpartum female. We offered these juveniles the choice between a shelter with their mother's odor and a shelter with no odor.

In a further experiment, we isolated 60 juveniles from their mother directly after birth, and kept them for 2 days in individual terraria. We offered them a choice between a shelter containing the odor of their mother and a shelter containing their own odor.

Siblings

Just after hatching, juveniles from each litter were separated from their mother and split into two or three groups. Each juvenile was

Table 1 Sample size of subjects used in each odor treatment according to the rearing condition that subjects experienced (*n* is the sample size of juveniles used (each juvenile only participated in one experiment), *L* indicates the number of litters used). Juveniles were reared with their mother in the group 1, they were reared with only a subset of their siblings in the group 2, and they were reared with an unrelated adult female in the group 3

Odor treatments	Rearing groups		
	Group 1	Group 2	Group 3
No odor (control trials)	$n = 25$ ($L = 23$)	$n = 28$ ($L = 19$)	$n = 9$ ($L = 9$)
Unfamiliar unrelated adult male	$n = 22$ ($L = 21$)	$n = 20$ ($L = 19$)	$n = 11$ ($L = 11$)
Unfamiliar unrelated adult female	$n = 21$ ($L = 20$)	$n = 19$ ($L = 19$)	$n = 12$ ($L = 12$)
Unfamiliar unrelated juveniles	$n = 16$ ($L = 15$)	$n = 38$ ($L = 31$)	$n = 6$ ($L = 6$)
Unfamiliar siblings		$n = 58$ ($L = 36$)	
Familiar siblings		$n = 60$ ($L = 37$)	
Unfamiliar mother		$n = 35$ (L = 32)	$n = 33$ (L = 29)
Familiar mother	$n = 55$ ($L = 31$)		
Unfamiliar mother versus own odor		$n = 60$ ($L = 40$)	

therefore familiar with some of its siblings and unfamiliar with others. We offered these juveniles a choice between a shelter containing the odor of their siblings ($n = 60$ for familiar siblings and $n = 58$ for unfamiliar siblings), and a shelter containing no odor.

Data analysis

From the three observations of each juvenile we recorded the number of times it was in a shelter and the number of times it selected a given shelter.

To test if the presence of an odor influenced juvenile choice, we compared the experiments where at least one odor was offered in a shelter to the control experiments where no odors were offered. In the same way, we tested whether the shelter choice differed from random expectation. All analyses were performed using logistic models (Procedure GENMOD, SAS Institute 1990) selected using log-likelihood ratio tests.

Results

Unrelated and unfamiliar adult males or females

When the odor of an unrelated unfamiliar adult male was offered, significantly fewer juvenile males than female entered a shelter ($n = 36$, $X_1^2 = 7.48$, $P = 0.006$, Fig. 1), and fewer juvenile males entered a shelter than in control trials ($n = 30$, $X_1^2 = 5.52$, $P = 0.019$). This was not the case for juvenile females ($n = 50$, $X_1^2 = 0.86$, $P > 0.10$). The 28 juveniles that entered a shelter did not significantly select or avoid the shelter containing the odor of an adult male ($n = 28$, $X_1^2 = 0.41$, $P > 0.10$, Fig. 2).

When the odor of an unrelated unfamiliar adult female was offered, the sex of the juvenile did not influence the probability of entering a shelter ($n = 34$, $X_1^2 = 1.05$, $P > 0.10$, Fig. 1), and they entered shelters as often as in control trials ($n = 114$, $X_1^2 = 0.36$, $P > 0.10$). The 34 juveniles that entered a shelter did not significantly select or avoid the shelter containing the odor of an unrelated adult female ($n = 34$, $X_1^2 = 2.82$, $P = 0.093$, Fig. 2).

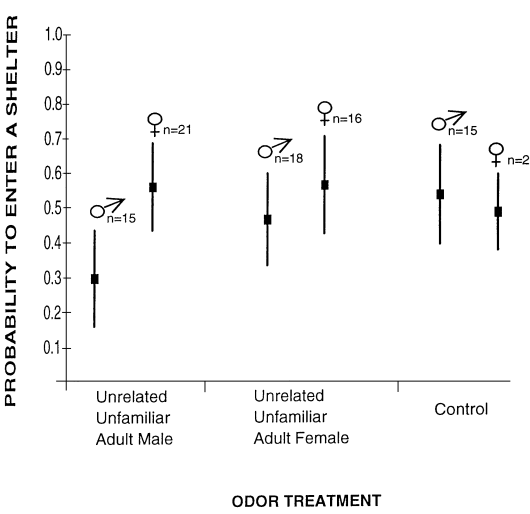

Fig. 1 Probability that juvenile males and females will enter a shelter when the odor of an unrelated unfamiliar adult male or female is offered. *Bars* indicate individual errors recorded at the 3 visits

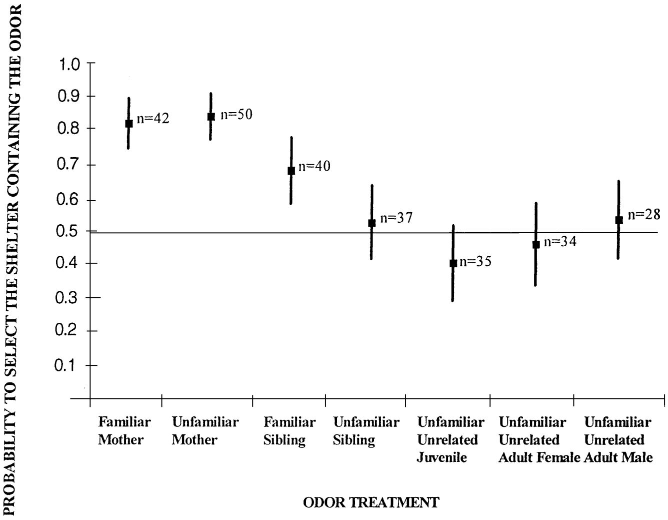

Fig. 2 Probability that a juvenile will select the shelter containing the odor according to the odor offered. *Bars* indicate individual errors recorded at the 3 visits

Unrelated unfamiliar juveniles

The presence of the odor of an unfamiliar unrelated juvenile did not influence the probability that a juvenile would enter a shelter ($n = 122$, $X_1^2 = 3.09$, $P = 0.078$) nor did it influence the choice of the shelter ($n = 35$, $X_1^2 = 0.36$, $P > 0.10$; Fig. 2).

Mothers

Neither the sex of the juveniles nor the rearing conditions that the juveniles experienced influenced whether they entered a shelter when one of the shelters contained the odor of the mother (Table 2). Juveniles entered the shelters as often when one of them contained the odor of their mother as in the control trials ($n = 185$, $X_1^2 = 1.208$, $P > 0.10$). However, independent of the sex of the juvenile, those juveniles which entered a shelter significantly more often selected the one containing the mother's odor ($n = 92$, $X_1^2 = 100.56$, $P < 0.0001$) whether they were familiar with their mother or not (Fig. 2). Juveniles significantly selected the mother's odor even if they had been reared for 2 days with an unrelated female ($n = 27$, $X_1^2 = 42.74$, $P < 0.0001$), or kept isolated from conspecific adults for 2 days ($n = 23$, $X_1^2 = 15.60$, $P = 0.0001$). Juveniles selected a shelter containing the odor of an unfamiliar mother significantly more often than a shelter containing odor of an unfamiliar and unrelated female ($n = 84$, $X_1^2 = 21.66$, $P < 0.0001$).

Juveniles showed no significant preference for the shelter containing their own odor over one containing the odor of their mother ($n = 48$, $X_1^2 = 0.0$, $P = 1$).

Siblings

When offered the odor of unfamiliar siblings, juveniles entered a shelter as often as in control trials ($n = 120$, $X_1^2 = 0.61$, $P > 0.10$). Those juveniles that entered shelters showed no preference or avoidance of the shelter with odor (Fig. 2).

When offered the odor of familiar siblings, juveniles did not enter the shelters more often than in control trials when both the shelters contained no odor ($n = 122$, $X_1^2 = 0.67$, $P > 0.10$). However those juveniles which entered a shelter significantly more often selected the shelter containing the familiar sibling's odor ($n = 40$, $X_1^2 = 6.11$, $P = 0.013$, Fig. 2). Comparing the trials, there was a not quite significant trend for juveniles to be more attracted by the shelter containing the familiar siblings odor than when the shelter contained odor of unfamiliar unrelated juveniles ($n = 75$, $X_1^2 = 3.62$, $P = 0.057$).

Discussion

The results suggest that juvenile lizards are able to discriminate their mother from other lizards on the basis of olfactory cues alone. Juveniles of both sexes were attracted by the odor of their mother, but not by the odor of an unrelated unfamiliar female. Attraction to the mother's odor was not diminished in juveniles separated from their mother from birth, suggesting pre-natal determination. Juveniles were also attracted by the odor of their siblings, but this attraction vanished if siblings were not reared together, suggesting post-natal determination. Male juveniles were also sensitive to the sex of unrelated unfamiliar adults.

Laboratory results are not always relevant to the field. In our study, a relatively large fraction of juveniles stayed outside the shelters, even when neither shelter contained an odor. Common lizards normally spend the night in a burrow (Stamps 1977), so juveniles which refused to enter the shelters may have been stressed by laboratory conditions. However, stress cannot explain the choices made by juveniles which entered a shelter. Choice of a given shelter was not visit-dependent, since 78 out of the 111 juveniles which were found in a shelter at each of the three visits never moved from one shelter to the other (all experiments pooled).

Response to the odor of unrelated unfamiliar individuals: influence of sex and age

Juveniles did not seem to be influenced by the odor of an unrelated juvenile or an unrelated unfamiliar adult female. However, the odor of an unrelated unfamiliar adult male decreased the probability that juvenile males would enter a shelter.

Table 2 Effect of both the juvenile sex and the rearing condition on the probability to enter a shelter and on the probability to select the shelter containing the odor when the mother's odor is offered. The analyses were performed using logistic regression. Non-significant interaction terms were removed from the analysis. Since only 81 out of 123 juveniles were sexed, we also removed the main effect "juvenile sex" (when non-significant) to test the influence of the rearing condition

Source of deviance	Probability of entering a shelter				Probability of selecting the shelter containing the odor			
	n	*df*	X^2	*P*	*n*	*df*	X^2	*P*
Rearing condition	123	2	3.15	0.21	92	2	3.33	0.19
Sex	81	1	0.45	0.50	61	1	0.26	0.61
Rearing condition × sex	81	2	0.93	0.63	61	2	0.06	0.97

In this species, adult males are usually dominant over subadult males whereas females are less aggressive towards younger individuals of both sexes (Lecomte 1993; Lecomte et al. 1994). In particular, adult males display aggressive behavior towards smaller individuals, when food is offered (authors, personal observations), and males may cannibalize juveniles in captive conditions. The avoidance by juvenile males of shelters with adult male odor may reflect avoidance of adult males by juveniles, which probably results from intrasexual competition. The absence of avoidance of shelter with adult female odor may reflect the low level of agonistic interaction between females and younger individuals. This also suggests that juveniles are able to recognize the sex of adults on olfactory cues alone.

Response to kin's odor: evidence for mother recognition

Juveniles responded positively both to the odor of their mother and to the odor of their siblings. We believe that only the recognition of the mothers has an ecological function. Juveniles of the common lizard are very active as soon as they hatch, so that spatial association of kin declines rapidly in the wild. Because of this, kin discrimination would have to be rapidly formed in order to be functional (Evans 1980; Gubernick 1980; Waldman 1988), and familiarity cannot be a reliable cue to assess kinship.

Self-recognition and species recognition based on chemical cues have been reported in several species of reptiles (Porter and Czaplicki 1974; Cooper and Vitt 1986; Graves and Halpern 1991; Alberts and Werner 1993; Waye and Gregory 1993). If individual odors are genetically based, odors of kin would be more closely related than the odors of non-kin (Grafen 1990), so attraction to kin odors may be a side effect of species recognition and/or of self-recognition. Several considerations led us to think that this is not the case in this species. First, juveniles did not prefer their own odor to the odor of their mother, which is contrary to the prediction of self-recognition. Second, juvenile males avoided the odor of unrelated adult males, and juveniles of both sexes were not attracted to the odor of unrelated females. This is contrary to the prediction of species recognition. We can conclude that juveniles of the common lizard show mother recognition, rather than self-recognition or species recognition.

Advantages of mother recognition when there is no parental care

There are three possible advantages from recognition of parents, even in the absence of parental care, in the common lizard: reduction of cannibalism, selection of optimal habitat, and avoidance of kin competition.

Parent-offspring recognition can reduce aggressiveness or cannibalism of a parent towards its progeny (Linsenmair 1987; Elwood 1991, 1992; Fitzgerald and Whoriskey 1992; de Fraipont et al. 1992) provided that the recognition is reciprocal (Halpin 1981; Holmes and Sherman 1982; Hurst and Barnard 1991). In the common lizard, adult males prey on juveniles when kept together in terraria for a long time (M. Massot, unpublished work). However, cannibalism was reduced in semi-natural enclosures. In addition, in 7 years of study, only 1 adult female out of more than 400 (M. Massot, personal communication) was found to prey on a juvenile which was not her offspring. Cannibalism also does not explain why more juvenile males than females avoid the odor of an adult male.

The odor of the mother can be used to facilitate the establishment of her offspring. This may help juveniles to locate suitable features in the habitat (Graves et al. 1986; Moses and Millar 1994). For example, the odor of the mother may help to locate safe shelters. In this species, several lizards can be found in the same burrow (Massot 1992a), which may indicate that selection of a good refuge for the night is critical.

Finally, the odor of the mother can serve as a cue to stay or leave the natal area. Dispersal is expected to decrease kin competition (Shields 1983; Moore 1992; Ferkin 1990; Ferkin et al. 1992). In the common lizard, juvenile dispersal, which can be as high as 80% (Massot 1992a,b; Massot et al. 1992), occurs shortly after birth (Clobert et al. 1994) and seems mostly determined by the avoidance of kin (Clobert et al. 1994; Massot and Clobert 1995; Léna et al., in press). Mother attraction may serve as the proximal mechanism promoting philopatry and this may explain why a large fraction of juveniles, perhaps potential dispersers, refused to enter the shelter when the odor of their mother was offered.

In conclusion, several functions may favor mother recognition in the absence of parental care. The avoidance of competition or the facilitation of juvenile establishment appears to be the most likely in this species. Further investigations are needed to evaluate their respective roles.

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