

Kin discrimination in the social lizard *Egernia saxatilis* (Scincidae)

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The ability to discriminate kin from nonkin is critical for the evolution of kin-based sociality. Black rock skinks, *Egernia saxatilis*, are viviparous lizards that typically live in “nuclear families” consisting of an adult male, adult female, and one or more cohorts of juveniles. Laboratory trials showed that juvenile lizards can discriminate between the scent of adults from their own social group versus that of unfamiliar adults. Experiments in which we translocated individuals among family groups revealed that this discriminatory ability was based on familiarity with other individuals rather than genetic relatedness. For example, neither “fostered” juveniles nor their mothers displayed any scent-based kin discrimination when brought together after 2 months’ separation. Thus, unlike the closely related (and also social) *Egernia striolata*, black rock skinks base kin discrimination on familiarity rather than genotypic similarity. **Key words:** kin discrimination, Scincidae, sociality. [*Behav Ecol* 17:206–211 (2006)]

Kin recognition (the neural processes involved in the classification of kin) and subsequent kin discrimination (differences in behavioral responses toward kin vs. nonkin: Tang-Martinez, 2001) are essential components of the evolution of “social” behavior (Komdeur and Hatchwell, 1999). If animals have long-term relationships with other specific individuals (e.g., as members of the same social group), we expect selection to favor the ability to quickly and reliably discriminate these familiar individuals from other conspecifics. Indeed, it is difficult to envisage the evolution of family groups, for example, in the absence of such discriminatory ability. The ability of an individual animal to identify genetically related conspecifics and alter its behavior based on this recognition has been documented among an extraordinarily diverse array of animals (e.g., both social, Panek and Gamboa, 2000, and nonsocial insects, Agarwala and Dixon, 1993; Faraji et al., 2000; fish, Arnold, 2000; Fitzgerald and Morrisette, 1992; lizards, Bull et al., 2001; Lena and De Fraipont, 1998; mammals, Heth et al., 1998; Mateo and Johnston, 2000; birds, Shorey et al., 1999; and amphibians, Masters and Forester, 1995; Pfennig et al., 1993).

Two main mechanisms have been proposed as to how individuals determine whether or not conspecifics are related to them. “Recognition by association” occurs when an animal learns the individually distinctive signals of familiar animals around it and treats these as kin, whereas “phenotype matching” is the use of a reference phenotype (either self or kin) against which other individuals are judged (Halpin, 1991). Recognition by association thereby requires individuals to have a period of association with one another before being recognized as kin. Phenotype matching, on the other hand, requires no such period of prior association, with the relatedness of newly encountered individuals being assessed based on how similar they are to the reference phenotype. Further research is required to determine the relative frequencies of phenotype matching versus recognition by association and the situations where each occurs (for further discussion of this issue, see Tang-Martinez, 2001; Todrank and Heth, 2001). The ability of individuals to recognize kin of varying re-

latedness is also expected to vary in different social systems (Pusey and Wolf, 1996), as is the recognition mechanism utilized.

The most robust tests of any theory are provided by comparing results across as wide a range of taxonomic groups as is possible. While there is increasing evidence of the presence of kin recognition mechanisms in reptiles, amphibians, and fish, studies on these taxa to date generally have interpreted this behavior as either a mechanism to avoid eating relatives in cannibalistic species (e.g., Gabor, 1996; Pfennig et al., 1993) or a mechanism to facilitate kin-based aggregation (e.g., Arnold, 2000). Due to the perceived lack of suitable study organisms, previous research on kin discrimination mechanisms in social vertebrates has concentrated on birds and mammals. There have been relatively few studies in other vertebrate taxa examining whether recognition by association or phenotype matching is used in the respective kin discrimination systems. However, recent research has documented a remarkable range of social systems within reptiles (see Clark, 2004; Greene et al., 2002; O'Connor and Shine, 2004) and amphibians (e.g., Gibbons et al., 2003). Reptiles, in particular, offer substantial benefits as study organisms in this field. They are generally easier to catch, house, and use in experiments than mammals and birds. Additionally, the juveniles of almost all mammal and bird species live with their parents when young. Such systems do not allow us to address the more fundamental issue of the evolution of family groups: why did juveniles “originally” start living with their parents? Australian lizards in the *Mabuya* skink lineage are of particular interest in this regard. At least half of the 29 species within the genus *Egernia* show some form of sociality, ranging from mother-offspring associations and short-term pairing by adults to large, long-term, extended family groups (Cogger, 2000; Gardner, 2000; Gardner et al., 2001).

If the type of social system affects mechanisms of kin discrimination, then we would expect to see variation in such mechanisms within *Egernia*. Although kin discrimination in this lineage has so far attracted little scientific attention, there is already evidence of variation in discrimination mechanisms. Vomeronasal cues are used by female sleepy lizards (*Tiliqua rugosa*) and gidgee skinks (*Egernia stokesii*) to recognize their own offspring, albeit possibly based on familiarity rather than genetic cues (Bull et al., 1994; Main and Bull, 1996). In contrast, juvenile tree skinks (*Egernia striolata*) discriminate between individuals using phenotypic similarity, not familiarity (Bull et al., 2001). By comparing the recognition mechanisms

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of closely related species with different social systems (as occurs within the *Egernia* lineage), we can begin to identify the selective forces involved in the evolution of these discrimination systems.

We examined kin recognition in the social lizard *Egernia saxatilis* to determine if kin discrimination was present in this species and, if so, whether discrimination was due to prior association or phenotype matching. To answer these questions we conducted the following trials. (1) Do mothers and juveniles recognize each other's scent? We tested whether juveniles and mothers could discriminate between the scent of their parent/offspring versus scent from an unrelated animal. (2) Is parent-offspring discrimination driven by familiarity or genetic similarity? On finding that juveniles raised with their mothers could discriminate between her scent and that of unrelated females, we tested whether this ability was based on recognition of genetically similar animals or a learned response to familiar individuals.

METHODS

Study species

E. saxatilis is a medium-sized viviparous skink (up to 130-mm snout-vent length [SVL]) that inhabits rocky outcrops throughout southeastern Australia (Cogger, 2000). It lives in groups, with the degree of sociality ranging from solitary animals to large aggregations (up to 13 individuals, including offspring from several cohorts), but it is most commonly found in small territorial "nuclear family" groups (one adult male, one adult female, and their current year's offspring; O'Connor and Shine, 2003). One to four offspring (mean 2.5) are born in late February/early March (unpublished data).

In January 2001, we hand captured 27 adult female *E. saxatilis* thought to be gravid (based on body mass) and an additional 14 males found with them. All animals were collected from Kanangra-Boyd National Park, Blue Mountains, New South Wales (150°0'11"E, 33°3'29"S for more details, see O'Connor and Shine, 2003), brought into the laboratory, and housed in the same groups in which they had been captured. At the completion of observations, all animals were released at their point of capture. Where a family group had been brought into captivity, all group members were released together. Animals were held in captivity for 3–4 months. Based on mass relative to SVL, at the time of their release all animals were in as good, or better, condition as animals in the wild. The sex of juveniles was not determined for this study as it is difficult to do so at such a young age and risks possible injury to the juvenile.

Experimental procedures

While in captivity, all lizards were housed in plastic nally bins (40 cm wide × 62 cm long × 40 cm high), each heated by a 60-W bulb suspended in the center of, and 10 cm above, the bin floor in a temperature-controlled room set at 25°C. Heat lamps came on daily at 0900 h and went off at 1700 h. A constant supply of water was available in the bins, and the lizards were fed three times a week (crickets, cat food, or cockroaches with Rep-Cal calcium and Herptivite dietary supplements added). Gravid females were housed in identical conditions to other lizards, and on giving birth all juveniles remained in their parents' enclosures (except for those used in the "adoption" experiment—see below).

To allow animals to attain their preferred body temperatures before trials commenced, recognition experiments were run in the afternoon between 1200 and 1600 h. Trials

were run in containers identical to those used to house the lizards, in rooms also set at 25°C. In the center of each bin, a basking area was formed by placing a terracotta tile (20 × 20 × 1 cm) on the floor with a heat lamp suspended 10 cm above it. A single test animal was placed in each bin and allowed 10 min to settle down. During this period, scents were obtained from the two scent source animals by running a 2-cm-long cotton wool bud six times along their dorsal surface and six times across their ventral surface (avoiding the cloacal area). These buds, one from a familiar/related animal and one from an unrelated unfamiliar animal, were then placed on the tile, in the middle of the opposite edges of the tile. The buds were held in place using small balls of adhesive (Blutak).

All trials were videotaped for 15 min using an overhead camera. Scoring commenced when a lizard first encountered one of the buds and continued for 10 min. If a lizard did not encounter one of the buds within 5 min, we scored the last 10 min of the trial. Pilot studies indicated that 10 min provided enough time for multiple investigations of each scent source. Scent stimuli were randomly allocated with respect to side on the tile, and the scorer was unaware of which stimulus was in which position. If an animal did not "visit" both scent stimuli during the scoring period, the trial was excluded from analysis (because no comparison of response intensity was possible). Likewise, trials were excluded if the animal moved a cotton bud out of the field of view of the camera (by knocking the bud over or carrying it away).

Individuals were used a maximum of twice in trials as the focal animal. For example, a juvenile that had been "fostered out" was used in a trial to determine if it could determine the scent of its genetic mother and again in a trial to see if it could recognize the scent of its foster mother. Similarly, the scent of that juvenile was used in trials with the two adults as focal animals. In such cases, at least 48 h lapsed between successive trials using the same individual (either as a scent source or as a focal animal). All treatments were run in random order. Equipment was washed with 70% alcohol between experiments.

A visit to a scent occurred when the test animal's head was within 2 cm of the cotton bud. For each visit, we scored:

1. Time—time spent with neck or head within 2 cm of the bud;
2. Tongue flicks—number of times the tongue was flicked in and out within 2 cm of the scent; and
3. Bites—cotton bud taken into the mouth.

For all trials, for an individual to classify as "unfamiliar," it had to be from an outcrop at least 100 m away from the animal that was the focus of the trial (range, 100–5000 m); it is unlikely that these animals had encountered each other previously. All animals used in trials (both test and scent source) were captured at the same time and housed in identical conditions in the laboratory. Given the subpopulation structure of *E. saxatilis* (unpublished data), it is unlikely that any of the unfamiliar animals had a similar genotype to the test animal. Hence, the animals involved were unfamiliar as well as being genetically dissimilar. We conducted trials to answer the following questions.

Do mothers and juveniles recognize each other's scent?

We tested to see if juveniles responded more to the scent of their mothers than to the scent of an unrelated female and tested maternal recognition of offspring scent in a similar fashion. Because unfamiliar animals are also likely to be genetically dissimilar, it is possible that any discrimination in these trials confounds genetic similarity with familiarity. This confounding effect is dealt with in the cross-fostering experiment below.

Is parent-offspring discrimination driven by familiarity or genetic similarity?

As juvenile-mother dyads (above) had had up to 2 months to form bonds and learn to recognize each other, we also conducted a second set of trials where juveniles and mothers were separated within 24 h of birth—the “fostering” manipulation. In this experiment, when two females gave birth to two or more juveniles within a day of each other, then one of the juveniles from each female was reciprocally cross-fostered. This manipulation left these females with one (or more) offspring of their own plus one from another female. If a third offspring was present or no other females gave birth within a day, then one juvenile was placed in a “kindergarten” with other juveniles but no adults. This procedure provided four categories of scents:

1. Related familiar—own offspring “living with mother”;
2. Related unfamiliar—own offspring fostered out (to either another female or the kindergarten);
3. Unrelated familiar—unrelated offspring “fostered in”; and
4. Unrelated unfamiliar—unrelated offspring housed elsewhere (control).

All juveniles were born in captivity in the summer of 2000/2001, separated at birth, and tested 44–62 days later (mean of 51 days). Ten juveniles were fostered out, and 12 were left with their mothers. The 10 juveniles fostered out also comprised the fostered in treatment in regard to recognition of their new foster mothers’ scent.

As the aim of this experiment was to test whether discrimination was via phenotype matching or recognition by association, we cross-fostered offspring to females that had been collected from different outcrops. It is unlikely that any of the foster families were genetically similar to the juveniles that we fostered to them. Thus, if juveniles (and mothers) show similar levels of response to familiar relatives (living with mother treatment) as they do to familiar foster animals (fostered in) and no difference in response to an unfamiliar but related individual (fostered out treatment) as compared to the control lizards (unfamiliar, unrelated), then phenotype matching cannot be invoked as a basis for any observed kin discrimination.

At the same time as the fostering experiment, we had 11 juveniles living in captivity with both parents. These were included in the above trials as living with mother. We also used these juveniles to test kin discrimination by, and of, adult males in the group.

Both diet and local environment can influence an individual’s scent (Schellinck et al., 1997). To remove these possible confounding influences, all animals were housed in the same environment and fed the same food for 2–3 months prior to the experiments.

All animals were released at their original point of capture on completion of the trials. Where juveniles had been fostered out, these were released adjacent to their mother’s original point of capture (at the same time as their mother was released nearby), thus maintaining the genetic structuring of the population while reducing the possibility of parental aggression toward unfamiliar offspring.

Statistical analysis

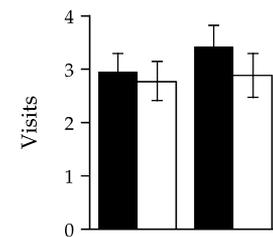
Data were nonnormally distributed and thus were analyzed nonparametrically. Analyses were corrected for ties and run in Systat 9.0 (SPSS, 1998) or Statview 5.0 (SAS Institute, 1998).

RESULTS

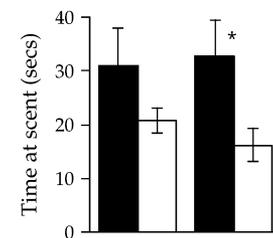
Do juveniles discriminate between scent of their mothers versus scent from unrelated females?

Combining the “related familiar” and “related unfamiliar” treatments, we found no indication that offspring discrimi-

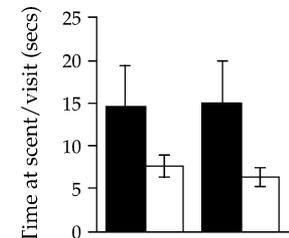
a) Average number of visits to each scent



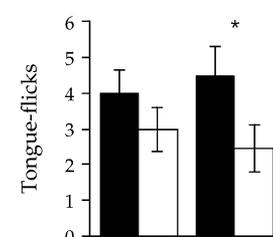
b) Total time spent at scents



c) Time at scent per visit



d) Tongue-flicks per trial



e) Tongue-flicks per visit

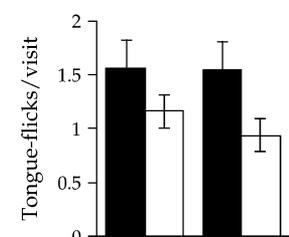


Figure 1

Responses (mean \pm SE) of juvenile black rock skinks (*E. saxatilis*) in the “Mother” and “Familiar” trials. “Mother” trials ($n = 34$) compare the response of juveniles to the scents of their birth mother (both familiar and unfamiliar) with that towards unfamiliar unrelated females, while the “Familiar” trials ($n = 32$) disregard the actual relatedness of the female-offspring dyads and simply compares the juveniles’ response to familiar adult females and unfamiliar females. Note: standard errors are presented for informational purposes only. All statistical analyses reported in the text are non-parametric (significant differences are indicated with an *).

nated between their own mother’s scent and that of an unrelated female (Wilcoxon signed-rank: $n = 34$, all nonsignificant; Figure 1). This result was not affected by whether or not the juvenile was living with its mother.

Do juveniles discriminate between scent from familiar females versus that from unfamiliar females?

Testing offspring that were familiar with an adult female’s scent regardless of relatedness (i.e., combining the related familiar and “unrelated familiar” treatments), offspring visited the scents of familiar and unfamiliar females equally (Wilcoxon signed-rank: $Z = 1.60$, $p = .11$, $n = 32$; Figure 1) but spent more time at the scent of the familiar female ($Z = 2.48$, $p = .013$, $n = 32$; time per visit: $Z = 1.90$, $p = .057$, $n = 32$; Figure 1) and tongue flicked this scent more often ($Z = 2.349$,

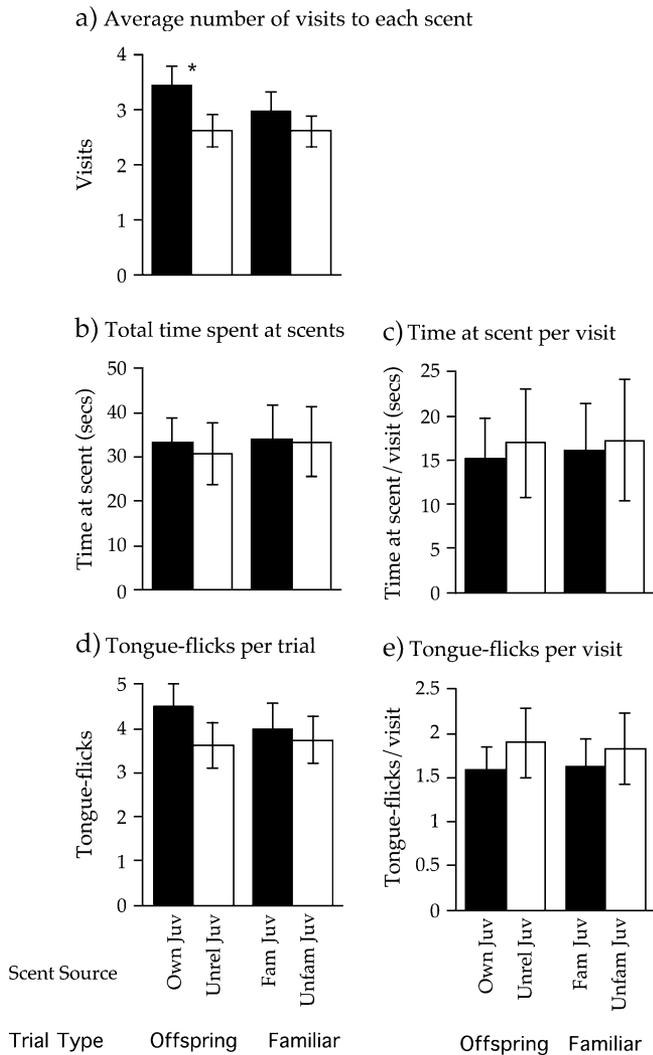


Figure 2
Responses (mean ± SE) of adult female black rock skinks (*E. saxatilis*) in the “Offspring” and “Familiar” trials. “Offspring” trials ($n = 41$) compare the response of adult females to the scents of their own offspring (both familiar and unfamiliar) with that towards unrelated unfamiliar unrelated juveniles (Unrel Juv), while the “Familiar” trials ($n = 35$) disregard the actual relatedness of the female-offspring dyads and simply compares the adult females’ response to familiar juveniles (Fam Juv) and unfamiliar juveniles (Unfam Juv). Note: standard errors are presented for informational purposes only. All statistical analyses reported in the text are non-parametric (significant differences are indicated with an *).

$p = .019$, $n = 32$; flicks per visit: $Z = 1.67$, $p = .095$, $n = 32$; Figure 1). There was no difference in this respect between familiar females based on actual maternity (i.e., genetic mothers vs. foster mothers; all comparisons nonsignificant).

Do mothers discriminate between the scent of their own offspring versus scent from unrelated offspring?

Females visited the scent from their own offspring more often than the scent from an unrelated unfamiliar juvenile (Wilcoxon signed-rank: $Z = -2.56$, $p = .011$, $n = 41$; Figure 2). The results were similar regardless of whether the juvenile was familiar or not (living with mother: $Z = -1.78$, $p = .076$, $n = 24$; fostered out: $Z = -1.94$, $p = .052$, $n = 17$; Figure 2). All other comparisons were nonsignificant.

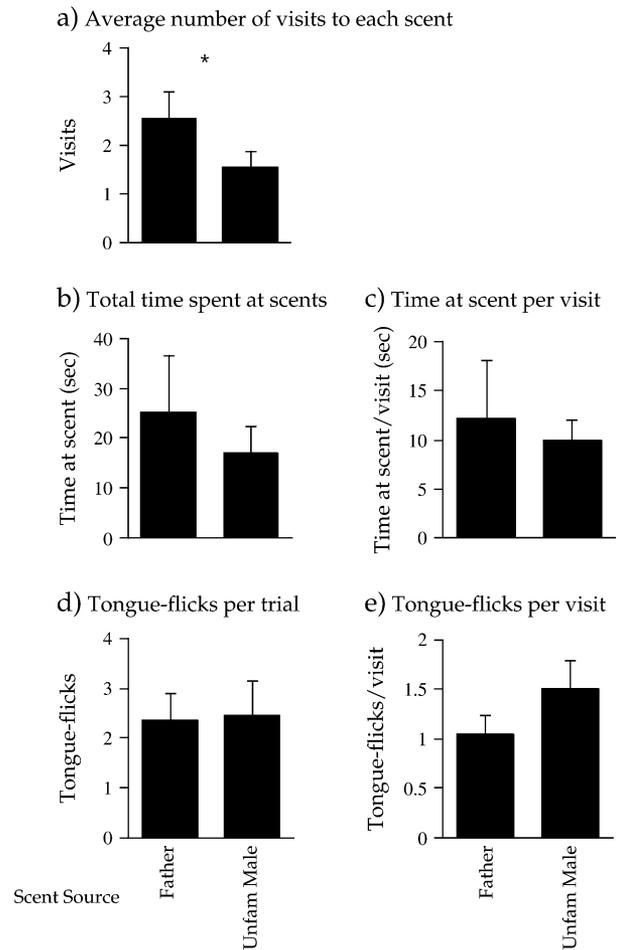


Figure 3
Mean responses of juvenile black rock skinks (*E. saxatilis*) to the scent of their genetic father versus that of an unfamiliar male ($n = 11$; mean ± SE). Note: standard errors are presented for informational purposes only. All statistical analyses reported in the text are non-parametric (significant differences are indicated with an *).

Do mothers discriminate between the scent of a familiar juvenile versus scent from an unfamiliar juvenile?

There was no significant difference in any behavior in any treatment between that shown toward scent from a familiar juvenile and toward scent from a control juvenile (Figure 2).

Do juveniles discriminate between the scent of their fathers versus that from unrelated males?

Juveniles visited the scent of their father more often (Wilcoxon signed-rank: $Z = -2.06$, $p = .04$, $n = 11$; Figure 3), and tongue flicks per visit approached significance ($Z = -1.90$, $p = .058$, $n = 11$; Figure 3). All other comparisons were nonsignificant.

Do fathers discriminate between the scent of their offspring and scent from unrelated juveniles?

Adult males showed no differences in their responses to the scent of their offspring versus that of control juveniles (Figure 4).

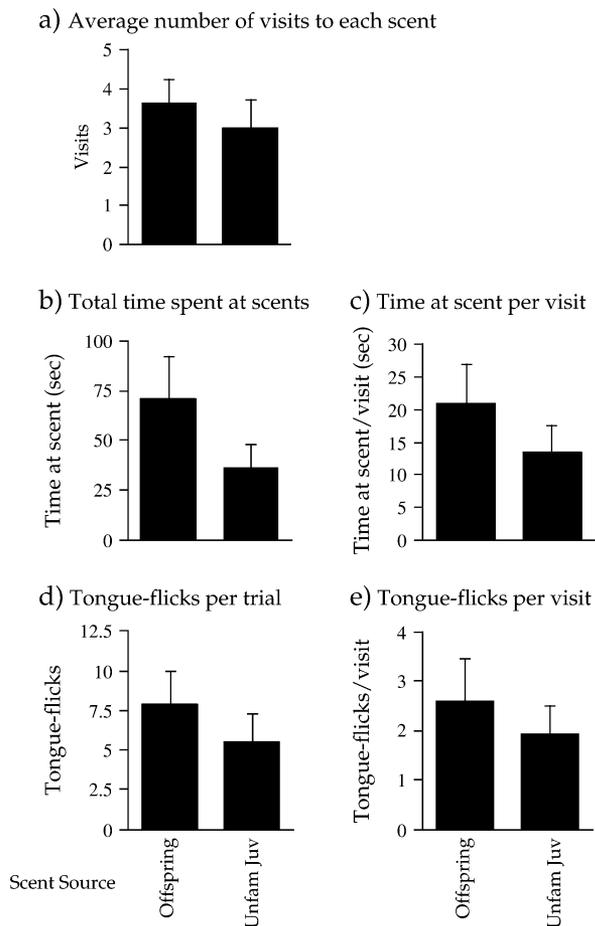


Figure 4
Mean responses of adult male black rock skinks (*E. saxatilis*) to the scent of their own offspring versus that of an unfamiliar juvenile ($n = 11$; mean \pm SE). Note: standard errors are presented for informational purposes only. All statistical analyses reported in the text are non-parametric (none of the responses in Figure 4 are statistically different).

DISCUSSION

Using scent alone, juvenile *E. saxatilis* were able to discriminate between the scent of adults from their own family group and scent from unfamiliar unrelated adults. Juveniles did not discriminate between the scent of their unfamiliar biological mother and that of a control female. They did, however, distinguish the scent of familiar females (whether their biological mother or unrelated) from that of other females. Juveniles also discriminated between the scent of their familiar biological father and that of an unfamiliar, unrelated adult male. Thus, juvenile black rock skinks use recognition by association to distinguish kin from nonkin.

Our field and laboratory studies on *E. saxatilis* suggest that such an ability to distinguish between kin and nonkin (especially, for juveniles to recognize their own parents) would confer substantial fitness advantages in this species. Juvenile black rock skinks are the focus of adult aggression throughout the year. This aggression is so intense that it may have been a major selective force for sociality within the species (O'Connor and Shine, 2004). In laboratory trials, the presence of a related adult significantly reduced the amount of aggression directed against the juvenile by an unfamiliar adult (O'Connor and Shine, 2004). Under this scenario, there would be strong

selection on the ability of juveniles to avoid contact with unfamiliar (and thus unfriendly) adults and stay within their parents' territorial boundaries.

In species where adults commit infanticide, as occurs in *E. saxatilis*, we expect strong selection for kin discrimination by adults (e.g., Joseph et al., 1999; Pfennig et al., 1999). In contrast, we documented only one significant difference (number of visits) in the responses of adults to the scent of their offspring (whether familiar or not) versus that of unrelated juveniles. This apparent lack of discrimination by adults toward offspring is surprising, given the presence of parental care in *E. saxatilis*. For parents to care only for their own offspring, they must have some method of identifying these offspring. *E. saxatilis* provides indirect care for its offspring by allowing them to remain within the parental territory (O'Connor and Shine, 2004). The scarcity of unrelated offspring in the parental territory and high aggression, including infanticide, shown by adults toward juveniles other than their own (O'Connor and Shine, 2004) indicate some mechanism of group recognition, though not one detected in this study. It is important to emphasize that a lack of discrimination, such as that found in our study, does not necessarily mean a lack of recognition: simply that recognition was not detected using our methodology.

Where the costs of making errors in recognizing kin are high, kin recognition by phenotype matching is unlikely to evolve (Keller, 1997; Reeve, 1989). As a result of access to higher quality resources and protection from conspecific aggression, juvenile *E. saxatilis* living within parental territories are likely to have higher fitness than those living outside parental territories (O'Connor DE and Shine R, unpublished data). Therefore, in *E. saxatilis*, if the inclusive fitness cost of excluding kin from the territory is high and the confidence in paternity is also high, then recognition by association is likely to offer a more reliable method for kin recognition than would phenotype matching. Although our study found no evidence for phenotype matching within *E. saxatilis*, it should also be noted that we did not explicitly test for this among familiar animals. That is, we did not test whether individuals could determine familiar kin from familiar nonkin. Although recognition using indirect indicators such as spatial and temporal cues has been proposed in other systems, these are unlikely to apply to black rock skinks. Field observations have confirmed that nongroup members travel through the territories of social groups, and the physical boundaries of the territories fluctuate. Use of indirect cues in such a system would result in a continual shifting of group membership.

Because *E. saxatilis* appears to recognize kin based on prior association rather than phenotype matching, the results of our study contrast with those from research on the closely related species *E. striolata*. A study by Bull et al. (2001) concluded that *E. striolata* recognize their kin based on phenotype recognition. The precise social system of *E. striolata* is currently unclear: this species is mainly solitary in some parts of its range (Bustard, 1970) but found in social groups in others (Bonnett, 1999). In saxicoline habitats, *E. striolata* appears to have a similar social system to that of *E. saxatilis* (personal observation). The two taxa are morphologically very similar and probably sister species (reviewed in Chapple, 2003). Why then do they apparently use different systems to recognize related conspecifics? The answer may lie in different experimental designs rather than species divergence per se. We presented *E. saxatilis* with a mixture of either familiar or unfamiliar animals, whereas Bull et al. (2001) presented *E. striolata* with a range of individuals that were all unfamiliar but differed in their degree of genetic similarity to the focal animal. If kin recognition in these species is context dependent, these differing designs might have revealed different

results. That is, both species may be able to use both mechanisms, with the two studies differing in which type of kin discrimination system is most powerfully detectable. Regardless, our study tested lizards against cues that mimic those in the natural environment; and in the *E. saxatilis* system at least (where the fragmented habitat results in high within-outcrop relatedness; O'Connor, 2003), familiarity may provide a more reliable signal of relatedness than would phenotype matching alone.

Clearly, it would be useful to resolve the apparent difference in kin recognition mechanisms utilized by *E. striolata* and *E. saxatilis*, by applying the same methods to studies of both taxa. More generally, species within the *Egernia* lineage provide ideal opportunities for further research into the relationship between social systems and kin recognition mechanisms. Contrasting the kin recognition mechanisms of social reptiles with those of other social animals (both vertebrate and invertebrate) will also provide further insight into the evolution of this widespread behavior.

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REFERENCES

- Agarwala BK, Dixon AFG, 1993. Kin recognition: egg and larval cannibalism in *Adalia bipunctata* (Coleoptera: Coccinellidae). *Eur J Entomol* 90:45–50.
- Arnold KE, 2000. Kin recognition in rainbowfish (*Melanotaenia eachamensis*): sex, sibs and shoaling. *Behav Ecol Sociobiol* 48:385–391.
- Bonnett M, 1999. The ecology, behaviour and genetic relationships of a population of *Egernia striolata* (Honours thesis). Adelaide: Flinders University of South Australia.
- Bull CM, Doherty M, Schulze LR, Pamula Y, 1994. Recognition of offspring by females of the Australian skink, *Tiliqua rugosa*. *J Herpetol* 28:117–120.
- Bull CM, Griffin CL, Bonnett M, Gardner MG, Cooper SJB, 2001. Discrimination between related and unrelated individuals in the Australian lizard *Egernia striolata*. *Behav Ecol Sociobiol* 50:173–179.
- Bustard HR, 1970. A population study of the scincid lizard *Egernia striolata* in northern New South Wales. I. *Proc K Ned Akad Wet* 73:186–213.
- Chapple D, 2003. The evolution of complex sociality in reptiles: a review of ecology, life-history and behavior in the Australian scincid genus *Egernia*. *Herpetol Monogr* 17:145–180.
- Clark RW, 2004. Kin recognition in rattlesnakes. *Proc R Soc Lond B* 271 (suppl.):243–245.
- Cogger HG, 2000. Reptiles and amphibians of Australia, 6th ed. Frenchs Forest: Reed New Holland.
- Faraji F, Janssen A, Van Rijn PC, Sabelis MW, 2000. Kin recognition by the predatory mite *Iphiseius degenerans*: discrimination among own, conspecific, and heterospecific eggs. *Ecol Entomol* 25:147–155.
- Fitzgerald GJ, Morrissette J, 1992. Kin recognition and choice of shoal mates by threespine sticklebacks. *Ethol Ecol Evol* 4:273–283.
- Gabor CR, 1996. Differential kin discrimination by red-spotted newts (*Notophthalmus viridescens*) and smooth newts (*Triturus vulgaris*). *Ethology* 102:649–659.
- Gardner M, 2000. A genetic investigation of sociality in the Australian group living lizard, *Egernia stokesii* (PhD dissertation). Adelaide: Flinders University of South Australia.
- Gardner MG, Bull CM, Cooper SJB, Duffield GA, 2001. Genetic evidence for a family structure in stable social aggregations of the Australian lizard *Egernia stokesii*. *Mol Ecol* 10:175–183.
- Gibbons ME, Ferguson AM, Lee DR, Jaeger RG, 2003. Mother-offspring discrimination in the red-backed salamander may be context dependent. *Herpetologica* 59:322–333.
- Greene HW, May PG, Hardy DL, Sciturro JM, Farrell TM, 2002. Parental behavior in vipers. In: *Biology of the pitvipers* (Schuett GW, Höggren M, Douglas ME, Greene HW, eds). Eagle Mountain, Utah: Eagle Mountain Publishing; 179–205.
- Halpin Z, 1991. Kin recognition cues of vertebrates. In: *Kin recognition* (Hepper P, ed). Cambridge: Cambridge University Press; 220–258.
- Heth G, Todrank J, Johnston RE, 1998. Kin recognition in golden hamsters: evidence for phenotype matching. *Anim Behav* 56:409–417.
- Joseph SB, Snyder WE, Moore AJ, 1999. Cannibalizing *Harmonia axyridis* (Coleoptera: Coccinellidae) larvae use endogenous cues to avoid eating relatives. *J Evol Biol* 12:792–797.
- Keller L, 1997. Indiscriminate altruism: unduly nice parents and siblings. *Trends Ecol Evol* 12:99–103.
- Komdeur J, Hatchwell B, 1999. Kin recognition: function and mechanism in avian societies. *Trends Ecol Evol* 14:237–241.
- Lena J-P, De Fraipont M, 1998. Kin recognition in the common lizard. *Behav Ecol Sociobiol* 42:341–347.
- Main AR, Bull CM, 1996. Mother-offspring recognition in two Australian lizards, *Tiliqua rugosa* and *Egernia stokesii*. *Anim Behav* 52:193–200.
- Masters BS, Forester DC, 1995. Kin recognition in a brooding salamander. *Proc R Soc Lond B* 261:43–48.
- Mateo JM, Johnston RE, 2000. Kin recognition and the 'armpit effect': evidence of self-referent phenotype matching. *Proc R Soc Lond B* 267:695–700.
- O'Connor D, 2003. The evolution of sociality in the black rock skink, *Egernia saxatilis* (PhD dissertation). Sydney: University of Sydney.
- O'Connor D, Shine R, 2003. Lizards in 'nuclear families': a novel reptilian social system in *Egernia saxatilis* (Scincidae). *Mol Ecol* 12:743–752.
- O'Connor D, Shine R, 2004. Parental care protects against infanticide in the lizard *Egernia saxatilis* (Scincidae). *Anim Behav* 68:1361–1369.
- Panek LM, Gamboa GJ, 2000. Queens of the paper wasp *Polistes fuscatus* (Hymenoptera: Vespidae) discriminate among larvae on the basis of relatedness. *Ethology* 106:159–170.
- Pfennig D, Collins J, Ziemba R, 1999. A test of alternative hypotheses for kin recognition in cannibalistic tiger salamanders. *Behav Ecol* 10:436–443.
- Pfennig DW, Reeve HK, Sherman PW, 1993. Kin recognition and cannibalism in spadefoot toad tadpoles. *Anim Behav* 46:87–94.
- Pusey A, Wolf M, 1996. Inbreeding avoidance in animals. *Trends Ecol Evol* 11:201–206.
- Reeve HK, 1989. The evolution of conspecific acceptance thresholds. *Am Nat* 133:407–435.
- SAS Institute, 1998. Statview 5.0. Cary, North Carolina: SAS Institute.
- Schellinck HM, Slotnick BM, Brown RE, 1997. Odors of individuality originating from the major histocompatibility complex are masked by diet cues in the urine of rats. *Anim Learn Behav* 25:193–199.
- Shorey L, Piertney S, Stone J, Hoglund J, 1999. Fine-scale genetic structuring on *Manacus manacus* leks. *Nature* 408:352–353.
- SPSS, 1998. Systat 9.0. Chicago, Illinois: SPSS Inc.
- Tang-Martinez Z, 2001. The mechanisms of kin discrimination and the evolution of kin recognition in vertebrates: a critical re-evaluation. *Behav Process* 53:21–40.
- Todrank J, Heth G, 2001. Rethinking cross-fostering designs for studying kin recognition mechanisms. *Anim Behav* 61:503–505.