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Mother–offspring recognition in two Australian lizards, *Tiliqua rugosa* and *Egernia stokesii*

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Abstract. Kin recognition has been reported in many animal taxa, but rarely in lizards. Newly born clutches from two viviparous Australian skink species, *Tiliqua rugosa* and *Egernia stokesii*, were either left with their mothers, separated at birth and kept with a foster mother, or kept completely isolated from any adults. In experimental trials mothers were presented with their own and with non-related young in gauze bags, and their attention to each young lizard was measured by the number of directed tongue flicks and the time in contact. There was a consistent tendency in both species for mothers to direct more attention to their own young, whether they had been kept together or apart. Foster mothers directed more attention to their own non-familiar young than to their familiar foster young. In reciprocal experiments, young lizards of both species consistently directed more attention to their own mothers than to unrelated females, even when they had been isolated from their mothers from birth. Olfactory cues are probably important for recognition. Using these cues, lizards can recognize kin, and discriminate between kin and non-kin even if the latter have been in close association. It was not possible to determine if the discrimination was genetically based, or if it was acquired during or shortly after birth. The presence of mother–offspring recognition suggests that family groups may be a component in the social organization of these species.

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Mother–offspring recognition is one form of kin recognition. Kin recognition is the ability of individuals to discriminate between kin and non-kin, and it contributes to the social structure and organization of an animal population. Recognition and association with related individuals is advantageous for parental care and for group breeding. Recognition and avoidance of related individuals is advantageous for outbreeding and to reduce kin competition. Kin recognition is a widely reported phenomenon among the higher vertebrates (Hepper 1986; Fletcher & Michener 1987). Among lower vertebrates, it has been reported in species of amphibia (Blaustein & Waldman 1992) and fish (Winburg & Olsén 1992; Moore et al. 1994), but seldom among reptiles (Werner et al. 1987). This has led to a common perception that one group of reptiles, the lizards, have simple social structures relative to other vertebrates (Bull 1994). There are few accounts of lizards with a social organization beyond territoriality (Stamps 1983).

There has been one, unsuccessful attempt to detect mother–offspring recognition in lizards (Vitt & Cooper 1989). Furthermore, beyond egg brooding (Noble & Mason 1933; Hasegawa 1985; Vitt & Cooper 1989), and assisting young to escape embryonic membranes (Cowles 1944), there are no records of maternal care of young for lizards. Troyer (1982) reported that young iguanas, *Iguana iguana*, associated with adults, and ingested adult faeces to aid digestion of their herbivorous diets, but those adults were not established to be parents. Thus there is little in the literature to suggest either mother–offspring recognition, or the parental behaviour that would require it, among lizard species. This is surprising, because adult lizards have the ability to discriminate between conspecific individuals using undetermined cues (Glinsky & Krekorian 1985), femoral pore secretions (Alberts 1990, 1991;

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Alberts & Werner 1993), cloacal glands (Cooper et al. 1986), faeces (Carpenter & Duvall 1995), or skin secretions (Graves & Halpern 1991). It has been suggested that more complex social relationships, including the recognition and association of mothers and young, may be more likely in those lizard species with relatively long lives and delayed maturity (Bull 1994). Furthermore, social groupings and associated interactions are more likely in non-territorial species (Stamps 1983).

We investigated mother–offspring recognition in two viviparous Australian skinks (*Tiliqua rugosa* and *Egernia stokesii*). Both are long lived, up to 30 years in *T. rugosa* (Bull 1995) and up to 25 years in *E. stokesii* (Swan 1990), and take at least 2 years to reach maturity (Greer 1989; Hutchinson 1993). *Tiliqua rugosa* live in overlapping home ranges (Bull 1978, 1987; Satrawaha & Bull 1981), and demonstrate long-term pair fidelity, a component of social structuring previously unreported in lizards (Bull 1988, 1994). *Egernia stokesii* have been reported to live in groups which share rock crevice refuges, and which are suspected to be family units (Greer 1989; Swan 1990; Hutchinson 1993).

Previous experiments with *T. rugosa* (Bull et al. 1994) showed that mothers kept with their clutches directed more attention to their own young than to non-related, non-familiar young. In this paper we expand the investigation to show that *T. rugosa* offspring also recognize their mothers, that this recognition does not depend on the young being kept with their mothers, and that the same abilities are shown by *E. stokesii*. These results substantially increase the repertoire of social behaviour reported in lizards.

METHODS

We collected gravid females, of unknown age, from near Mt Mary (34°06′S; 139°26′E) (*T. rugosa*) and near Hawker (31°54′S; 138°25′E) (*E. stokesii*), South Australia, between December 1993 and February 1994. We housed them outside until February (*E. stokesii*) or March (*T. rugosa*) 1994, then brought them inside into individual glass terraria (75 × 40 × 35 cm) in a room at 25°C with a 12:12 h photoperiod. Light globes (60 W), suspended above each terrarium, were turned on from 0900 to 1600 hours each day, and lizards basking under them were able to maintain body temperatures of 30–35°C. We provided permanent water in plastic petri dishes, and, on alternate days, a varied diet of mealworms, canned dog food and fresh, chopped fruit and vegetables. We lined the sides of the terraria with paper to maintain visual isolation. The terraria were cleaned twice each week and fresh paper substrate was provided. Three out of 117 lizards died during the study.

As females started to produce clutches, we checked them twice daily. Between 18 February and 30 March 1994, 53 young *E. stokesii* were produced by 12 females in clutches of two to seven. Between 22 March and 26 April 1994, 37 young *T. rugosa* were produced by 15 females in clutches of one to five. All births occurred in the light phase, after the heating lamps were on, but the actual time of birth varied between females.

We treated clutches in one of three ways. For *T. rugosa* there was a control group of five clutches in which we left the young with their natural mothers. In a second group of six clutches we removed the young from their mother immediately after birth, and placed them with a foster mother. In practice, we swapped clutches between three pairs of mothers. In the third group of four clutches we kept the young isolated from both their mothers and all other adults from birth. For *E. stokesii* we applied the same three treatments, with five control clutches kept with their mothers, four clutches cross-fostered, and three clutches isolated. Mortality reduced the cross-fostering treatment to two clutches in *E. stokesii*, but apart from that, growth and survival of the young did not differ between treatments for either species. Although the treatment design was to remove young from their mother immediately after birth, in practice we left some individual young with their mothers for several minutes up to 2 h before separation.

We conducted trials in a separate 25°C room, under artificial light, between 0900 and 1500 hours. Prior to each trial, each lizard was held in a separate heating tank (40 × 20 × 15 cm) under a 200 W light globe for 15 min. Preliminary results showed this was sufficient time to raise the body temperature of all lizards to the 30–35°C range. In each trial we recorded the responses of one lizard, the subject lizard. The subject lizard was placed in an experimental terrarium (75 × 30 × 35 cm). A 150 W light globe suspended 20 cm above the centre of the terrarium allowed lizards to maintain body temperatures. Three sides of the terrarium were lined with white paper to eliminate external visual cues. The fourth side also had white paper around a 30 × 30 cm section of one-way mirror, which allowed observation without disturbing the subject lizard. Before each trial we cleaned the terrarium with 95% ethyl alcohol, rinsed it with distilled water, and provided it with a fresh newspaper substrate.

We left the subject lizard undisturbed in this terrarium for 10 min. Then we lowered two gauze bags into the terrarium, 10 cm apart, to a position 10 cm from the nose of the subject lizard. They were suspended by nylon fishing line from a wooden rod, which rested on the top of the terrarium. The bags contained the other two lizards, the test lizards. Usually one bag contained a test lizard related to the subject lizard, while the other bag contained a test lizard unrelated to the subject lizard. In each trial we determined the side on which the related test lizard was placed by random coin toss. Bags were cleaned in 95% ethyl alcohol, detergent and distilled water, and then dried before use in a trial.

After we had lowered the bags into the terrarium, we observed the subject lizard for the next 10 min through the one-way mirror, and recorded the number of tongue flicks it directed towards each bag. For a directed tongue flick, the subject lizard had to be facing the bag, and the tongue flick had to come to within 5 cm of the bag. Lizards also made many undirected tongue flicks during trials. In some trials, the subject lizard moved to a bag and lay alongside it, or curled its body around it. We also recorded the amount of time during the 10-min observation that a subject lizard spent exclusively in contact with each bag. At the end of the trial we measured the body temperature of each lizard with a cloacal probe. If any lizards in the trial were below 30°C at this time, we abandoned the results from that trial.

For each of the two species, we ran six sets of trials, three investigating the response of mothers to young, and three investigating the response of young to mothers. The three trials per age class represented the three experimental treatments. For mothers, the first set of subject lizards were females that had remained with their own clutch. The test lizards were their own young (familiar, related) and from a different clutch (unfamiliar, unrelated). The second set of subject lizards were the females with cross-fostered clutches. The test lizards were their own young (unfamiliar, related) and their fostered young (familiar, unrelated). The third set of subject lizards were the females that we had kept isolated from any clutches. They were tested with their own young (unfamiliar, related) and young from another clutch (unfamiliar, unrelated).

We ran reciprocal trials where the subject lizards were the offspring. Those that had been kept with their mothers had their mother and an unrelated female as test lizards. Cross-fostered young were tested with their real and their foster mother. Isolated young were tested with their real but unfamiliar mother, and an unrelated female.

We conducted trials in random order over 5 months (April–September 1994). We usually used individual lizards less than once per week in trials, and never more than twice per week. Each individual female was the subject lizard in 1–10 trials. Each individual offspring was the subject lizard in one or two trials. Replicates with individuals were to allow for variable responses. In the analysis, where an individual was the subject lizard in more than one trial, we used the average response of that individual over all of its trials, to avoid pseudoreplication.

We used analyses of variance to compare the responses (number of directed tongue flicks, time in contact) of the subject lizards to the two test lizards in the different experimental treatments. Repeated measures ANOVAs were used, because each subject lizard was responding to two test lizards, so the responses were not independent. We organized the data for analysis in two ways. First, the data from all three treatments were classified according to whether the subject lizard was responding to a related or to an unrelated test lizard. Second, the data from the first two experimental treatments were classified according to whether the subject lizard was responding to a familiar or an unfamiliar test lizard. We omitted the third treatment in this case, because neither test lizard was familiar.

When analysing the responses of young lizards to related and unrelated females we also pooled all young from a clutch and used the average response from each clutch in the analysis. We took results consistent with those from analyses with individual young to imply that there was no clutch bias in the behaviour. A clutch bias may have arisen because more young were tested from some clutches than from others.

Table I. Responses of female *Tiliqua rugosa* to young

Treatment	*N*	Tongue flicks	Time in contact
1 Related	5	5.23 (1.42)	1.25 (0.60)
Unrelated	5	1.27 (0.64)	0.30 (0.26)
2 Related	6	7.06 (2.29)	1.70 (0.65)
Unrelated	6	4.92 (0.70)	0.86 (0.37)
3 Related	4	5.50 (2.37)	0.44 (0.31)
Unrelated	4	2.21 (0.96)	0.16 (0.09)

Mean responses (SE) to related and unrelated young in the three treatments measured by the number of tongue flicks directed towards young and the time (min) in contact with young during a 10-min trial. Treatment 1: young were raised with their mother; treatment 2: young were raised with a foster mother; treatment 3: young were separated from their mother and raised without a female. In treatment 2 the non-related young are the foster young of the females.

Table II. Responses of female *Egernia stokesii* to young

Treatment	*N*	Tongue flicks	Time in contact
1 Related	5	4.90 (1.67)	0.37 (0.14)
Unrelated	5	1.41 (0.66)	0.14 (0.11)
2 Related	2	4.20 (1.20)	0.26 (0.03)
Unrelated	2	1.75 (0.55)	0.06 (0.06)
3 Related	3	6.25 (0.24)	0.73 (0.14)
Unrelated	3	2.08 (0.49)	0.18 (0.05)

Data presented as in Table I.

Table III. Responses of young *Tiliqua rugosa* to females

Treatment	*N*	Tongue flicks	Time in contact
1 Related	7	18.79 (6.92)	1.88 (0.72)
Unrelated	7	11.57 (3.66)	0.93 (0.32)
2 Related	10	14.80 (5.71)	0.42 (0.19)
Unrelated	10	14.80 (5.38)	0.24 (0.13)
3 Related	9	13.44 (4.09)	0.94 (0.59)
Unrelated	9	7.56 (3.39)	0.19 (0.16)

Data presented as in Table I. In treatment 2 the non-related females are the foster mothers of the young.

We returned the females and their offspring to the field in October 1994.

RESULTS

Female Response to Young in *T. rugosa*

Table I shows the responses of female *T. rugosa* to young in each treatment. The repeated measures ANOVAs considering related versus non-related offspring showed no effect of treatment, but significantly more tongue flicks towards related than non-related young ($F_{1,12}=11.82$, $P=0.005$). There were no interaction effects, indicating the difference was consistent over all treatments. Although the trend was similar with time in contact, there were no significant effects. When the data were rearranged to compare responses to familiar versus non-familiar offspring in treatments 1 and 2, the analyses showed no overall difference between treatments, or between responses to familiar and non-familiar young, but a significant interaction effect ($F_{1,9}=7.78$, $P=0.020$) as a result of females tongue flicking more to familiar young in treatment 1, and to non-familiar young in treatment 2.

Female Response to Young in *E. stokesii*

Table II shows the responses of female *E. stokesii* to young in each treatment. The analyses considering related versus non-related offspring showed no overall effect of treatment, but significantly more tongue flicks towards ($F_{1,12}=20.25$, $P=0.003$), and significantly more time in contact with ($F_{1,12}=12.33$, $P=0.010$), related than non-related young. There were no interaction effects, again indicating the differences were consistent over all treatments. Analyses to compare responses to familiar and non-familiar young in treatments 1 and 2 showed no significant effects, although the small sample size for treatment 2 reduced the power of this test.

Young Response to Females in *T. rugosa*

Table III shows the responses of young *T. rugosa* to females in each treatment. When comparing responses to related or non-related females, there were no differences between treatments. Young spent significantly more time with related females (their natural mothers) than with non-related females ($F_{1,23}=5.75$, $P=0.025$), and there were no interaction effects, implying the responses were consistent over all treatments.

Table IV. Responses of young *Egernia stokesii* to females

Treatment		N	Tongue flicks	Time in contact
1	Related	9	10.78 (3.42)	0.45 (0.18)
	Unrelated	9	5.22 (1.64)	0.17 (0.07)
2	Related	10	16.90 (3.89)	0.51 (0.22)
	Unrelated	10	10.70 (2.59)	0.96 (0.83)
3	Related	10	13.10 (2.79)	0.68 (0.95)
	Unrelated	10	5.70 (1.81)	0.21 (0.12)

Data presented as in Table III.

When clutch data were pooled, the overall average time that young spent in contact with related females ($\bar{X} \pm \mathrm{SE} = 0.81 \pm 0.42$ min) was higher than with unrelated females (0.21 ± 0.17 min), but the difference was not quite significant ($F_{1,9}=4.30$, $P=0.068$). No other effects or interactions were significant ($P>0.20$) in the analyses of responses to related and unrelated females using pooled clutch data.

Responses to familiar and non-familiar females in treatments 1 and 2 showed a significant effect of treatment on time in contact ($F_{1,15}=6.42$, $P=0.023$). Young from treatment 1 (controls) spent more time in contact with females than those from treatment 2 (cross-fostered). There were no overall differences in responses to familiar and non-familiar females, but there was a significant interaction effect ($F_{1,15}=4.85$, $P=0.044$). Young spent more time in contact with familiar females in treatment 1 and with non-familiar females in treatment 2. In both cases those females were their natural mothers.

Young Response to Females in *E. stokesii*

Table IV shows the response of young *E. stokesii* to females in each treatment. Comparing responses to related and non-related females, the young tongue flicked significantly more to their natural mothers than to other females ($F_{1,26}=14.40$, $P<0.001$). There were no differences between treatments, nor any interaction effects. There was a consistent result from the analysis with data pooled from within clutches. Overall average tongue flicks were significantly higher to related females ($\bar{X} \pm \mathrm{SE} = 14.22 \pm 1.29$) than to unrelated females (7.58 ± 0.93; $F_{1,6}=38.72$, $P<0.001$).

The analysis comparing responses to familiar and non-familiar females showed no differences between treatments 1 and 2, no differences between familiar and non-familiar females, and a significant interaction effect for number of tongue flicks ($F_{1,17}=5.94$, $P=0.026$). More were directed towards the familiar female in treatment 1, and towards the non-familiar female in treatment 2. Again in both cases those females were the natural mothers. The analyses of time in contact showed no significant effects.

DISCUSSION

The data show a trend for both mothers and offspring to discriminate between related and non-related individuals. In all four cases there was a trend for there to be more tongue flicks directed towards, and more time spent in contact with, related than non-related test lizards. In three of the four cases the tongue flick differences were significant, and in two cases the differences in time in contact were significant. There were no effects of treatment. The lack of significant interaction effects implied that the enhanced responses to related individuals were consistent across treatments in all cases. For both species, the responses of young to related and unrelated females were consistent whether individual young or pooled clutch data were considered. This indicates that a clutch bias did not influence the results.

Bull et al. (1994) reported a preferential response of female *T. rugosa* towards their own young, but could not determine whether females were responding specifically to related young, or just to familiar young. The present paper expands our understanding of mother–offspring recognition in reptiles in three ways. (1) We have now shown a reciprocal set of responses. Mothers recognize their offspring, and offspring recognize their mothers. (2) We have shown those responses are present in both *E. stokesii* and *T. rugosa*. (3) We have shown that the response remains when young are isolated from their mothers soon after birth, and that familiar but non-related individuals do not stimulate the same response. There were no significant differences in responses towards familiar and non-familiar lizards in treatments 1 and 2 for any case. However, in three of the four cases there was a significant interaction effect because lizards responded more strongly to related non-familiar lizards than to non-related familiar lizards.

The data provide support for the hypothesis that mothers can recognize their own young, and young can recognize their mothers, even when they have not been housed together. Although not significant, there was a trend in both species for a stronger response to unrelated individuals in treatment 2 (when unrelated individuals were familiar) than in the other treatments. With larger sample sizes these differences may have become significant, so we cannot completely eliminate the role of familiarity in recognition. Our data suggest that relatedness has a stronger role.

We could not differentiate between two groups of hypotheses to explain the recognition. Recognition may be based on phenotype matching (Lacy & Sherman 1983) or recognition alleles (Blaustein 1983) shared by mother and offspring. Alternatively, some learned association (Waldman 1988) may have developed soon after birth, during the short time interval (up to 2 h) before the experimental separation of mothers from their young. In observed births of *T. rugosa* (Bull et al. 1993b) and *E. stokesii* (A. Duffield & C. M. Bull, unpublished data), there were no obvious interactions, such as tongue flicking that either mother or offspring directed towards the other. However, both mother and offspring tongue flick the substrate repeatedly immediately after birth, and excess birth fluids and tissues are consumed by both. Perhaps they learn cues about each other in these activities. Independent of the mechanism of recognition, the results demonstrate that isolated lizards retain a memory of their mothers or offspring, and respond as strongly as controls even after several months of separation.

The cues used for recognition are probably chemical. We deduce this because the gauze bags containing the test lizards would have obscured visual cues, and because tongue flicking in reptiles is usually associated with the vomeronasal organ which is an olfactory receptor (Graves 1993). During tongue flicks, lizards sample chemicals in the surrounding environment, and deliver molecules to the vomeronasal organ (Cooper & Burghardt 1990; Cooper 1994).

One function of recognition could be to reduce inbreeding later in the life of the juveniles. Another possible function is to increase the probability of mothers and young staying together. Advantages for offspring survival (and thus for the mother's reproductive success) include efficient finding of suitable refuges, protection from predators, and transmission of gut fauna for digestion of herbivorous diets (Troyer 1982, 1984), although we have evidence for none of these. *Tiliqua rugosa* live mostly in deep refuges from the time of birth (autumn) until the following spring, and we know little of their behaviour over that period. In early spring, juveniles are sometimes found with or close to adults (Bull 1987) which may or may not be their parents. Adult *T. rugosa* have stable home ranges (Bull 1978, 1987; Satrawaha & Bull 1981), long-term pair fidelity (Bull 1988, 1994), and the ability to relocate displaced partners (Bull et al. 1993a), which imply a complex social organization with individual recognition and long-term memory. An additional parent–offspring bond, resulting from kin recognition, may not be unexpected in such a long-lived species (Bull 1995).

Less is known about the social behaviour of *E. stokesii*, but it is one of several *Egernia* species in which groups of individuals occupy refuges together (Hutchinson 1993). These may be social groupings, or random assemblages, but, near Hawker, *E. stokesii* occurs in temporally stable groups containing adults and juveniles (G. A. Duffield, personal communication) which we suspect are related. In this case, mother–offspring recognition would consolidate group structure.

The conclusions from this study, that in two species of skinks, mothers and their offspring can recognize each other, may not seem surprising to those who have studied higher vertebrates. What is unusual is that this level of recognition and potential social structuring has rarely been reported in reptiles. This may be because many reptile species are secretive, and infrequently active, so observations relevant to social organization are harder to accumulate. We deliberately chose two Australian skink species for which there were previous suggestions of complex social organization. It remains to be determined how widespread mother–offspring recognition is among other lizard species. Mother–offspring recognition may be more pronounced among viviparous lizard species, because there is more certainty about the maternal relationship without an intervening period as an egg, and because the mother has already invested extra reproductive effort in carrying the developing young.

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