



Parental care protects against infanticide in the lizard *Egernia saxatilis* (Scincidae)

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Reports of postpartum parental care in squamate reptiles (lizards and snakes) are rare and generally anecdotal. We investigated parental care in black rock skinks, *Egernia saxatilis*, from southeastern Australia. These lizards live in small family groups, with adults defending territories against conspecifics. Juvenile lizards live within their parents' territory and may thus be protected from infanticide. In staged encounters in the laboratory, adults frequently attacked unrelated juveniles but not their own offspring, and the parent's presence significantly reduced the incidence of this infanticidal aggression. This protection arose not through specific 'parental' behaviours, but because adults tended to ignore juveniles when another (potentially threatening) adult was present. When two family groups were placed in the same enclosure, one family rapidly became dominant over the other. Juveniles of the dominant family derived thermoregulatory and foraging benefits from their parents' status. Thus, some lizards do show postpartum parental care, and may thereby significantly benefit their progeny via reduced risk of infanticide and better access to thermal and nutritional resources.

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Parental care can be defined as any behaviour by an individual that appears likely to increase the fitness of its own offspring (Clutton-Brock 1991). While mammals and birds typically have prolonged associations between parents and their offspring, parental contributions to offspring viability have evolved in many phylogenetic lineages of animals (e.g. Shine 1988; Van Schaik & Dunbar 1990; Abe 1998; Bhoopathy 1998; Annett et al. 1999; Greene et al. 2002). In fact, the near ubiquity of parental care in endothermic vertebrates makes it difficult to develop and test hypotheses about the initial evolution of parental care in these taxa.

The tight linkage between endothermy and parental care may reflect adaptation, with the latter trait acting as a selective force for the former (Farmer 2000). To clarify this hypothesis and others like it, we need to understand more about the forms (including costs and benefits) of parental care in ectothermic terrestrial vertebrates. Many fish and amphibians display complex parental behaviours (e.g. Wells 1978; Bachmann 1984; Abe 1998; Annett et al. 1999; Burrowes 2000; Cook et al. 2001), but the closest phylogenetic and ecological comparison to terrestrial

endotherms comes from the reptiles. Parental care is ubiquitous in crocodylians (reviewed in Shine 1988), unknown in turtles (but see Barrett & Humphrey 1986; Iverson 1990), and sporadically distributed in squamates (lizards and snakes: Shine 1988; Somma 1990). Although offspring disperse soon after hatching/birth in most squamate species, a few taxa of lizards have longer-term associations between offspring and their parents, in particular their mothers (e.g. *Xenosaurus newmanorum*: Lemos-Espinal et al. 1997; *Cordylus cataphractus*: Mouton et al. 1999). Lizards thus offer an opportunity to examine relatively simple forms of parental care, providing a robust comparison with the more complex conditions in endothermic vertebrates.

One hypothesis of particular interest is the idea that infanticide has been a major selective force favouring parental protection of offspring. Infanticide (killing of juvenile animals by older conspecifics) is a significant source of juvenile mortality in more than 1300 animal taxa (Jenssen et al. 1989). Wolff & Peterson (1998) suggested that female territoriality in semisocial mammals may have evolved to protect young from such conspecific infanticide (the 'offspring defence' hypothesis for the evolution of territoriality).

The same arguments may apply to lizards. For example, Jenssen et al. (1989) found that juvenile curly-tailed

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lizards, *Leiocephalus schreibersi*, live entirely within the home ranges of a single adult male and a single adult female. Unfamiliar juveniles that enter the home ranges of other adults are attacked, and in some instances consumed, by resident adults. A case of territorial defence resulting in indirect parental care was also observed in this species.

Similarly, the tropidurid lizard *Liolaemus huacahuasicus viviparus* lives in groups consisting of one adult female, up to 11 juveniles and sometimes an adult male (Halloy & Halloy 1997). Adults defend a 'family' territory containing the juveniles. Infanticide was observed in the laboratory, and postpartum females assumed distinctive threat postures when an observer approached them and their young.

To test the 'offspring defence' hypothesis for the evolution of territoriality in reptiles, we need a species in which the parent and offspring remain associated after birth or hatching and where we can determine whether observed adult–juvenile associations in the field are indeed parents with their offspring. Australian scincid lizards of the genus *Egernia* fulfil this condition: they show long-term stable pair bonds and parent–offspring associations, and microsatellite primers are available that amplify across most taxa. Offspring remain with their parents until the next litter of young is born (e.g. *E. whitii*: Milton 1990) or for even longer (up to several years: e.g. *E. cunninghami*, *E. stokesii* and *E. saxatilis*: Gardner 2000; Gardner et al. 2001; Stow et al. 2001; O'Connor & Shine 2003). Intriguingly, infanticide has also been observed in these taxa (Bartlett 1981; Bruyn 1994; Lanham & Bull 2000; for *E. saxatilis*, see below). In such a system, we can ask the following questions. (1) Are juveniles threatened by infanticide and if so, is this threat present throughout the active season? (2) Do parents act differently (i.e. more aggressively) towards unrelated juveniles than towards their own offspring? (3) Does the parent's presence enhance the fitness of its offspring and, if so, by what process (e.g. protection against infanticide or access to resources)?

We have addressed these questions with experimental studies on the black rock skink, *E. saxatilis*. Fieldwork has shown that these lizards form stable 'family' units with offspring remaining within the parental territory for up to 3 years (O'Connor & Shine 2003). Although these descriptive data are essential to document the overall patterns of association among individuals, they do not enable robust tests of hypotheses about the putative advantages of parental presence for juvenile lizards. To conduct such tests, we captured lizards, brought them into contact with each other in the laboratory, and monitored the results of these staged encounters.

METHODS

Study Species and Area

Egernia saxatilis is a medium-sized viviparous skink (up to 130 mm snout–vent length, SVL), found in rocky areas throughout southeastern Australia (Cogger 2000). These animals are primarily insectivorous, although larger specimens also consume plant food during some seasons (Brown 1991). During the active season (October to March) the lizards emerge on warm days from their

overnight shelters (crevices beneath boulders and exfoliations on rocky outcrops), to forage and to interact socially. One to four offspring are born in late February/early March (unpublished data).

Within our study population, some *E. saxatilis* live singly but the majority are found in small nuclear family groups: microsatellite parentage analysis confirmed that the adults in these groups are the parents of the juveniles that share their home range (O'Connor & Shine 2003). Both adults and subadults chase and bite smaller individuals in the field (personal observation). They also commit infanticide in laboratory enclosures, killing juveniles (and consuming smaller ones: personal observation). In the field, we saw one intruding adult chase a juvenile only to be chased off by the territorial parent of the juvenile. This observation suggests parental protection of offspring, but the inference remains weak without experimental evidence.

We studied lizards on granite outcrops in the Kanangra-Boyd National Park, Blue Mountains, New South Wales (GR 150°03'E, 33°58'S) at an elevation of 1200 m above sea level (for more detail see O'Connor & Shine 2003). Permits were provided by the NSW National Parks and Wildlife Service and the Animal Ethics Committee of the University of Sydney. Lizards were captured by hand, brought back to the laboratory and housed in the same groups in which they had been captured. We classified individuals as adult based on the minimum SVL at sexual maturity (95 mm males; 100 mm females, from dissection: G. Shea, unpublished data). All animals smaller than these sizes were classified as juveniles. All experiments were completed within 2 months of capture. 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.

Experimental Procedures

Lizards were housed in plastic bins (40 × 62 cm and 40 cm high) heated by a 60-W bulb suspended in the centre of, and 10 cm above, the bin floor in a room kept at 25 °C. Each bin contained a shelter crevice formed by two terracotta tiles (20 × 20 × 1 cm). Heat lamps came on daily from 0900 to 1700 hours. Each bin contained water ad libitum, and food (crickets, cockroaches or cat food) was added thrice weekly. All experiments were conducted in similar bins, in one of two adjoining rooms, and were run in the afternoon between 1200 and 1600 hours so that animals could attain their preferred body temperatures before each trial. For trials involving mother–offspring pairs, these juveniles were born in captivity in late February/early March and housed with their mothers in the same conditions as all other lizards. For other groups (i.e. those where both adults and juveniles were caught in the field), we used microsatellite loci to confirm that the juveniles were the offspring of the adults with which they were found (see O'Connor & Shine 2003 for further details).

Interactions between lizards

Before the main experiments, we ran a series of pilot studies (using different individuals to those used in the

trials reported below). In these we directly observed individual trials (via a monitor connected to the video camera) to ensure no animals were injured during the aggression trials. In these pilots we intervened in all trials after an aggressive act had taken place to check the health of the animals. At most, they received superficial bite marks. The only exception to this was in trials involving juveniles, where juveniles occasionally lost parts of their tails. From these pilots we determined that 15 min was long enough for lizards to accustom themselves to the enclosures and interact, but was short enough that any aggressive interactions did not occur frequently enough for the health of the animals to be affected. Juveniles that had lost part of their tails were not used in any subsequent trials. All animals were released in good health at the completion of the trials.

To quantify the levels of aggression targeted towards juveniles by conspecific adults, in the next series of trials we placed an adult (either male or female) with an unrelated juvenile and observed them (1) to quantify levels of aggression; and (2) to identify factors (adult sex, or the season when trials were run) that affect these levels of aggression.

Within each category (adult male, AM, adult female, AF, juvenile, J), lizards were randomly paired for trials, with each pair of animals encountering each other only once. Individuals collected together (and thus housed together) were not tested against each other except for trials in which we examined effects of group membership on aggression (e.g. mother versus offspring). For identification during trials, lizards were marked on the neck with nontoxic short-term (<2 days) paint. To remove the effect of territory status, we introduced the lizards to the experimental enclosure in a random order within 1 min of each other, so that both were on unfamiliar (and hence neutral) territory. All encounters were videotaped for 15 min (see above), with minutes 3–12 scored for aggressive interactions. Three types of interaction were scored in each trial. (1) Bite: one lizard bites any portion of another. Only the aggressor in an encounter was scored as having taken a bite (i.e. if the bitten animal retaliated by biting at the animal holding it, this was not scored as a bite). (2) Chase: one lizard runs directly towards the other. (3) Follow/Approach: lizard changes direction and walks directly towards the other individual.

To generate an overall aggression score for each trial, we summed the number of occurrences of each behaviour multiplied by subjectively selected weightings (Bite \times 4, Chase \times 1, Follow \times 0.5) to reflect the level of agonistic interaction involved. Varying these weightings did not significantly alter the results presented below. We washed bins with 70% alcohol between experiments and each lizard was tested only once each day. We ran the following sets of trials.

(1) To examine whether juveniles were under threat of infanticide year round, we ran trials in October, January and March 2001, encompassing the active season of the lizards. Both the individuals used in trials and the trial categories (AF versus J; AM versus J) were randomized within and between trial days.

(2) To examine whether agonistic responses were modified by the presence of a parent, we ran trials with three

animals rather than two (i.e. with mother–offspring pairs plus one unfamiliar adult).

(3) To clarify influences on aggression levels, we ran additional trials in which the same 15 mother–offspring combinations were tested under different circumstances: mother only, mother plus offspring, or offspring only against (a) an adult male, (b) an adult female and (c) an unrelated juvenile. For consistency, the same individual within each of these latter categories was used for all trials for any particular mother–offspring pair.

(4) As we found that unrelated adults directed less aggression to juveniles if their mothers were also present (see below), we conducted additional trials in which two adults were present with the offspring but neither was related to the younger animal. This experiment was designed to test the possibility that the presence of an additional adult (not necessarily the mother) somehow redirected aggression away from the juvenile, independently of 'parental' behaviour.

Interactions between groups

Pilot studies showed that if two pairs or family groups of lizards (each consisting of an adult male and an adult female, with or without their offspring) were brought together in the same area, one pair remained active and basked whereas the other group retreated to a shelter and rarely emerged. Thus, in practice it was straightforward to rate one of the groups as dominant and the other as subordinate. We took advantage of this fact to see whether juveniles from the dominant family benefited from their parents' status in terms of basking frequencies and duration.

An oval arena (120 \times 90 cm and 38 cm high) was constructed from pliable polystyrene sheets 1 mm thick. In the centre of each half of the arena we suspended a 60-W bulb, 10 cm above terracotta tiles (20 \times 20 \times 1 cm) arranged to form a crevice with a gap of 7 mm above floor level at one end, sloping up to 17 mm at the other. These tiles thus provided both shelter crevices and basking sites. A third smaller tile (11 \times 11 \times 1 cm) was placed in the centre of the arena, providing a 7-mm crevice large enough to provide shelter for juveniles but not for adult lizards. This 'juvenile-only' tile was added to protect juveniles from adult aggression and possible infanticide. No heating was provided above the juvenile-only tile.

On the night before a trial, two families (each consisting of one adult male, one adult female and one of their offspring aged between 2–3 months) were introduced to the bin and placed under their respective family shelter tile. Each lizard was given a unique combination of paint marks. In all trials families remained under their respective tiles until 0900 hours the following day when the basking lights above each tile were turned on. All trials were recorded via time-lapse video recording for 16 s per segment with an interval of 4 min between successive segments. Room temperature was set at a constant 25 °C. Trials ended at 1700 hours.

For each 16-s segment, we scored animals as: (1) basking on a tile (if they remained completely on the tile for the entire 16-s segment); (2) active (moving around the arena); (3) sheltering (not visible); or (4) partially sheltered

(head emerging from shelter). We also counted the basking sessions (i.e. times the animal moved on to a tile, remained for a minimum of one complete segment, then later moved off) per animal. For analysis, all results were calculated as percentages of the total number of observations.

One of the families in each trial was defined as dominant if (1) there was obvious aggression by adults of one family against the second (eight cases), or (2) no aggression was observed but adults of the 'subordinate' family spent most of the trial sheltering (three cases). Two trials were excluded because no aggression was observed and there was no significant difference in the basking rates of adults from the two families.

To characterize the behaviour of juveniles in the same arena when no unfamiliar adults were present, we ran four trials using only one family. A further three trials were run with no adults present; the arena contained only four juvenile lizards, one of which was randomly selected for comparison with the behaviour of juveniles in other trials.

To minimize stress to our experimental animals, we monitored a pilot set of trials directly so that we could intervene and stop trials if any animal appeared to be under severe stress or in danger of actual injury. No such outcomes were observed, so we conducted the experimental trials without any human presence. Inspection of individuals after the trials did not reveal any detectable injuries to any of the participants.

Data Analysis

Because some of the lizard interaction trials did not evoke any agonistic behaviour, distributions for aggression scores contained many zero values and hence were non-normally distributed. No transformation could resolve this problem, so we conducted nonparametric analyses on the entire data set (i.e. including cases with zero scores, probabilities corrected for ties). All analyses were run using either Systat 9.0 (SPSS 1998) or Statview 5.0 (SAS Institute 1998). We used two-tailed statistical tests.

Some individuals were used in more than one trial of the same type (i.e. AM versus J) to investigate changes in aggression over multiple trials, to assess the degree of individual variation in level of aggression, or simply because of logistical restrictions. The same two individuals were never used against each other more than once. Our analyses thus used the mean aggression score of each individual for each trial type, to avoid pseudoreplication; thus each individual contributes only a single score to any given analysis. The text reports mean values ± 1 SE.

As the interactions were bidirectional, some of the trials were used in more than one analysis. For example, where two adults and a juvenile were present in the same trial, we looked at the mother's aggression towards the second adult and also at the second adult's aggression towards the mother. Although the behaviour of one animal will undoubtedly influence the other, this analysis provides an accurate indication of the behaviour of the animal of interest in the respective trial type.

RESULTS

Interactions between Lizards

Adult aggression towards juveniles

There were no significant differences in the amount of aggression directed against juveniles by either sex (Mann-Whitney test: $Z = -0.559$, $N_{\text{Females}} = 97$, $N_{\text{Males}} = 46$, $P = 0.58$), or over the season (Kruskal-Wallis: both sexes: $H_2 = 0.91$, $N_{\text{Oct}} = 55$, $N_{\text{Jan}} = 26$, $N_{\text{Mar}} = 62$, $P = 0.63$; females: $H_2 = 2.02$, $N_{\text{Oct}} = 27$, $N_{\text{Jan}} = 21$, $N_{\text{Mar}} = 49$, $P = 0.36$; males: $H_2 = 0.52$, $N_{\text{Oct}} = 28$, $N_{\text{Jan}} = 5$, $N_{\text{Mar}} = 13$, $P = 0.77$; Fig. 1).

Attacks on own and unrelated juveniles

Adult lizards of both sexes were less aggressive to their own offspring than they were to unrelated juveniles, but owing to differing sample sizes this trend was statistically significant only for females (Mann-Whitney test: females: $Z = -3.351$, $N_{\text{Own}} = 50$, $N_{\text{Unrelated}} = 85$, $P < 0.001$; males: $Z = -0.220$, $N_{\text{Own}} = 7$, $N_{\text{Unrelated}} = 29$, $P = 0.83$; Fig. 2).

Attacks on other lizards

Postpartum females showed similar levels of aggression towards unrelated juveniles whether or not their own neonate was present (aggression against unrelated juvenile: own neonate absent: 2.94 ± 1.23 ; own neonate present: 1.54 ± 0.98 ; Mann-Whitney test: $U = 144.5$, $N_{\text{Present}} = 19$, $N_{\text{Absent}} = 17$, $P = 0.52$). Neither did the presence of a mother's offspring affect her level of aggression towards the second adult (Mann-Whitney test: $Z = -1.003$, $N_{\text{Present}} = 38$, $N_{\text{Absent}} = 117$, $P = 0.32$; females: $U = 629.5$, $N_{\text{Present}} = 19$, $N_{\text{Absent}} = 67$, $P = 0.94$; males: $U = 395.0$, $N_{\text{Present}} = 19$, $N_{\text{Absent}} = 50$, $P = 0.16$; Fig. 3a). In fact, in the few cases where the second adult attacked the juvenile during a trial, the mother showed no obvious response.

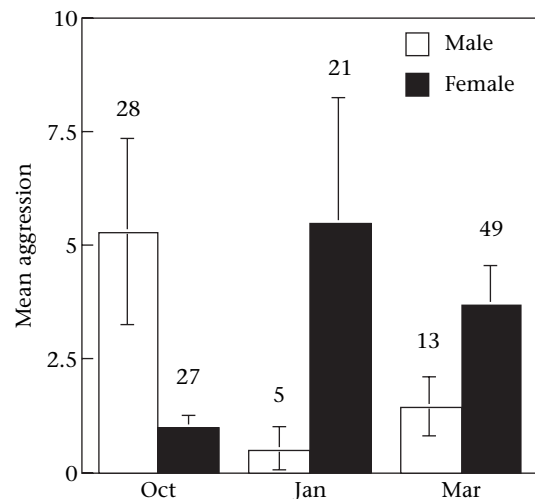


Figure 1. Mean aggression scores ± 1 SE of male and female black rock skinks in paired laboratory encounters against juveniles in October, January and March. Sample sizes are given above the bars.

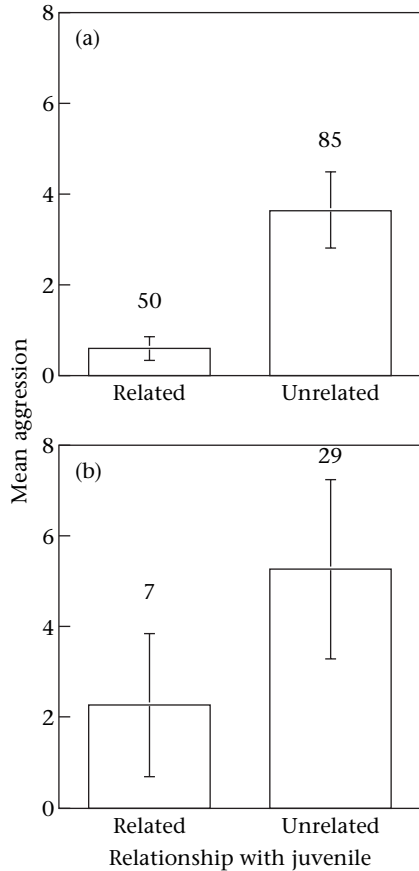


Figure 2. Mean aggression scores ± 1 SE of (a) female and (b) male black rock skinks in laboratory encounters against related and unrelated juveniles. Sample sizes are given above the bars.

Attacks by adults on mother

The presence of a juvenile decreased the amount of aggression directed against the juvenile's mother by the second unrelated adult (Mann-Whitney test: $U = 254.5$, $N_{\text{Present}} = 22$, $N_{\text{Absent}} = 31$, $P = 0.022$; Fig. 3b), although this trend fell short of significance when the responses of males and females were analysed separately (females: $U = 32.0$, $N_{\text{Present}} = 7$, $N_{\text{Absent}} = 13$, $P = 0.19$; males: $U = 105.0$, $N_{\text{Present}} = 15$, $N_{\text{Absent}} = 18$, $P = 0.06$).

Attacks in presence of mother

Significantly less aggression was directed against a juvenile when its mother was also present than when it was alone with an unrelated adult (Mann-Whitney test: $Z = -4.596$, $N_{\text{Present}} = 57$, $N_{\text{Absent}} = 118$, $P < 0.0001$; Fig. 4). The same pattern was observed in the paired trials (Wilcoxon signed-ranks test: overall: $Z = 2.54$, $N = 64$, $P = 0.01$; females: $Z = 1.70$, $N = 41$, $P = 0.09$; males: $Z = 1.96$, $N = 23$, $P = 0.05$).

Attacks in presence of unrelated adult

In the trials in which we placed a juvenile with two unrelated adults, the level of aggression directed at the juvenile was intermediate between that in trials using only one adult and those where the mother was also present (Kruskal-Wallis: $H_2 = 16.8$, $P < 0.0001$; Fig. 4).

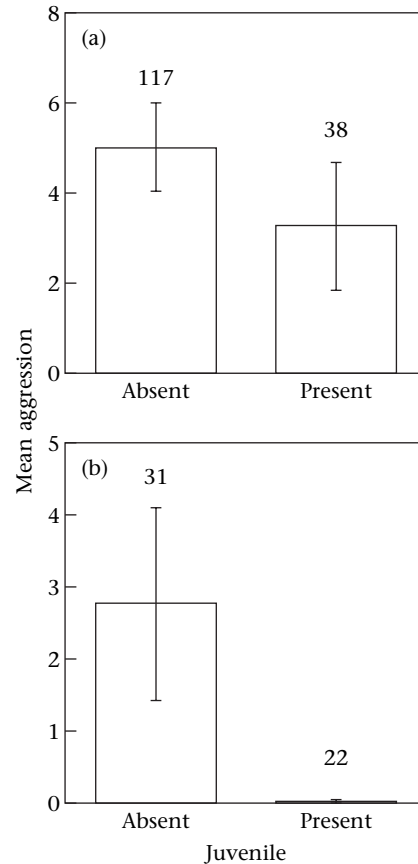


Figure 3. Mean aggression scores ± 1 SE in black rock skinks in laboratory encounters with (a) mother against second adult with and without a juvenile present, and (b) second adult (unrelated to juvenile) towards the juvenile's mother with and without a juvenile present. Sample sizes are given above the bars.

Pairwise comparisons of the 'two random adult' trials with the 'single adult' and the 'mother present' trials both approached statistical significance (Mann-Whitney test: single adult comparison: $Z = -1.764$, $N_{\text{Single adult}} = 118$, $N_{2 \text{ random adults}} = 25$, $P = 0.08$; mother present: $Z = -1.907$, $N_{\text{Mother}} = 57$, $N_{2 \text{ random adults}} = 25$, $P = 0.06$).

Interactions between Groups

When two families were placed in an arena together, the juvenile from the dominant family basked for longer, and more often, than did the juvenile from the subordinate family (Wilcoxon signed-ranks test: time spent basking: $T = 2$, $N = 10$, $P < 0.01$; number of times basking: $T = 3$, $N = 10$, $P < 0.02$; Fig. 5a, b; all other behaviours showed strong but nonsignificant trends with $P < 0.20$; time half out of shelter: $T = 10$, $N = 9$; number of times half out: $T = 1.5$, $N = 6$; time out basking: $T = 4$, $N = 6$; time under shelter: $T = 10$, $N = 10$; Fig. 5c-f).

Juveniles from dominant families behaved similarly to juveniles in trials with only one family (the juvenile's parents) present, and to juveniles in trials where no adults were present (Mann-Whitney test: all nonsignificant except for neonates in the 'juveniles only' trials which

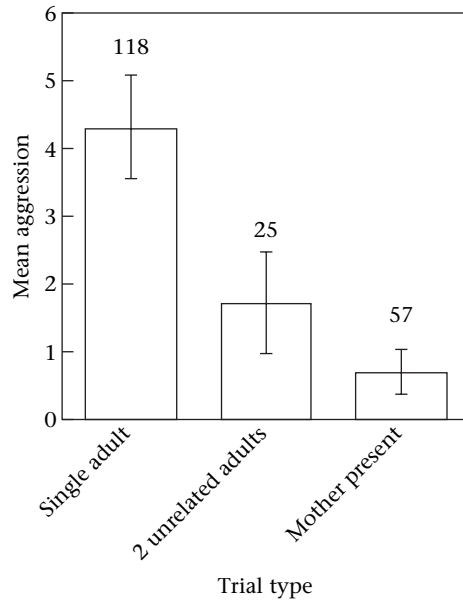


Figure 4. Mean aggression scores ± 1 SE of black rock skinks in laboratory encounters. The histograms show amounts of aggression directed at juveniles by unrelated adults when the juvenile was alone with an unrelated adult, alone with two unrelated adults, and when its mother was present as well as the second adult. Sample sizes are given above the bars.

spent less time sheltering than did juveniles in trials with their parents: $U = 0$, N_2 families = 11, $N_{\text{juv only}} = 3$, $N_{\text{juv+parents}} = 4$, $P < 0.03$). Juveniles from subordinate families spent most of their time hidden in shelters rather than active or basking (versus juveniles in trials with only their own family present: time spent basking: $U = 0$, $N_1 = N_2 = 11$, $P = 0.003$; number of times basked: $U = 0$, $N_1 = N_2 = 11$, $P = 0.003$; time spent out active: $U = 7$, $N_1 = N_2 = 11$, $P < 0.015$; time spent half out of shelter: $U = 10.5$, $N_1 = N_2 = 11$, $P = 0.12$; times half out of shelter: $U = 10$, $N_1 = N_2 = 11$, $P = 0.08$; time in shelter: $U = 1$, $N_1 = N_2 = 11$, $P = 0.007$; Fig. 5).

DISCUSSION

To show unequivocally that a species exhibits parental care, we need to show that offspring benefit from the parent's activities, and that parents perform such activities selectively towards their own offspring rather than to other (unrelated) offspring. Using these criteria, our study provides the first clear demonstration of parental care for any squamate reptile. The benefits of parental care for *E. saxatilis* may be complex, involving access to resources such as thermoregulatory and feeding opportunities, but the primary mechanism by which such advantages were conferred in our study involved protection against attack from other lizards.

Adult *E. saxatilis* showed frequent aggression towards conspecifics, attacking juveniles as well as other adults. In captivity at least, juveniles that accidentally trespass into a cage containing another family group are quickly killed (and often eaten; personal observation). Adult females were less aggressive towards their own offspring than

towards unrelated juveniles, and our data suggest (although they do not demonstrate) that males show the same tolerance of their own offspring. Because adult skinks often move widely around the outcrop well outside the boundaries of their own territories (unpublished data), juveniles undoubtedly encounter unrelated adults. Limited field observations of aggression by adults towards juveniles probably reflect such encounters. As parents tolerate their own offspring, however, a juvenile inside its parents' territory will experience far fewer risky encounters with unrelated adults. Even if a stranger enters the territory, the parents' presence provides substantial protection to the young lizard.

The mechanism of this protection is indirect. That is, parents did not behave differently when their offspring was present (even when it was being attacked); their sole 'parental' behaviour was tolerance of the juvenile's presence. Thus, the protection conferred by parental presence was due to adult skinks virtually ignoring any juveniles when another unrelated adult was nearby (as demonstrated by the 'two unrelated adults' trials). Given the highly aggressive nature of these animals, that reduced level of aggression towards juveniles presumably reflects the tendency for the two adults to focus on each other rather than on a smaller, less threatening, adversary. Despite the indirect nature of this interaction, the end result is effective parental protection of offspring.

One could argue that in such an indirect system, a juvenile would also benefit if the two adults close to it were unrelated animals. However, this situation is unstable. As soon as one of the adults leaves (perhaps because of agonistic interactions with the other), the remaining adult is likely to attack the juvenile. Thus, it is only the juvenile's parents, the only adult lizards not likely to attack it, that confer some measure of security for the young animal.

As black rock skinks live in 'nuclear families' (O'Connor & Shine 2003), many of the potentially dangerous encounters for a juvenile lizard occur not as a result of meeting wide-ranging adult 'strangers', but in conflicts with the adults from family groups occupying neighbouring territories. Family-level dominance hierarchies played a critical role in these interactions in this study: one family (including its juveniles) continued to behave normally (basking, feeding, etc.), whereas the other family retreated to shelter. Despite the presence of unfamiliar adults in our 'two families' trials, juveniles from dominant families spent most of their time basking or exploring the enclosure, and little time sheltering. Thus, parental protection against conspecific aggression has both direct fitness benefits to the offspring (they are less likely to be injured or killed by infanticidal conspecifics) and indirect benefits (opportunities to bask, feed, etc.). Food supply and basking opportunities can substantially affect fitness-related traits such as growth rates and escape speeds (Crowley & Pietruszka 1983; Sinervo 1990; Mautz et al. 1992; Autumn & De Nardo 1995; Niewiarowski 2001).

In common with a number of other lizard species (e.g. *Scincella lateralis*: Akin 1998; *Abronia vasconcelosii*: Formanowicz et al. 1990), *E. saxatilis* males are more aggressive than females and win most aggressive

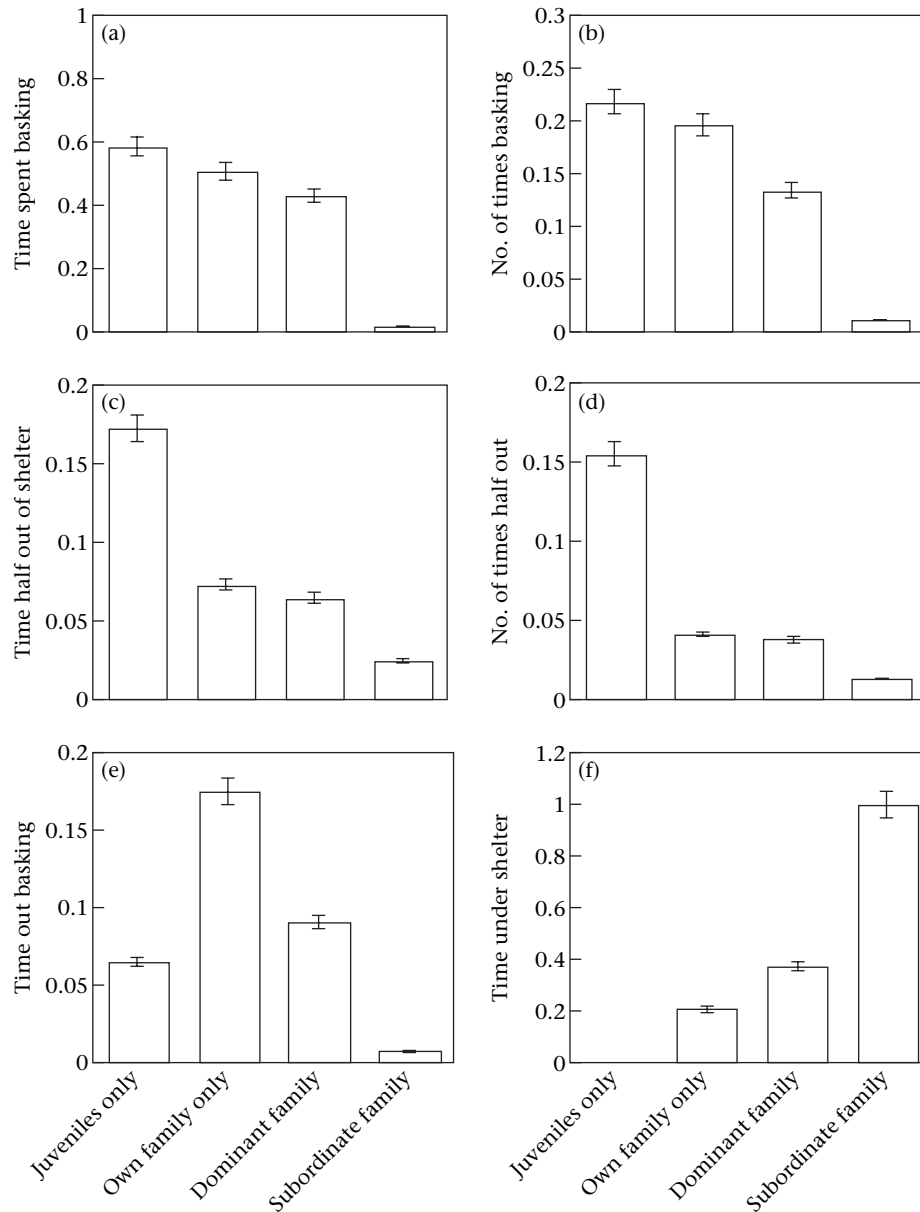


Figure 5. Behaviour of juvenile black rock skinks in paired laboratory encounters. The histograms show mean proportion of observations ± 1 SE for behaviour of juveniles in the juvenile only ($N = 3$), juvenile plus own parents ($N = 4$) and paired two family trials ($N = 11$).

interactions between the two sexes (unpublished data). Thus, adult females are unlikely to be able to defend their offspring successfully against attacks by males, nor is it probable that they would confront male intruders. In such situations, females may protect offspring from male infanticide by strategies such as multiple mating (Agrell et al. 1998) or the formation of pair bonds with territorial males. Although multiple mating within *E. saxatilis* occurs at similar rates to that found in related species (ca. 20% of clutches show some form of multiple paternity; O'Connor 2003), the rate of extragroup multiple paternity is significantly lower (7%; O'Connor 2003), suggesting that pair bonding is a more important strategy within *E. saxatilis* than multiple mating. Paired males then protect juveniles against infanticide by excluding male intruders from the family territory.

Protection from male conspecific infanticide is thought to be the primary selective force in the evolution of year-round male–female associations in primates (Van Schaik & Kappeler 1997). Long-term pair bonding is unusual among reptiles, albeit with occasional records from several lineages (e.g. *Chamaeleo hoehnelii*: Toxopeus et al. 1988). The Australian scincid lineage *Egernia* is exceptional in this respect, with long-term pair bonding apparently the rule rather than the exception (e.g. *E. cunninghami*: Stow et al. 2001; *E. stokesii*: Gardner et al. 2002; *Tiliqua rugosa*: Bull 1988, 1994). *Egernia saxatilis* also form long-term pair bonds with the same individuals, breeding together for up to 3 years, and possibly longer (O'Connor & Shine 2003). Our field study showed that these lizards form pairs even if no offspring are present (O'Connor & Shine 2003). Once pair bonding has evolved, tolerating offspring within the

parental territory may entail few additional costs but substantial benefits. Such protection by adult pairs thus meets the requirements of the offspring defence hypothesis for the evolution of territoriality.

If this behaviour provides the benefits detailed above, why do not all black rock skinks live in family groups? In reality, our study population of *E. saxatilis* displays a range of sociality with some juveniles living singly, some in small 'juvenile only' groups and most others in family groups (O'Connor & Shine 2003). Resource limitation may curtail the numbers of family groups. For example, many territories that contain ideal (large) crevices for adult lizards do not have any small (juvenile-sized) crevices nearby. Partitioning of food resources is less likely, given that the species is a generalist insectivore, but none the less some territories may be disproportionately suitable in this respect for either juveniles or adults, but not both groups. The wide variation in social structure both within and between *Egernia* species (Chapple 2003) provides immense opportunities to explore such issues.

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