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Parental care in the long-tailed skink, *Mabuya longicaudata*, on a tropical Asian island

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Parental care has been reported in more than 140 species of reptiles (about 3%), but few records unambiguously demonstrate the selective value of that care. I experimentally investigated the influence of maternal attendance on survival of eggs in the long-tailed skink, *Mabuya longicaudata*, on Orchid Island, Taiwan, by placing sympatric reptiles, both predators and nonpredators, into nests. Without maternal care, most lizard eggs were eaten by the egg-eating snake, *Oligodon formosanus*. Female lizards with eggs attacked snakes more often and escaped from snakes less often than did females without eggs. Survival of eggs was lower when females were removed from clutches than when they were left in attendance. All egg loss in unprotected nests on Orchid Island was due to predation by *O. formosanus*. Size of snakes did not determine whether lizards abandoned egg-free nests or nests with eggs when attacked. Females that attacked egg predators had larger clutches than those that did not attack. Females recognized sympatric lizards and did not attack species that do not prey on eggs or on *M. longicaudata*, but recognized the predatory snake *Elaphe carinata* and escaped when that species entered the nest. These findings emphasize the ecological importance of an increased understanding of the function of parental care in reptiles.

Most animals are exposed to the highest risks of mortality during the earliest stages of their life cycle, and various studies have suggested the importance of parental care at these times (Roff 1992; Olsson & Shine 1998). The amount of parental effort invested during defence of offspring should be determined by the degree of risk to future reproductive potential, the value of present offspring compared with the parent's expected future contribution, and the expected increase in offspring welfare resulting from such parental expenditure (Pressley 1981). Accordingly, natural selection should favour an optimum level of defence based on the risk incurred by the parent and the expected benefit derived by the offspring (Shine 1988).

Parental care in reptiles can be divided into four categories: (1) egg attending: a parent remains with the eggs, but never actively defends its nest; (2) egg brooding: a parent facilitates incubation by raising nest temperatures above ambient; (3) egg guarding: a parent actively defends its nest against potential predators; and (4) complex active defence behaviours: this is a special case in crocodilians, including guarding of eggs and young, nest opening, and mouth transport of eggs and young (Shine 1988). Parental care has been reported in more than 140 species of reptiles (about 3%), but many records are either ambiguous or inadequate. For example, most records are based on an association of females and eggs with no direct evidence of parental care, and actual defence against predators has rarely been reported in natural environments (Somma 1990). However, Greene et al. (2002) found that pit viper, *Crotalus molossus*, females remained with the nest until the neonates shed their skin and attending females were sometimes more aggressive against natural predators than they had been before birth or after neonate ecdysis.

Maternal aggression, a component of parental care, involves an increase in aggression towards conspecifics or heterospecifics (Figler et al. 2001), and can occur from early pregnancy until independence of the progeny (Archer 1988; Maestripieri 1992). However, maternal aggression in reptiles has rarely been reported except in crocodilians (Rand 1968; Shine 1988). Female crocodiles remain in the vicinity of the nest after laying, and return to it at intervals. Potential predators near the eggs may be attacked, but nonpredatory species are ignored (Dietz & Jackson 1979). The females help open the nest and carry

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the hatchlings to the water. The hatchlings stay with the parents for days or weeks and the adults actively defend offspring against potential predators.

Populations of the long-tailed skink, *Mabuya longicaudata*, on Orchid Island show parental care, but other conspecific populations do not (Huang 2004). In this study, I followed a natural population of *M. longicaudata* during the breeding season on Orchid Island to determine what proportion of the population showed parental care, and whether the size of an intruding snake affected the willingness of female *Mabuya* to defend their eggs. I placed sympatric lizards, *Japalura swinhonis* and *Sphenomorphus incognitus*, the lizard-eating snake *Elaphe carnita*, male *M. longicaudata* and an egg-eating snake *Oligodon formosanus* into nests to test the responses of attending females to intruding predators and nonpredators. I also recorded how clutch size affected whether lizards escaped or attacked. Finally, I tested the responses of male *M. longicaudata* to intruding snakes.

METHODS

Study Area and Species

Individual *M. longicaudata* spend most of the active season dispersed over large areas but they congregate in high densities at holes to lay eggs. The breeding period lasts for 7 months (February–August, Huang 2004).

All field data were collected in 2001–2003 at a study site in low-elevation rainforest in the central part of Orchid Island, Taiwan. At this site plastic drainage tubes were present in the concrete walls along the mountain road. Because some of the pipes were blocked by rocks, they provided good nest sites for *M. longicaudata*. There were nearly 1200 pipes (diameter 7.5–12.5 cm, length 120 cm) spread sparsely along 2 km of the road.

I visited all nests in the area at the peak of the breeding season from May to August. To ensure that all breeding attempts were detected, I checked all the nests every 6 h, with the exact hour varied so that each hour in a day was used at least three times in every year. For example, if the first time a nest was checked was 0600, 1200, 1800 and 2400 hours, the following day it was checked at 0700, 1300, 1900 and 0100 hours. Female lizards were recorded as present at the nest or not. I investigated all the nests on the first day I arrived on Orchid Island, and visited the study site four to six times per day between May and August. I recorded clutch size, oviposition date and hatching date. Hatching success was calculated on the basis of number of hatchlings, that is, before the young had left their nests.

Experimental Intruders

Oligodon formosanus is a major predator of reptile eggs on Orchid Island (Huang 2004). In a 6-year study on Orchid Island I observed female *M. longicaudata* attacking this species on 15 occasions.

I caught snakes on the beach by hand. They were kept in a rectangular plastic cage (35 × 25 cm and 20 cm high) that was half full of sand and had a cardboard box for shelter. All snakes were measured and weighed at the time of capture (Huang 2004) and regularly thereafter. Snakes were fed egg yolk once a day and provided with water. At the conclusion of the study, the snakes were released at their initial capture site no more than 24 h after capture.

I used 20 individual *O. formosanus* 4–22 times (average: 8.85; snout–vent lengths (SVLs) 33.5–63.5 cm; weight 25.5–174 g). To generate an encounter, I gently put a snake into the open end of a pipe (the other end being sealed) that contained a female lizard with or without eggs ($N = 177$ females). I recorded responses after the snakes reached the nest. The SVL and body mass of snakes were recorded for each encounter, and I used body size as a variable in assessing the lizards' responses (attack, escape from the nest or ignores if the lizard neither attacked nor escaped).

To test for parental defence by *M. longicaudata* to other sympatric reptiles, I also used sympatric lizards (*Japalura swinhonis*, *Sphenomorphus incognitus*, male *M. longicaudata*) and a potential snake predator on adult lizards (*Elaphe carinata*). I also recorded the responses of 58 male *M. longicaudata* to *O. formosanus* when they were in holes. All male *M. longicaudata*, selected randomly on Orchid Island, were tested once. Sympatric lizards and *E. carinata* were kept in cages (35 × 25 cm) that were half full of sand, with a cardboard box for shelter. They were fed crickets and chicken egg, respectively, once a day and provided with water. At the conclusion of the study, the sympatric reptiles were released at their initial capture site no more than 24 h after capture.

Egg Survival Experiment

This experiment was designed to detect possible effects of maternal care on egg survival. I removed 32 female lizards to simulate clutch desertion after oviposition (unprotected treatment), and compared them to a normal, egg-guarding group ($N = 70$, protected treatment). I checked the nests at least once a day until the eggs were gone or hatched. I recorded the hatching dates and hatchling numbers and body sizes.

Ethical Note

I observed no injuries to any animals tested in this study. When they met, lizards violently pushed snakes away from the nest, usually biting the snake's head or neck. After the snake was pushed away from the nest, the lizard released its bite immediately and returned to its eggs. Sometimes, a snake returned to the nest, and the lizard again chased the snake away. Lizard bites appeared not to be harmful to the snakes since I never saw females puncture the skin of the snakes. To minimize stress to the tested animals, I carried out each treatment a maximum of 56 times. To test for impacts of treatments, I followed females that were individually marked with a piece of numbered, coloured, plastic paper 1 cm^2 (Tunyin, Taipei, Taiwan) glued on the back. The plastic paper had no apparent adverse effects on the lizards and fell off within 10 weeks. I resighted 56 females, and the 32 removed females, 1–92 days after the initial experimentation: 80 of the 88 were depositing a new clutch of eggs suggesting little impact of the experimental procedures on survival or reproductive performance. It is recommended, however, that future studies involving similar experiments use appropriate continuous assessment of the data as they are generated, which may allow a smaller sample size to be used. Lizards removed from egg guarding were released immediately above the concrete wall where their nest was. If the egg-guarding lizards did not return to the nests after the test, I used plastic nets to protect their nests from snake attacks. Clutches that were not predated hatched normally. The study was approved by the National Museum of Natural Science, Taiwan.

Statistical Analyses

I used sign tests to determine the response of the lizards when *O. formosanus* entered nests. Mann–Whitney tests were used to test the differences in egg numbers between attacked and unattacked groups (including escape and ignore responses) and the proportion of eggs hatching in protected and unprotected nests. To test for possible block effects caused by repeated use of individual snakes, I used Monte Carlo permutation tests (Wolframe Research 2003) to test for heterogeneity in the proportion of attack responses of the lizards when *O. formosanus* entered nests. I conducted separate analyses in the two groups of lizards with and without eggs. A nonsignificant result would indicate that all snakes generated about the same proportion of attack responses, allowing data to be combined across snakes. I used a chi-square test to determine the responses (attack, escape and ignore) of the lizards when *O. formosanus*, the other sympatric lizards (*J. swinhonis*, *S. incognitus*) and the lizard-eating snake *E. carinata* entered nests. Regression analyses were used to determine whether the proportion of lizards' responses that were attacks was affected by the snake's body size (SVL). All data conformed to normality and homogeneity of variance before analyses.

RESULTS

Response to *O. formosanus*

Females

Over the 3 years, I placed 20 snakes in holes containing females without eggs 107 times and I placed 14 of the 20 snakes in holes containing females with eggs 70 times. The differences in attack rate between the 20 snakes in the without-egg group and the14 snakes in the with-egg group were both nonsignificant (permutation test: without-egg group: $P = 0.66$; with-egg group: $P = 0.42$). Block effects caused by individual snakes can therefore be ignored in later data analysis. At nests with eggs females usually reacted strongly to snakes (53 attack, 11 escape, 6 ignore), but they usually escaped at nests without eggs (12 attack, 86 escape, 9 ignore; $\chi^2_2 = 80.22$, $P < 0.0001$). Most of the lizards returned to their holes even when they had initially escaped (55 returned to and 15 abandoned their nests; sign test: $Z = 4.66$, $P < 0.05$).

The SVL of snakes did not affect the tendency to abandon egg-free nests (regression analysis: $F_{1,17} = 0.17$, $P = 0.682$; Fig. 1). Similarly, lizards attacked snakes at nests with eggs regardless of snake body size ($F_{1,12} = 0.11$, $P = 0.746$; Fig. 1).

Males

I introduced snakes to 58 pipes containing male *M. longicaudata*, and found that none of them attacked the intruder: all males escaped immediately.

Relation Between Clutch Size and Parental Care

I divided all responses into two groups, female attacked or female did not attack (including ignore and escape), and compared clutch sizes between groups. The mean clutch size ±SE of females that attacked (6.73 ± 0.33; range 3–11, $N = 30$) was higher than for those that did not attack (4.25 ± 0.411; range 2–7, $N = 12$; Mann–Whitney U test: $U = 775.3$, $P = 0.0003$).

Response to Other Intruders

Egg-guarding females generally ignored conspecifics and other lizards (two attacks and 54 ignores for male *M. longicaudata*; 0 attacks, 56 ignores for *J. swinhonis*; 5 attacks

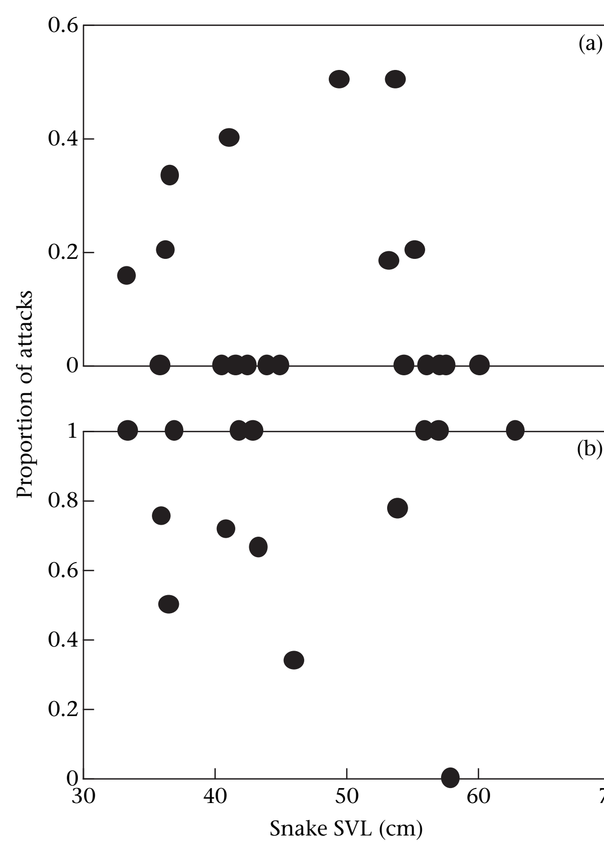

Figure 1. Relation between lizard attacks and snake snout∼vent length (SVL) for (a) egg-free nests and (b) nests that contained eggs.

and 51 ignores for *S. incognitus*), whereas female lizards always escaped when I put the lizard-eating snake *E. carinata* into the holes (two initially attacked but then escaped and 54 escaped immediately; overall test comparing all types of intruders; $\chi^2_6 = 221.65$, $P < 0.0001$). The lizards never returned when the intruders were *E. carinata*.

Egg Survival

Most egg loss was caused by fungal infections (12 eggs, 2.8%) or by the attacks of ants (19 eggs, 4.5%) and snakes (36 eggs, 8.6%). If eggs were attacked by fungi or by ants, eggshells remained visible at the nest site; eggs disappeared if they were eaten by snakes. The major factor that caused egg death in unprotected nests was predation by snakes.

The percentage of eggs hatching was higher for protected (guarded) nests than for unprotected nests (protected nests: median 81%, range 50–100%, $N = 70$; unprotected nests: median 18%, range 0–100%, $N = 32$; Mann–Whitney U test: $U = 3638.19$, $P < 0.0001$). All egg loss in the unprotected nests was due to *O. formosanus*.

DISCUSSION

Parental Care

Egg guarding is among the most basic and primitive forms of parental care, and an understanding of its evolution might lead to insights into the origin of parental care in other animals (Reynolds et al. 2002). The adaptive significance of egg guarding in *M. longicaudata* was demonstrated here by the dramatic reduction in hatching success (70%) after experimental removal of females. Few females abandoned their eggs in the field, further supporting the suggestion that egg guarding radically improves parental fitness. This result matches that for female treehoppers, *Publilia concave*, where early abandonment of eggs was also associated with a nearly 50% reduction in hatching success (Zink 2003).

Clearly, defence of eggs against attack by oophagous snakes was the primary factor that elicited attacks by mothers in *M. longicaudata*. However, *M. longicaudata* showed a unique type and intensity of maternal defence behaviour, one that is sensitive to local factors. Clutch size affected the level of maternal aggression. Little or no maternal aggression was provoked in empty nests, and females abandoning eggs had smaller clutches. Similar phenomena have been reported in the cichlid fish *Oreochromis mossambicus* (Oliveira & Almada 1998), lizards (genus *Egernia*: Chapple 2003; *E. saxatilis*: O'Connor & Shine 2003, 2004) and mice, *Mesocricetus auratus* (Giordano et al. 1984). In cichlid fish, when the brood was removed from the mouth of a female, the level of aggression quickly declined, and a day later her agonistic profile and colour pattern could not be distinguished from those of nonbrooding females (Oliveira & Almada 1998). Similarly, when female mice are separated from their pups they become markedly less aggressive (Giordano et al. 1984).

Of 107 female *M. longicaudata*, 12 showed attack behaviours even when they were tested at empty nests. However, 10 of these 12 females were carrying eggs and might already have been under the influence of the neurohormonal mechanisms that underlie defence of eggs in the nests.

In multiple-clutch species, parents can be strongly constrained by time and/or energy, facing conflicts between breeding, hatching and the establishment of territories (Sanz & Tinbergen 1999). In birds, clutch size is generally thought to be limited by (1) the ability of parents to rear young (Lack 1947), depending on their condition and territory quality or (2) the cost incurred by the parents (subsequent fecundity and/or survival) when rearing too many young (Daan et al. 1996). Unlike birds, however, *M. longicaudata* does not rear or guard its hatchlings. In a lizard showing maternal care, a larger clutch size may be better because the cost of guarding is similar for large or small clutches. However, an alternative hypothesis postulates that whether the female attacks intruders or escapes may depend on experience with social aggression, such that subsequent encounters with the same species result in attacks (Kudryavtseva 2000). For example, mice given repeated opportunities to fight attack more than individuals lacking such experience (Parmigiani & Brain 1983). In *M. longicaudata*, escape behaviour and small clutches are correlated with small body size (Huang 2004); that is, if smaller females are less experienced at guarding eggs they might be having their first encounter with a snake, and thus they always escape. Further studies are necessary to test this learning hypothesis using marked individuals with known histories.

Experimental Intruders

There are many strategies by which prey may reduce the probability of capture by predators, including the avoidance of microhabitats where risk of predation is perceived to be high, or reducing activity during periods when predators are most active (Lima & Dill 1990; Mathis & Smith 1993). Prey survival often depends upon the effectiveness of patterns of antipredator behaviour that are performed only after a potential predator has encountered a prey item (Greene 1988). Furthermore, the ability of prey to distinguish predators from nonpredators has important implications. Failing to recognize a predator is likely to increase the probability of capture during an encounter (Hirsch & Bolles 1980), and defensive response to nonpredators may waste time and energy (Hansen & Slagsvold 2003).

Female *M. longicaudata* remain in the nests after laying and guard their eggs for long periods during incubation (Huang 2004). In this study, potential predators of the eggs (*O. formosanus*) were attacked, but species that are not egg predators were ignored (i.e. conspecific male *M. longicaudata*, *J. swinhonis* and *S. incognitus*). However, after exposure to a predatory snake, *E. carinata*, attending *M. longicaudata* ran away immediately and never returned to their nests. Females took greater risks for eggs but sometimes left them exposed to higher predation risk from egg-eating snakes. These results suggest that the benefits of desertion may depend on the female's ability to defend a nest or the potential for deserting females to lay another clutch in the same season. My observations also show that *M. longicaudata* responds differentially to a lizard predator *E. carinata* and an egg-predator *O. formosanus*, as well as to nonpredator lizards. Further study is necessary to determine which cues induce lizards to attack, escape or ignore an intruder.

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