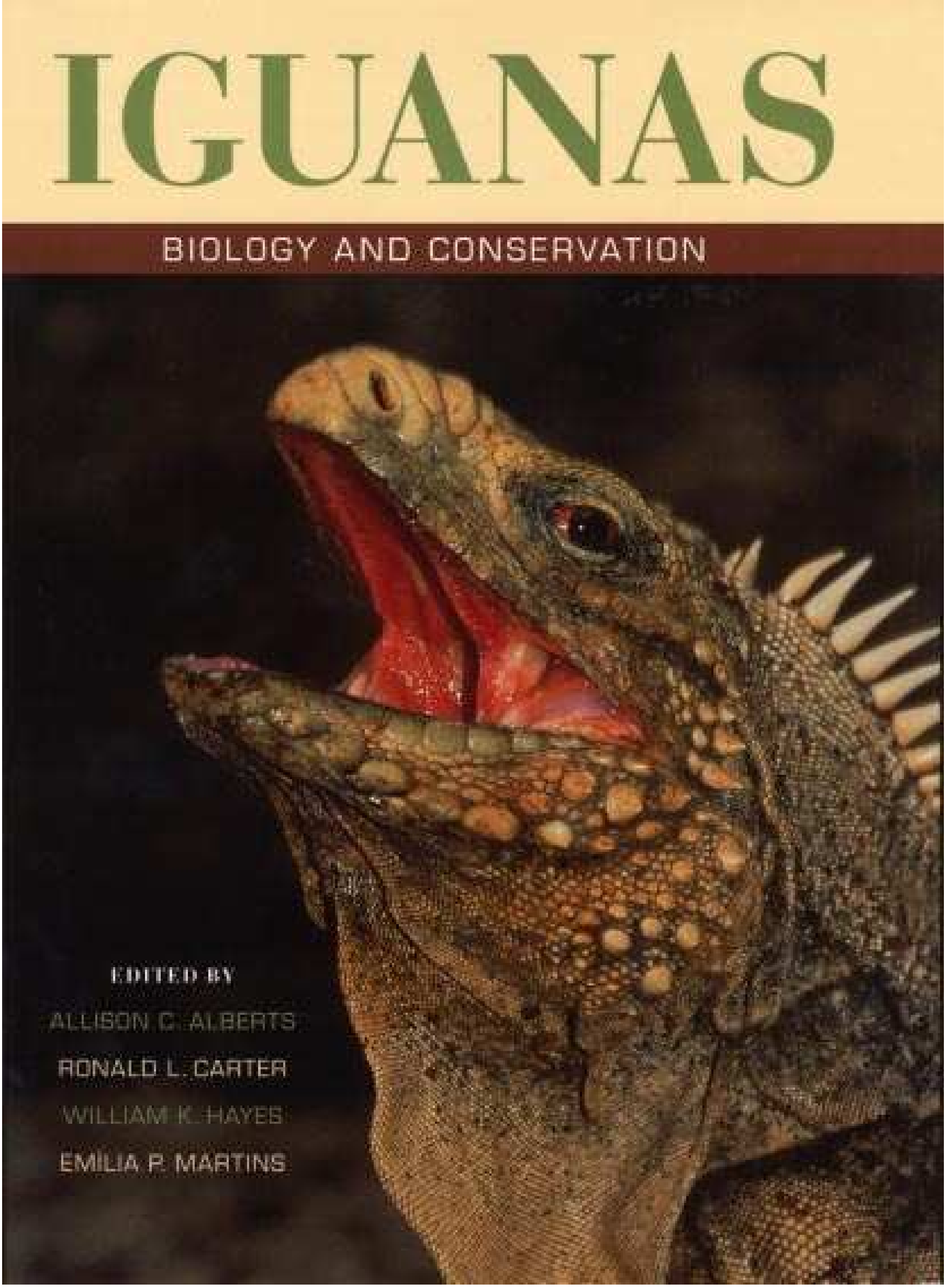

IGUANAS

BIOLOGY AND CONSERVATION

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9

Sexually Dimorphic Antipredator Behavior in Juvenile Green Iguanas

KIN SELECTION IN THE FORM OF FRATERNAL CARE?

Jesús A. Rivas and Luis E. Levín

THE BENEFITS OF SOCIALITY have been widely discussed. Because the probability of detecting an approaching predator increases with the number of guarding eyes, it has been proposed that animals gain protection against predators by living in groups (Brown and Brown, 1987; Da Silva and Therhune, 1988; Yáber and Herrera, 1994). Other benefits to sociality include decreased likelihood of predation through the selfish-herd effect (Hamilton, 1971), active deterrence of predators (Gross and MacMillan, 1981), and confusion of predators through a perceptual bottleneck that leads to lower capture efficiencies (Krakauer, 1995).

Studies of antipredator behavior in gregarious reptiles have not been thorough in any species (Greene, 1988). In particular, studies of social behavior in iguanas have focused on territorial interactions and mating behavior (Rand and Rand, 1976; Alberts et al., 1992a; Rodda, 1992; Phillips et al., 1993; Pratt et al., 1994). Although some attention has been given to the benefits of sociality in predator avoidance among green iguanas (Burghardt, 1977b; Burghardt et al., 1977; Greene et al., 1978; Burghardt, this volume), these studies have been observational rather than experimental. Most carnivorous species are expected to show the types of territoriality and intraspecific aggression that is widely documented among lizards (e.g., Stamps, 1983). However, as a result of their strictly herbivorous diets, iguanas might be expected to differ from other lizards due to decreased competition for food resources.

Cooperation among relatives has been reported in many species of social insects as a mechanism to increase fitness by increasing the reproductive output of related individuals (Hamilton, 1964). For example, in honeybees, there are a variety of social behaviors in which some siblings care for and brood younger ones (Wilson, 1971). Some vertebrates have been reported to show analogous behaviors (Alexander et al., 1991). To date, there have been no reports of any reptile performing similar altruistic acts. Indeed, we know of no vertebrate in which siblings protect other siblings of the same age.

From 1988 to 1991, we hatched eggs from both natural and artificially incubated nests of green iguanas *(Iguana iguana)* at Hato Masaguaral, a cattle ranch and biological field station located in Estado Guárico, Venezuela (8°34′ N, 67°35′ W). We repeatedly observed that when a researcher approached a naturally hatching nest, some animals remained immobile at the entrance to the nest, while one to several others fled. Such escape attempts were not usually directed toward cover, but rather toward the observer or into relatively open space. The animals typically ran along a straight trajectory with their tails raised.

When we handled iguanas incubated in artificial nests, they frequently ascended our arms, in an apparent escape maneuver potentially related to their natural tendency to escape by climbing trees. However, similar to the behavior we observed in the field, other individuals either froze or hid in the bottom of the enclosure. Their subsequent behavior depended on the observer's/intruder's behavior. Most iguanas remained immobile or hidden if we remained motionless, but if we chased the fugitive, then five or six additional individuals would flush from the nest. In the seven instances where we were able to capture the fugitive, it was a male. A similar behavior was observed in ten-month-old animals.

Given that the sex ratio at birth is 1:1 in green iguanas (J. Rivas, unpubl. data), we would have expected to find females among the fugitives if the likelihood of males and females exhibiting these behaviors were the same. That we did not prompted us to carry out two pilot studies of sexually dimorphic antipredator behavior in juvenile green iguanas. Such behavior has been reported in other juvenile squamata (Greene, 1988; Herzog et al., 1989). Here we present our preliminary observations and discuss their possible implications.

SIMULATED PREDATOR RESPONSES

Our initial field observations suggested that males reacted more actively than females to potential predators. However, because we did not know the sex ratio of the animals in the nest at the time we found them, we were unable to draw solid conclusions. To further explore this phenomenon, we observed the reactions of juvenile males and females to a simulated predator under controlled conditions. For five months, animals from different artificially incubated clutches were kept in separate outdoor enclosures measuring 60 × 60 × 80 cm and fed daily with a mixture of papaya and dog food supplemented with vitamins and minerals. Twelve groups were formed, each composed of five females and five males from the same clutch. Sex was determined through visual cloacal examination (Rivas and Ávila, 1996).

The experimental arena was a rectangular opaque plastic enclosure measuring 180 × 30 × 30 cm. Dimensions were chosen to limit the direction in which the animals could flee, thus making it easier to score the behaviors. The bottom of the arena was lined with foam rubber to provide traction, with a 10 × 10-cm refuge (consisting of an opaque cover supported by four 2-cm legs at its corners) placed at the center of the arena. The refuge was encircled by a removable 25 × 25 × 30-cm transparent plastic corral, which at the beginning of the trial enclosed the iguanas (figure 9.1). The trial was initiated by remotely lifting the corral to avoid disturbing the animals. The arena was illuminated by eight-reflector hood lights hanging from the room ceiling.

The simulated predator consisted of a model of a hawk species *(Falco femoralis)* known to prey on juvenile iguanas (Rivas et al., 1998). The body of the model was constructed of wood and the wings of cardboard (39 cm long × 52 cm wide). The shape, color, and body pattern were based on a descriptive illustration of the bird (Phelps and De Schauensee, 1978; figure 9.2). Eyes were simulated with two black dots (Gallup, 1973; Burger et al., 1991). To add a mechanical component to the stimulus, a celluloid sheet was hung below the model, which, when in contact with the wall of the enclosure, produced noise and vibration. Air movement, contact by the celluloid sheet (simulating the bird's feathers) and the shadow of the model (Prestude and Crawford, 1970) were additional components of the stimulus. The model was fixed to one end of a pen-

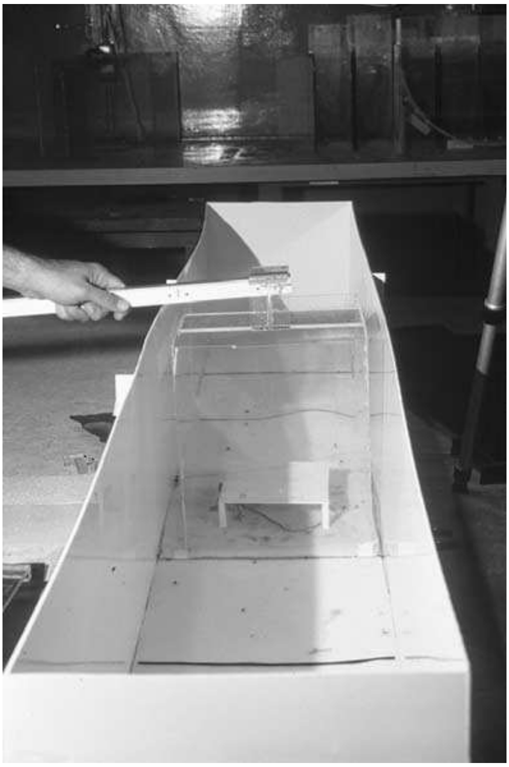

FIGURE 9.1. Test arena for simulated predator presentations to juvenile green iguanas.

dulum. The other end was articulated at a hinge joint on the ceiling above the refuge. The pendulum was held horizontally by an electromagnet fixed to the ceiling of the room. When the electromagnet was turned off in an adjacent observation room, the model swept down over the arena.

All observations were carried out during the normal daily activity period. For ease of recognition during experimental trials, females and males were labeled with black and white tape, respectively, on their backs. After two hours of acclimatization to the test arena, the plastic corral was removed, and five minutes later, the stimulus was presented. We let the model pass over the arena forward and backward three times and recorded the first movement performed by each animal during the three passages. After the trials, all animals were returned to the field and released at the site where the eggs were collected.

The iguanas' behavior was recorded with a video camera placed 2 m above the refuge. During preliminary trials, some iguanas concentrated at the end of the enclosure, and a second camera was directed at this area. Recording alternated between the two cameras by an electronic switch operating at one-second intervals. Trials were analyzed at one-fifth of actual speed, and frame by frame, where necessary. We scored the following mutually exclusive behaviors during each passage of the pendulum: moving ahead of the model running in the same direction as the model, moving in the opposite direction of the model, hiding under the refuge, and appearing from under the refuge and exposing either part or all of the body. We also observed an unexpected behavior that consisted of one animal climbing onto another animal and covering it with its body at the moment when the model was starting its downward movement.

Risky behaviors, such as running in front of the hawk, appearing from under the cover, and covering another iguana were performed most often by males (table 9.1). Females more often performed behaviors that increased safety, including hiding, immobility, and running in the opposite direction of the model. Only males (seven of twelve trials) showed the behavior of covering another iguana, and it was always directed toward females.

Both male and female iguanas responded more strongly when the model predator passed in a forward direction. This result suggests that the iguanas discriminated the shape of the model, responding more actively to the head-forward movement of the hawk model, as found by Tinbergen (1948) in gray geese. The forward movement of the hawk also might have presented additional predator cues (e.g., eyes) to the iguanas (Gallup, 1973; Burger et al., 1991).

In evolutionary terms, the higher responsiveness of the males to the simulated predator could have two opposing but not mutually exclusive explanations, one selfish and the other altruistic. First, this rapid response might surprise a searching predator and give the iguana more time to escape at the expense of the remaining

FIGURE 9.2. Frontal view of the hawk model presented to juvenile green iguanas.

TABLE 9.1

Responses by Male and Female Juvenile Green Iguanas to the Forward Passage of a Simulated Hawk Model

ACTION	NUMBER	
	FEMALES	MALES
Move ahead of the model	20	35
Move in the opposite direction	5	2
Hide	6	3
Appear	1	4
Cover another	0	7
Remain stationary	28	9

Notes: Only the first movement performed by each animal during the three passages of the model was scored. Moving ahead of the model, appearing from under the refuge, and covering another animal were lumped together as risky behaviors. Hiding and moving in the opposite direction of the model were labeled as risk-averse behaviors. The difference in the first behavior performed by individual females and males in response to the model was highly significant ($\chi^2_1 = 24.43$, $P < 0.001$), with males showing more risky behavior than did females. The hypothesis of equal probability for both sexes of covering another was rejected by a two-tailed binomial test ($P < 0.02$).

animals. Alternatively, it might serve to divert the predator away from others, giving his relatives the opportunity to escape. If the fugitive escapes, he accomplishes the double goal of surviving and helping his clutchmates to escape. If he fails to escape, he may still provide the opportunity for his siblings to escape.

The selfish explanation requires that the escapee start the escape early, when the probability of escaping successfully is high. Conversely, the altruistic explanation requires that the escapee wait until the attack on the group is imminent, and assumes that the predator does not know that additional animals are present. Our preliminary observations do not support one hypothesis over the other. However, in observations of natural nests, escapes took place after digging and harassing the animals for some time, which does not support the selfish hypothesis. The high synchrony of hatching, in which several hundred iguanas may emerge from a single nest site over approximately two or three weeks (Burghardt, 1977b; Burghardt et al., 1977; Rivas et al., 1998), may limit opportunities for predator learning. In fact, predators cueing on mass hatching events could have been an evolutionary force leading to such synchrony, as has been documented in tadpoles of *Bufo boreas* that metamorphose synchronously to decrease predation by garter snakes (Devito et al., 1998).

Our observations suggested that females stay motionless more often than males (table 9.1). Avoiding detection by predators is crucial for iguanas, given that a small iguana probably cannot repel a relatively large bird (Greene et al., 1978); one strategy to avoid being detected is to remain immobile (Prestude and Crawford, 1970). Greene et al. (1978) reported that a young iguana avoided being discovered by a hunting coati (*Nasua* sp.) by freezing.

Given the relatively high speed of an approaching falcon, to run in front of the predator, a behavior seen more frequently among males, is arguably more likely to attract the hawk's attention than to facilitate escape. Indeed, for an iguana attempting to escape by running, the best direction to run would be in the opposite direction of the flying hawk. Movements in the opposite direction of the model, which could have avoidance advantages, were more frequent in females than in males (table 9.1).

Covering behavior is particularly striking. In all likelihood, a male that covers a female with his body increases his risk of being predated while decreasing hers. Our observations strongly suggest the possibility of an altruistic behavior in which a male assumes the predation risk of his female clutchmates. That females never climbed on any other animal and males climbed only on females leads us to speculate that this behavior could be performed to protect the females that are being covered. Because males never climbed on each other or on the refuge, we find it unlikely that the observed instances of covering another may be misdirected climbing behavior in the presence of a stressful situation. Earlier studies have reported juvenile iguanas perching and sleeping in physical contact with each other and even on the top of each other (Burghardt, 1977b; Burghardt et al., 1977; personal observation), indicating that covering behavior occurs in other natural contexts. Unfortunately, inability to determine the sex of juveniles in these studies prevented collection of the information needed to document behavior in the wild. Future studies should address this issue.

NATURAL PREDATION

Responses to the simulated predator suggested that males may be more risk-prone than females in their antipredator behavior, a response pattern that could have opposing consequences for male survival. Males could surprise the predator, allowing them to escape more often than females who respond less actively. Another possibility is that the behavior of males attracts the attention of predators, facilitating higher survival of their female clutchmates. To see how our observations in captivity may be related to the wild, we examined survival probabilities of males and females facing free-ranging, natural predators.

We excavated eight nests from the communal nest at Hato Masaguaral (Rodda and Grajal, 1990) and incubated the eggs until hatching. A total of ten groups was used, each composed of seven females and seven males, up to two weeks old, randomly chosen from the same clutch. Animals were identified with a number drawn with ink on the ventral side. Snout-vent length (SVL), total length, and mass were measured for each animal. A 3 × 3-m outdoor escape-proof enclosure was constructed with 60-cm-wide zinc sheeting. The enclosure contained a shelter made from a 40 × 40-cm wood board on two cinder blocks, under which food and water were placed. Several 40-cm natural bushes were included in the enclosure to provide natural perches and hideouts for the animals. Animals were released into the enclosure at 0600 and exposed to natural predators until 1800 (twelve trials) or released at 1800 and exposed to natural predators until 0600 (six trials). At the end of each trial, we recorded which animals were present or absent. For animals that were present, we noted which were missing a piece of the tail, as evidence of attack. Absent animals were scored as predated.

During diurnal trials, we saw some avian predators flying nearby or perching next to the enclosure, including savanna hawks *(Heterospizias meridionalis)*, crane hawks *(Geranospizias caerulens)*, and great kiskadees *(Pitangus sulphuratus)*. A snake was also seen in the area *(Chironius charinatus)*. All of these animals are known to prey on juvenile iguanas (Rivas et al., 1998). Nocturnal predators seen included opossums *(Didelphis marsupialis)* and an unidentified rodent that entered the enclosure. Actual predation events could not be documented, as our proximity would have deterred predators from approaching the enclosure.

Of the 140 animals tested, twenty-one were predated and 71% of these were males ($\chi^2_1 = 3.86$,

TABLE 9.2

Number of Juvenile Iguanas of Each Sex That Were Predated Naturally in Outdoor Experimental Enclosures

TRIAL	FEMALES	MALES
1	0	2
2	2	2
3	0	1
4	0	2
5	1	0
6	1	1
7	0	1
8	0	2
9	1	3
10	1	1
Total	6	15

Note: Each trial was based on fourteen siblings (seven males and seven females).

$P = 0.05$; table 9.2). We compared the mean SVL of males (74.89 ± 3.04 cm) with that of females (74.59 ± 2.57 cm) and found no significant difference ($t_{138} = 0.63$, $P = 0.53$). Nor was there a difference between mean mass of males (12.44 ± 2.29 g) and females (12.45 ± 2.26 g; $t_{138} = 0.04$, $P = 0.97$). Neonate green iguanas are not sexually dimorphic; therefore, selective capture of larger animals by predators cannot explain the observed differences in predation rate between the sexes. We also compared the mean SVL and mass of animals that survived (74.89 ± 2.72 cm; 12.62 ± 2.26 g) with those that were predated (74.61 ± 2.87 cm; 11.93 ± 1.99 g). No significant effects were found for either SVL ($t_{138} = 0.41$, $P = 0.68$) or mass ($t_{138} = 1.32$, $P = 0.19$).

Among the surviving animals, seven (five females and two males) were missing a piece of tail, presumed evidence that they had sustained an attack. Our findings suggest that the high responsiveness of male juvenile green iguanas to predators does not contribute to their individual survival. Males were predated more often than females, lending little support to the hypothesis that the males enhance their probability of successful escape by surprising predators. Rather, the risky behavior of males seems to attract the attention of natural predators.

The refuge provided within the enclosure was large and protective enough for the iguanas to escape beneath it and avoid detection. Thus, the animals that were predated had the option of either hiding or being exposed. The larger number of males predated cannot be explained by sexual dimorphism in body size, as we did not detect any differences between the sexes in SVL or mass. We presume that the higher number of males predated is the result of behavioral differences, a conclusion supported by the observed differences in behavior between the sexes in their responses to the simulated predator. The larger number of females missing part of the tail suggests that females do get attacked by predators, but that they manage to escape predation more often than males. It is possible that covering behavior by males toward females explains these findings, but field experimentation is needed to document the extent to which these patterns occur in nature.

KIN SELECTION IN THE FORM OF FRATERNAL CARE?

We observed that male iguanas seem to show more risk-prone behavior than females when presented with a model predator and were predated more often than females by natural predators. Here we offer two nonmutually exclusive explanations that may help explain our observations, one involving mechanisms of control, and one involving adaptive function.

If it occurs in the wild, the risk-prone behavior of males that we saw in response to the simulated predator could attract attention, resulting in the higher mortality we observed in the field enclosure. One possible explanation for this behavior in males is a consequence of higher androgen levels, important for social dominance in early stages of maturation (Phillips et al., 1993; Pratt et al., 1994). To be dominant early may produce a larger payoff later in life that outweighs the cost of increased risk of predation. Thus, the higher risk incurred by males may be a by-product of the social system of green iguanas, in which dominant males perform the vast majority of mating as adults (Dugan 1982a; Rodda 1992). However, higher androgen levels do not explain the difference in the direction of runs performed in response to the predator model, in which males ran in front of the model more often, while females tended to run in the opposite direction. Nor do they explain the covering behavior exhibited by males directed toward females. In addition, this hypothesis requires that the benefits of high androgen levels outweigh the increased predation risk. Neonate green iguanas suffer extremely high predation pressure by a large variety of predators (Rivas et al., 1998), meaning that the benefits of increased androgens would have to be extremely high for this explanation to be tenable.

Another explanation for our results suggests adaptive reasons for the observed differences in behavior of males and females. Males react more actively than females, which may attract the attention of a predator and increase the chance for clutchmates to escape. This apparently altruistic behavior can be explained in terms of kin selection (Hamilton, 1964). Because they are from the same nest, the probability that such males and the individuals they assist are siblings is high. Hence, an individual could potentially increase its indirect fitness by increasing the survival probability of his peers. It has been reported that green iguana hatchlings show a tendency to remain in groups in the wild for many months (Burghardt, 1977b; Burghardt et al., 1977; Drummond and Burghardt, 1982; Burghardt and Rand, 1985) and that individuals recognize and prefer to group with their kin (Werner et al., 1987).

Female green iguanas perform seasonal migrations to lay eggs in communal aggregations, showing a high degree of philopatry (Bock et al., 1985; Rodda and Grajal, 1990). These nesting aggregations are isolated from one another, leading to low levels of heterozygosity (Bock and McCraken, 1988). This pattern suggests the possibility of breeding with relatives (Waldman and McKinnon, 1993) such that relatedness among the hatchlings would be higher than the expected 0.5, conditions under which cooperative behaviors are more likely to evolve (Michod, 1993). Thus, a male that attracts a predator toward himself and saves several clutchmates might be increasing his indirect fitness. Such fraternal care could help account for the maintenance of sociality in juvenile green iguanas. Because only animals within a cohesive social group will benefit from such risk-prone behavior, it benefits clutchmates to stay together.

A remaining question is why males should direct their altruistic behavior differentially toward females. One possible explanation derives from differential variability in the reproductive success of males and females. Iguanas breed in harems that are vigorously defended by dominant males (Dugan, 1982a; Rodda, 1992). A male cannot gain control of a harem until he reaches an appropriate size to fight and win contests. Dugan (1982a) suggests that a male needs six or seven years to reach the size at which he can defend a territory, and even then, only a fraction of males can successfully control a harem. Females, on the other hand, virtually all breed by their third year, with some breeding as early as 1.5 years. Once they reach maturity, females breed annually (Werner, 1991; Rand and Bock 1992). Due to high rates of predation in the wild and strong intrasexual competition, the probability of a male reaching breeding size and controlling a harem is very low. Given that variance in breeding success is so much lower for females than males, a male that protects his female clutchmates might be significantly increasing his inclusive fitness.

Future studies are needed to determine if the risk-prone behavior we observed in males occurs in the wild, and if so, whether it is maintained into adulthood. Dominance relations are established early in life among male green iguanas (Phillips at al., 1993), but their significance for adult mating success can only be speculated upon. One might expect risk-prone behaviors to be most beneficial to young, subordinate males that have a low probability of reproducing successfully as adults. For such males, the best option may be to enhance survival of their female clutchmates, for whom variance in adult reproductive success is considerably lower. Further testing would be helpful in determining if altruistic risk-prone behavior is more prevalent among males of lower competitive ability.

Energetic constraints associated with herbivory may be an important evolutionary force in maintaining altruistic behavior in green iguanas. In this species, variance in male reproductive success may be due in part to the very long period of time it takes for dominant males attain the large body size needed for successful territory defense and harem control. Larger size has been related to the evolution of increased colon complexity, necessary for high efficiency in digesting the energy-poor diet that characterizes herbivory (Iverson, 1982). That males with slow growth rates as a consequence of the low nutritional value of plant matter will remain small for extended periods with a low probability of breeding compared with larger, older males (Pough, 1973; Rand, 1978) may have led to alternative strategies for increasing individual fitness.

This is the first report of possible altruistic behavior in any reptile, excluding parental care. However, the traits that favor its evolution are not unique to green iguanas. All iguanines are folivorous and most have similar hierarchical social structures and mating systems. Therefore, the potential exists for altruism to be present in other related taxa. However, the evolution of altruistic behavior might not be favored or might be constrained in some groups. Taxa living on islands (e.g., *Amblyrhynchus, Brachylopus, Conolophus, Cyclura*) with lower predation pressure and smaller clutch size would not be predicted to exhibit the altruistic behaviors reported here. Similarly, iguanines living on the mainland that have an insectivorous stage in their life cycle *(Ctenosaura)* may be less likely to evolve altruistic behavior because the cost of sociality in juveniles might be much higher due to competition for limited food resources. Mainland species that are herbivorous throughout their lives would be good species to examine for the behaviors described here. In particular, the genus *Sauromalus* meets these conditions and is genetically closely related to the green iguana (Sites et al., 1996). The insular species *I. delicatissima* would be another interesting taxon to consider because it is very closely related to *I. Iguana,* but does not experience the putative environmental conditions expected to lead to altruism. More details on the phylogeny, ontogeny, consistency, and variance of these altruistic behaviors, as well as on their relationship to ultimate reproductive success of those that perform and benefit from them are needed to understand fully the potential role of altruism in iguanine lizards. We have shown how antipredator strategies of green iguanas, like other aspects of their behavior (Burghardt, 1977b), seem to be far more complex than previously believed. Our observations are the first report of possible fraternal care in a reptile, and suggest intriguing avenues for future research. Behavior of reptiles has been considered as primitive and simple, but may actually involve a level of intricacy not previously appreciated.

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