Social Behavior in Hatchling Green Iguanas: Life at a Reptile Rookery

Abstract. *Hatchling green iguanas (*Iguana iguana*) emerge from the ground in small groups in a communal nesting area on a small Panamanian islet and engage in complex social interactions. Iguanas from different clutches often join together before and during departure from the nest site. They also usually move around the islet and migrate from it to the larger adjacent landmass in social groups. These and other observations indicate that the sophistication of saurian social organization and neonate behavior has been underestimated.*

Recent summaries of social behavior in terrestrial vertebrates emphasize birds and mammals; at most, they imply that complex activities in reptiles are restricted to territorial-hierarchical systems in lizards and parental care in crocodilians (*1*). Our more than 500 hours of observations of free-living juvenile iguanas in the Panama Canal Zone counter this widespread view. We now report highly adaptive coordination and timing of nest emergence and island migration activities in hatchling iguanas. These findings indicate sophisticated behavioral mechanisms we believe to be previously unrecorded in reptiles, and they suggest changes in our thinking on the evolutionary origins of vertebrate social behavior.

Green iguanas (*Iguana iguana*) are large (as long as 2 m), widely distributed, arboreal, Neotropical lizards; although some general information is known (*2*), most observations of behavior in the wild are casual and limited. However, the ecological niche of *Iguana* (that of an arboreal herbivore) is rarely filled by a lizard anywhere in the world (*3*).

We studied iguanas on Barro Colorado Island (BCI) and the adjacent islet of Slothia in Gatun Lake, Panama, Canal Zone. Barro Colorado Island is a 1600-hectare research reserve of rugged terrain covered with lowland tropical moist forest.

In January and February, mated female iguanas migrate to clearings to lay eggs (*4*). The scarcity of open areas in tropical forests may be one reason why large numbers of females congregate in the same small clearings year after year and intensively compete for a space to dig their nests (*5*). On the main island, mammalian predators often excavate such areas and devour the eggs (*6*). However, on the islet of Slothia (0.3 hectare), which is free of mammalian predators, a clearing approximately 6 by 7 m attracts as many as 150 to 200 females (Fig. 1). No iguanas live year-round on Slothia.

Although possible factors leading to communal nesting on Slothia have been analyzed for females and their eggs (*7*), the hatchlings have hitherto been ignored. Hatchling iguanas begin to appear in the first week in May, the onset of the rainy season. We studied them on Slothia in 1974, 1975, and 1976 through the 3-week hatching period (*8*).

After hatching, the young iguanas dug an escape hole 1.5 to 2.5 cm in diameter. An animal did not typically leave immediately. Rather, one or a few hatchlings periodically pushed their heads out of the hole and scanned the surroundings, occasionally flicking their tongues. Such repeated head movements sometimes occurred for long periods. If weather conditions changed (cooler, darker, rain), no animals might emerge at all that day. Often, however, after periods upward of 2 hours, one animal would begin to emerge from its hole and would be followed by others within a few minutes (*9*). The animals, who often appeared simultaneously at the entrances of holes, usually coordinated their head and body movements and seemed aware of each other's presence. Sometimes the holes were close together (Fig. 2), but often they were separated by 2 to 3 m.

Seeing other lizards at the entrance of holes facilitated emergence as is shown by the greater latency between head emergence and departure from the hole when only one nest hole was active. The average time between the first head emergence and first departure was 82 minutes, but the latency from head emergence to departure when heads were visible from at least one other hole was 11.7 minutes ($P < .02$, two-tailed Mann-Whitney U test). Sometimes between three and eight animals simultaneously squeezed out of the same hole (cover). Tongue extensions at the nest opening almost always immediately preceded complete emergence.

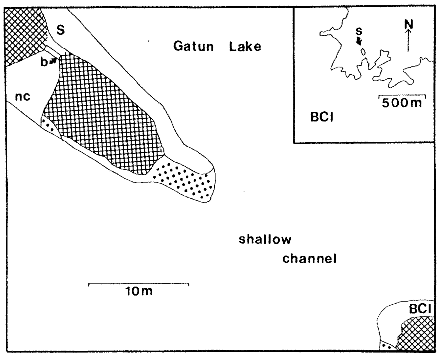

Fig. 1. Slothia (*S*) and the point of Barro Colorado Island (*BCI*) to which most iguanas migrated. Abbreviations: *nc*, nest clearing; *b*, blind. Dotted areas indicate reeds, and hatched areas, woods.

In 1975 we unobstrusively observed at the nest site from midmorning to early afternoon (approximately 0800 to 1300). On 6 days (not including those during which no animals were observed to emerge), a total of 89 animals left the clearing during a total of more than 20 hours. Only three of these animals left alone; one ran to a disturbance in the brush that may have been another lizard, and the other two each departed 5 minutes after other iguanas had left. The remaining iguana departures were either simultaneous or within 2 minutes of another. The emergence bouts totaled about 50 minutes out of the 20 hours.

Unlike singletons, the animals that emerged en masse from a single hole or from two or more holes often spent some minutes in the clearing, moving slowly and engaging in a variety of behavior patterns of presumed social import: vertical and lateral head movements, tongue licks at the substrate and other hatchlings, tail waving, thigh and belly rubbing, dewlap extension, and nipping at the abdomens and thighs of other iguanas. While most of these behaviors suggest visual communication, the tonguing and rubbing suggest chemical communication. Feeding on the sparse vegetation in the clearing was also observed. During the frequently synchronized movements that occurred at these times, animals from different clutches often moved off together (Fig. 3). If a disturbance occurred, particularly an aerial one, the animals scampered off rapidly. Surprisingly, few such instances occurred, which suggests that the many eyes of the group of iguanas at the hole entrances allow a good assessment of predator danger (*10*).

American crocodiles (*Crocodilus acutus*) and slider turtles (*Chrysemys scripta*) also hatch in the clearing in early May, but we saw no interactions between hatchling crocodiles and either turtles or iguanas. Hatchling crocodiles on Slothia emerge at night. Usually an adult, presumably the mother, excavates the nest in response to their peeping. The turtles emerge during the day, often at the same time as the iguanas. However, the two species seem mutually unaware of each other, and no interactions have been noted. The turtles migrated singly and more or less directly to the water. Such obliviousness between species ac-

Fig. 2 (left). Iguanas simultaneously emerging from three separate holes (marked with arrows) at Slothia nest site. Five iguanas are visible. Foreground hole is 9, directly behind it is hole 7, and off to the right is hole 8. The length of hatchling iguanas is, from snout to vent, 70 to 75 mm. Fig. 3 (right). Five iguanas from the three holes oriented to the right and are beginning to move off together (photographed a few minutes later than Fig. 2). The arrow indicates the head of a sixth iguana at hole 7.

centuates interactions and group movements of the iguanas.

Our observations suggest that iguanas usually emerge and move off in groups of from two or three to as many as twelve, although the larger groups could likely be broken down into subgroups by film analysis. Group size is probably affected by the number of hatched iguanas yet unemerged and the number of active nest holes. In 1975 the average group size (including the singletons) was 3.9. The iguanas moved off hesitantly with their heads raised high, their dewlaps often extended, and with frequent pauses and flicking of the tongue to the substrate. Groups moved together in the same direction and often seemed to influence the direction in which subsequent emerging lizards departed (*11*).

After leaving the nest area, most of the iguanas moved to the end of the islet closest to BCI, a narrow, reedy spot. Most eventually swam to BCI from there. During the 1974 and 1975 seasons, only 4 percent of 130 iguanas marked with paint at the nest site were sighted on Slothia more than 3 days after hatching (*12*). A few animals have been seen swimming the longer, 200-m route to the BCI shore from the other end of Slothia.

In the reeds, the cryptic iguanas usually perched close to each other, often in physical contact, and moved simultaneously or successively in spurts of activity. The animals sometimes moved about in groups of as many as a dozen and explored the rocky shore together. At night the lizards moved down into dense mats of grasses and reeds and were not visible. In the morning they began to move into the reeds, usually in groups. Chin, thigh, and belly rubbing, scratching, forelimb waving, and nipping of the body were noted. Eventually the animals moved far out onto the narrow point of Slothia. Here again they moved in groups over the reeds or with first one and then others running across the ground in virtually the same path.

The iguanas finally moved out onto the reeds extending over the water. As many as ten animals perched on the same set of reeds. Suddenly, first one and then another would either drop off the reeds or crawl out from the rocky shore. Of 47 iguanas we observed migrating to BCI from the reedy point, 43 left in groups of between 2 and 10 ($\bar{X}$ = 3.4, including singletons). Hours could elapse before another animal left, or no more might depart until the next day. Although the activities differed from those that occurred at the nest site, the temporal relations were similar.

There are several avian predators of the iguanas. We have also seen crocodiles and basilisk lizards (*Basiliscus basiliscus*) attack the migrating iguanas (*10*). However, the iguana can run swiftly and, if swimming, it can dive or run bipedally on the surface of the water to shore (we know of no other description of the latter activity).

In spite of the predators, most iguanas do reach BCI without incident. We conclude that two social factors aid their survival: (i) the coordinated social interactions, vigilance, and gregariousness of the young iguanas and (ii) the restriction of intense group activities to relatively brief periods of time. Both seem adapted to counter predators that are potentially able to exploit this yearly source of protein. The first factor is effective because predators are usually solitary and can capture no more than one iguana at a time. Further, the presence of several iguanas may cause confusion. The second factor creates difficulties for predators that cannot afford to wait indefinitely for the brief and unpredictable periods of activity.

We have confirmed synchronized activities and movements in neonate green iguanas. These lizards often virtually followed in the footsteps of each other, a behavior that has also been inferred from fossil footprints in dinosaurs but that seems to be uncommon in extant reptiles (*13*). Since such evidence is the only behavioral data that exist concerning the hypothesis that dinosaurs were behaviorally more advanced than extant reptiles (*14*), its existence in neonates of a living species should lead to caution in assessing such speculation (*15*).

According to widespread and traditional views, much of the complex social behavior in mammals and birds derives, ontogenetically or phylogenetically, from their often extended, intensive, and necessary parental care, behavior largely lacking in virtually all reptiles except crocodilians. Yet our observations show that much mammalian and avian social behavior may plausibly be influenced by ancient evolutionary mechanisms that were only refined and modulated by parental care once it appeared. Because there have been relatively few generations of iguanas (15 to 20) since Slothia was formed with the damming of the Chagres River in 1911, observations on other populations are now needed to investigate these broader concerns.

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8. Cine and still photographs were taken from a blind with no apparent disturbance to the animals. At other than observation times, animals were captured at the nest site and marked with paint so that we could trace their movements.
9. While the most intense emergence bouts occurred in late morning in bright sun, emergence also occurred during overcast days and from nest holes in the shade (Fig. 2). Thus, reaching a critical body temperature is not a satisfactory explanation, as animals emerged at substrate temperatures that varied from 27.5°C to more than 40°C. Temperatures at nest hole depth (50 cm) remained virtually constant during any one observation session; across days they ranged between 29° and 33°C. On 2 May 1975, we observed iguanas leaving in the rain. An animal was seen at the opening of a hole at 1000 hours. Its head was out momentarily and then gone for 2 minutes. The iguana popped up and down eight times in 42 minutes and had its head out almost 32 minutes. Within a minute, two new iguana heads appeared at the hole. After a total elapsed time of 65 minutes 40 seconds, one iguana ran off and was followed 80 seconds later by another.
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11. An impressive emergence bout was seen on 6 May 1975 (Figs. 2 and 3). At 0915 one lizard head was visible at hole 8. After 40 minutes a head appeared at hole 9 and 2 minutes later, another head at hole 7. During a 7-minute period beginning at 1013, six animals moved off to the right and then three to the left. One iguana from hole 7 went to an iguana head at hole 8 and both then left the clearing. Seven minutes later, four iguanas emerged and went to the left and were followed 6 minutes later by five more. During the next 52 minutes, no animals left the hatch area, but two departed from holes 7 and 9 oriented to the right, and another was at the entrance to 7. At this point, an iguana that had earlier gone to the right emerged from the vegetation and approached the group. After it and the others had engaged in some mutual head bobbings and tongue lickings, it moved through the group to the left. The three iguanas turned within about 5 seconds and followed the "stranger" to the left (filmed sequence). Five minutes later, five animals moved to the left and were followed 6 minutes later by first three and then five more. Three minutes later, 11 more left in over a 6-minute period in groups of two to four. Another 20 minutes of no activity was followed by a 5-minute explosive period in which 12 more emerged. From 1220 to 1225, four more animals left in groups of two. In the remaining period until 1245 hours, no more animals left the hole. A total of at least 61 lizards departed, all but nine leaving to the left. The emergence of the lizards over the 216-minute period (0910 to 1245) was not random [$\chi^2 = 85.95$ (the observation period was divided into 12 periods of equal length), d.f. = 11, $P < .001$].
12. Unlike observing at the nest site, observing at the reedy area did not require a blind. Standing or sitting quietly on shore or out in the water for several minutes was sufficient to habituate the iguanas to our presence. A portable blind was used during some photographic sessions.
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16. Quantitative results and expanded details of our studies on neonate green iguanas will be published elsewhere. Supported in part by grants from the National Institute of Mental Health, the National Science Foundation, and the Smithsonian Tropical Research Institute. We thank K. Milton and B. A. Dugan for comments on earlier drafts of this report. B. A. Dugan and J. A. Carter aided in the observations in 1976.

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21 May 1976; revised 8 September 1976

Pleistocene Avifaunas and the Overkill Hypothesis

Abstract. *At the end of the North American Pleistocene, birds and mammals suffered comparable degrees of generic extinction. Both the magnitude and pattern of avian extinction are incompatible with the hypothesis that humans played a major role in causing the demise of numerous North American mammalian genera at this time.*

The hypothesis that humans played a major role in causing massive extinctions of North American mammalian genera at the end of the Pleistocene has most recently been developed by Martin (*1–5*) in a lengthy series of ingenious and influential articles. After reviewing the archeological, biological, and geological records for the North American Pleistocene, Martin concluded that "prehistoric hunters ten to fifteen thousand years ago . . . exterminated far more large animals than has modern man" (*6*), that "man and man alone was responsible for the unique wave of late Pleistocene extinctions in North America" (*7*). Martin (*2*) has appropriately labeled this hypothesized phenomenon "Pleistocene overkill."

The overkill hypothesis is readily testable. Because it states that the end of the North American Pleistocene was marked by extraordinarily high rates of extinction of mammalian genera, this hypothesis requires terminal Pleistocene mammalian generic extinctions to have been relatively greater than generic extinctions within other classes of vertebrates at this time (*8*). Since 67 genera of North American mammals are known to have become extinct during the Pleistocene, of which as many as 32 disappeared between about 13,000 and 10,000 B.P. (before the present) (*4, 5, 9*), the overkill hypothesis predicts that in nonmammalian vertebrate classes, significantly fewer than 48 percent of the genera which became extinct during the Pleistocene became extinct at the end of this epoch. This prediction may be tested against the Pleistocene record for birds (*10*).

During the North American Pleistocene, 22 genera of birds are known to have become extinct (Table 1). In order to determine the proportion of these genera which became extinct at the end of the Pleistocene, it is necessary to turn to paleontological sites which contain avifaunas demonstrably deposited between about 13,000 and 10,000 B.P.

Such sites are exceedingly rare; of them, only Rancho La Brea contains a sizable and well-analyzed fauna. Located within metropolitan Los Angeles, Rancho La Brea deposits have provided over 85,000 bones and bone fragments pertaining to over 150 species of birds (*11*). A large proportion of these avian remains came from 13 excavation units. The faunas of five of these units (pits 10, 28, 36, 37, and A) lack the large Pleistocene mammals typical of the other Rancho La Brea units, are characterized by the predominance of the modern turkey vulture (*Cathartes aura*) over the extinct western black vulture (*Coragyps occidentalis*), and show relatively low proportions of large raptors and extinct avian species. Consideration of such attributes led Howard (*11*) to conclude that, of the 13 units with sizable avifaunas, pits 10, 28, 36, 37, and A lie closest to the Pleistocene-Holocene boundary.

Only one radiocarbon date is available for these five excavation units. This date (9000 ± 80 years, UCLA-1292 BB) was obtained for human bones from pit 10 which have long been recognized as occupying a vent which "passed through older asphalt deposits containing remnants of extinct late Pleistocene animals" (*12*). As a result, this date does not apply to the extinct avian genera of this unit. However, dates ranging from approximately 13,000 to over 40,000 years ago are available for seven of the eight remaining units (*13*). Coupled with Howard's arguments, these dates strongly suggest that pits 10, 28, 36, 37, and A postdate 13,000 to 14,000 years B.P.

The birds of these five units are represented by 1658 individuals belonging to 75 genera, of which 11 are extinct in at least North America (Table 2). With the exception of the passenger pigeon (*Ectopistes migratorius*), these genera are unknown in North American faunas which unquestionably postdate 10,000 years ago. It is reasonable to conclude that these genera became extinct during very late Pleistocene times.

Other North American faunas which date, or may date, to between 13,000 and 10,000 years ago simply provide additional instances of genera documented for this time span at Rancho La Brea (*14*). These other sites combined do not provide as substantial a record of terminal