

adult *Iguana iguana* (10 large males, nine medium and small males, and eight females) on a small island just off the Pacific coast of Panama, about 50 km from our study site. Our adult females were comparable in size to hers and had equivalent home range sizes. One of our juveniles (#9, a male) was large enough to be considered adult by Dugan's criterion. This and the next largest male in our study had Core Areas comparable to those reported by Dugan for small and medium sized males. However, the home range sizes for our two largest males were much greater than those reported by Dugan for large males. Whereas home range sizes of our large males were more than twice as large as those of the females, Dugan's large males maintained home range sizes only one quarter the mean size of her female home ranges.

Several factors may have influenced the differences in home range size between this study and Dugan (1982). Our study site receives more rain and supports lush vegetation than does Dugan's site (Rand and Rand, 1982), so it seems unlikely that our males had to range farther for food. Casual observations on repeated visits to both sites suggested that iguana densities were lower at our site, so our large males may have ranged more widely because they were less constrained by other territorial males. Alternatively, perhaps our two large males were behaviorally in Dugan's medium male class and subordinate to the larger males observed in our study area. Without further information the discrepancy between the two studies cannot be resolved.

Our finding that males have larger home ranges than females is consistent with reports for other iguanines (Iverson, 1979; Christian and Waldschmidt, 1984; Stamps, 1983), although the magnitude of the difference reported here is substantially greater. Our male iguanas maintained home ranges with substantially larger Core Areas than those reported for other iguanine lizards (with comparable data) by Christian and Waldschmidt (1984), whereas the Core Areas of our female iguanas were comparable.

Within other iguanine species, home range size is larger where food is scarcer (Krekorian, 1976; Iverson, 1979). It is unlikely that this explains the unusually large home range sizes of the adult male iguanas documented here because males and females have similar diets. It may be related to the fact that these *I. iguana*

do not have the same dependence on a burrow or refuge that many iguanines do.

In summary, *I. iguana* in central Panama are sedentary outside of the breeding season, restricting their movements to small home ranges, apparently largely along shoreline habitat. The adult male home range sizes documented here were larger than those of the females. Experienced females may migrate directly from their home range to a nesting area and back. Information on iguana movement patterns during the establishment and maintenance of breeding territories is still lacking.

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EGG FORMATION IN CROCODILES: AVIAN AFFINITIES IN YOLK DEPOSITION.—The evolutionary relationship between crocodilians and birds is clear at morphological levels, with general consensus that both groups arose from archosaurian ancestors (Romer, 1945; Feduccia, 1980; Martín, 1983). Crocodilians, the only extant archosaurs, therefore may be expected to share some behavioral and physiological traits with birds. Certainly, in nest construction, maternal nest guarding and hatching care, crocodilian parental behavior closely resembles that of some birds (Garrick and Lang, 1977). Though reproductive strategies adopted by reptiles include a spectrum of variations in the flexibility and degree of viviparous development (Shine, 1983, 1985), crocodilians are obligate in their oviparous habit and very little development occurs in the oviduct (Webb et al.,

1987). Similarly, crocodilian eggs share many general structural, biochemical and developmental properties with their avian counterparts (Packard et al., 1977; Ferguson, 1982). These similarities, along with their large yolked, calcium carbonate-shelled egg invited a comparison of yolk structure between crocodiles and birds.

Recent avian studies have revealed that there is more intraspecific variability in the timing and rates of egg formation than previously assumed from studies of domestic hen (Roudybush et al., 1979; Grau, 1984). Much of this understanding derives from analysis of the structure of fresh yolk which reveals a record of yolk deposition as a series of concentric layers (Riddle, 1911; Grau, 1976). These layers represent circadian periodicity with light-staining yolk being deposited nocturnally and dark staining yolk being deposited diurnally (Grau, 1976). Thus, the duration of vitellogenesis in days can be determined, as well as the rate of yolk deposition. Because yolk material is transported from the liver where it is synthesized to the ovary via the blood, a small dose of non-toxic, lipophilic dye administered to a prelaying female will color all yolk lipids transported through the follicle wall on the day of dosing. This results in a discrete, dyed yolk layer within the completed yolk and serves as a "date marker" in all eggs undergoing rapid yolk deposition (Grau, 1976). We have used this marker as an experimental tool in avian eggs to determine the dates of yolk initiation and completion and the timing relationships between eggs of the same clutch. Such studies have been significant in understanding possible energetic and ecological adaptations for reproduction (Grau, 1984; Astheimer, 1985, 1986).

Previous examinations of non-crocodilian reptile eggs (including several freshwater turtles and North American snakes) have not revealed any structure in the pattern of yolk deposition (Grau and Astheimer, unpubl.). To our knowledge, the data presented below constitute the first report of crocodilian yolk structure.

Materials and methods.—Fifteen infertile, freshly laid eggs of *Crocodylus porosus* (five nests) and five eggs of *C. johnstoni* (four nests) were collected in March 1986 and Aug. 1986, respectively, from the Northern Territory, Australia. The eggs were weighed and refrigerated until transferred to the University of Tasmania where

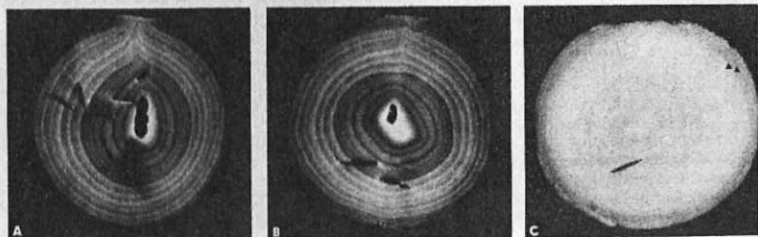


Fig. 1. Central yolk slices of two eggs from a clutch laid by a female *Crocodylus porosus* given lipophilic dye. Yolk halves in 1A and 1B have been treated with potassium dichromate and show enhanced ring structure. Note the similarity in the pattern of yolk layers. The yolk slice in 1C is from the unstained half of the yolk in 1B. Two yolk layers stained with Sudan red are indicated. Other variations in grey tones do not correspond to red stain. Mean yolk diameter is 43 mm.

they were treated as per Grau (1976). Briefly, intact eggs were placed under vacuum overnight to remove air dissolved in the yolk. Whole eggs were then frozen overnight at -20°C ; upon partial thawing, yolks were carefully removed and preserved in 4% formalin at 65°C for 16–18 h. After weighing, one-half of each yolk, bisected to one side of the blastodisc, was immersed in 6% potassium dichromate and kept at 65°C for 16–18 h. This staining procedure enhances the definition of the layers, revealing alternating pairs of pale and dark-staining yolk rings (Grau, 1976). Thick, central slices (1–2 mm) were made of the stained and unstained yolk for examination and photography.

A female *C. porosus* housed at Yarrawonga Zoo, Northern Territory was used in an experiment to place a date marker in the yolk. On 22 Oct. 1986, she was fed a 3 g dose of Sudan IV dye (red) contained in three No. 0 gelatin capsules which were concealed in a fish. Our original design called for 2–3 doses of different colored dyes to determine depositional rates over a known period. However, this female became refractory to feeding making a second dose impossible. Additionally, she was not interacting normally with her mate, who had seriously attacked her earlier in the year. Observers watched for traces of the dye in her excreta over the next 2 wk to estimate gut transit time, but none were found. Eggs laid by this female on 20 Dec. 1986 were collected and nine (the first five and last four laid) were treated as above; one was examined for fertility and embryonic development.

Results.—Yolk rings were found in all eggs examined from both crocodylian species. Layered structure was apparent in yolk before staining with potassium dichromate, but rings were poorly differentiated due to a lack of dietary pigment in the pale yellow yolk. Potassium dichromate treatment greatly enhanced the distinction between pale- and dark-staining rings which appear as clearly as those in avian eggs (Fig. 1A–B). The mean number of pairs of light and dark yolk rings in *C. porosus* was 14.9 ± 0.27 SD ($n = 20$). Intraclutch differences were even less, with the pattern of deposition being almost identical in all available eggs from the same clutch. Yolk rings in eggs of *C. johnstoni* were difficult to determine due to poor fixation.

The single dye-fed *C. porosus* laid her eggs 60 d after the dose was administered. The yolks of all 10 eggs examined contained two discrete pink layers near the outer margin of the yolk (Fig. 1C). These dyed layers occurred in the same position in the yolks of eggs laid earliest (1–3, 6–7) and latest (37–38, 40, 43–44) in the clutch. Comparison of untreated slices and those from the same yolk treated with potassium dichromate revealed that the dye rings corresponded to the 12th and 13th pairs of yolk rings deposited from a total of 15 (Fig. 1B–C).

The mean yolk mass for eggs of *C. porosus* was 51.59 ± 5.12 SD g ($n = 18$), representing an average of 46.2% of total egg mass. Intraclutch variations were much less, with SD ranging from 0.66–1.2 in small samples of eggs from three clutches. Taken with the similar intra-clutch pattern of deposition, these data

suggest uniform yolk deposition on all ovarian follicles.

Discussion.—*Crocodylus porosus* and *C. johnstoni* deposit yolk in a regular, periodic manner similar to that seen in avian eggs. The total number of yolk layers, 14–16, is found in eggs of both crocodile species and in a single yolk examined from an egg of *Alligator mississippiensis* (Grau and Lance, unpubl.). The pattern of yolk deposition in eggs from the same clutch is nearly identical, with the dye rings occurring in exactly the same position for all eggs examined from the dosed female *C. porosus*. This indicates that yolk deposition occurs evenly and simultaneously on a cohort of enlarging ova, without a follicular hierarchy. In addition, the total number of yolk rings varies little in eggs of *C. porosus* collected during two different seasons. These findings suggest that egg formation is a conservative process in crocodylians, as has been noted in birds (Grau, 1984).

Yolk deposition in crocodile eggs clearly represents a periodic function of yolk deposition, although it is not possible to determine the rate of deposition from the present data. In all avian species studied to date, each pair of light and dark yolk rings represents a 24 h period of deposition (Astheimer, 1986; Grau, unpubl.). Studies of crocodile thermoregulation and metabolism indicate that the female *C. porosus* would have completely assimilated the fish containing the dye dose within 1–3 d (Lang, 1979; Gatten, 1980; Coulson, 1984). Presumably the dye would also bind to plasma lipids and be deposited on enlarging yolks within the same period. The two dyed yolk layers observed in eggs of the dosed *C. porosus* were discrete, suggesting rapid deposition of dye-stained lipids. If these lipids had been stored, we would expect less well-defined dye rings with dye bleeding over many layers. Given these considerations, our initial impression was that yolk layers in crocodiles represented circadian deposition, similar to that seen in avian eggs. However, some evidence suggests longer periods of yolk deposition, as discussed below.

Daily deposition of yolk layers would require either retention of completed yolks for a very long period (57 d) before ovulation or holding fertilized eggs in the oviduct for part or all of this period. The latter possibility seems unlikely for freshly laid crocodile eggs normally contain embryos at a very early stage of development

(15–20 somites; Webb et al., 1987). Oviducal development beyond this stage is rare, unlike that seen in squamate reptiles (Shine, 1985), and extended periods of oviducal retention can be detrimental to normal embryo development (Manolis, pers. obs.). On the other hand, yolk retention or delay of ovulation for specific periods occurs in many avian species, although this "lag" period is not known to exceed 12 d (Astheimer and Grau, 1985; Astheimer, 1986). Nevertheless, we cannot dismiss the possibility that our dosed female exhibited abnormal nesting behavior and retained her eggs much longer than normal.

Evidence placing doubt on a circadian pattern of yolk deposition comes from a preliminary study of alligator eggs (Grau and Lance, unpubl.). One female *A. mississippiensis* was given two doses of dye 2 wk apart. In the single egg that was undamaged in shipping, the dye was apparent in two broad layers with only three pairs of yolk rings between them, rather than the expected 14. This suggests that each light and dark pair of yolk rings should represent approx. 5 d of deposition in this egg. Dye bleeding did occur from the innermost dye layer towards the subsequent layers, unlike the case in *C. porosus* where only two discrete dye rings were seen. When the date of yolk completion is calculated based on a 5 d interval between each yolk layer, this egg of *A. mississippiensis* would have been laid 30 d after completion of yolk deposition. This period corresponds well with the 21–25 d interval between ovulation and laying estimated from necropsies of female alligators killed early in the breeding season (Johanen and McNease, 1980; Lance, 1987).

Regardless of whether crocodiles retain completed yolks in the ovary or partially shelled eggs in the uterus, yolks begin enlarging up to 3 mo in advance of laying. In the Northern Territory, *C. porosus* synchronize egg laying with the onset of the wet season, which can vary from late Nov.–early Jan. (Webb et al., 1977). Delaying oviposition, by either follicular or oviducal retention in a late wet season, would have advantages over resorbing yolks produced too early and starting again, particularly for a species which rarely produces a second clutch. Interestingly, although some birds retain yolks in the follicle, this "lag" or "holding" period is of fixed duration and does not appear to be modulated by environmental conditions (Astheimer, 1986). Further studies of the timing of crocodile egg formation are needed to determine the rate of

yolk deposition and what, if any, environmental conditions account for its periodicity.

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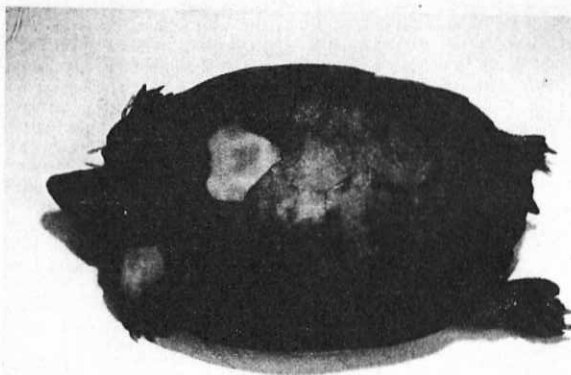


Fig. 1. Neotype of *Heosemys leytensis*, CAS 60930. Dorsal view.

The description of the cotypes comprises virtually the entire literature on this taxon, excluding regional or global lists and keys of chelonian species (Loveridge, 1945; Wermuth and Mertens, 1961; Pritchard, 1967, 1979; Obst, 1986; Iverson, 1986). No further specimens have been recorded, despite active searching recently by collectors sent from Silliman University to southern Leyte (Alcala, pers. comm.). The type specimens, a male and a juvenile originally kept in the laboratory of the University of the Philippines, were reported by Taylor (1944) to have been moved to the Bureau of Science in Manila. At the end of the Second World War, aerial bombardment reduced the Bureau of Science

to rubble along with the zoological specimens it contained.

The CAS possesses the only known specimen of *H. leytensis*, a female, CAS 60930 (Figs. 1-4). Records show that it was received by the CAS on 24 Dec. 1922; the original catalogue entry is at the bottom of a page devoted to reptiles collected at Cabalian, Leyte, by G. Lopez. However, where the collector's name would have been entered in the appropriate column, the pencilled notation "exchange from the University of the Philippines" was written. The original number given the specimen was 2385. It is highly probable that this sole female representative of *H. leytensis* was also collected by G.

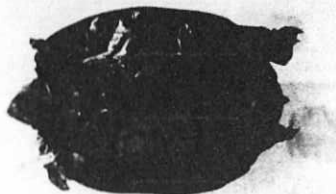


Fig. 2. Neotype of *Heosemys leytensis*, CAS 60930. Ventral view.



Fig. 3. Neotype of *Heosemys leytensis*, CAS 60930. Anterio-lateral view.

A THIRD SPECIMEN AND NEOTYPE OF *HEOSEMYS LEYTENSIS* (CHELONIA: EMYDIDAE).—Taylor described *Heosemys leytensis* in 1920 on the basis of two specimens collected near Cabalian, Leyte, the Philippines, by Lopez-

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