MOVEMENTS OF JUVENILE AMERICAN CROCODILES IN GATUN LAKE, PANAMA

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Abstract: The movement patterns of juvenile American crocodiles, *Crocodylus acutus*, were observed in Gatun Lake, Panama, by nighttime censusing and radiotelemetry in February and March 1981. Ten juveniles (nine 10 mo old, one 22 mo old) were radiotelemetered for an average of 233 fixes for each individual. The 10 mo old animals stayed within 300 m of the nest and had home ranges averaging 330 m of shoreline; 80% of movements occurred within core areas averaging less than 200 m. The 22 mo old animal dispersed about twice as far and included within its range at least twice as much shoreline as the younger animals.

On the basis of sharp reductions in the strength of the radio signals when animals submerged, I inferred that 35–45% of the animals were in exposed locations on the surface during the day, and <65% at night. Movements between locations were rare from 0900–1700 h, increased markedly after dusk, peaked around 0300 h, and dropped to near zero 2 h after dawn. Nocturnal movements were significantly reduced during periods of bright moonlight, although the percentage of animals exposed at the surface did not noticeably change.

Key words: *Crocodylus acutus*; Crocodylia; Panama; Movements; Dispersal; Home range; Radiotelemetry

THE American crocodile, *Crocodylus acutus*, lives in coastal areas throughout the New World tropics (Ogden, 1978). Systematic studies of its life history are lacking, although published observations (e.g., Alvarez del Toro, 1974) suggest similarities to the other large estuarine crocodiles (Cott, 1961; Messel et al., 1980). Like most crocodilians, the American crocodile is difficult to observe directly. Underwater radiotelemetry is difficult in the salty waters in which it is usually found. However, American crocodiles also inhabit some fresh water bodies, such as Gatun Lake in Panama. I radiotracked 10 juvenile crocodiles in Gatun Lake in order to determine the extent of movements, the daily pattern of activity, and the environmental factors influencing activity.

Methods

The 10 crocodiles were all found in the immediate vicinity of a nest site at the edge of a small lighthouse clearing on the mainland peninsula ending in Buena Vista Point, near Barro Colorado Island (Fig. 1). This was the only known nest site on the peninsula (Rand, unpublished data). In February and March 1981, I censused the 11.2 km southern shoreline of the pen-

insula four times by boat at night. All crocodilians were located by their conspicuous red eyeshine and were approached until the size and species could be determined. Nine other censuses were conducted away from the peninsula to obtain size distributions and observe the dispersion of juveniles around other nest sites.

The area used for radiotracking was typical of the relatively wave-protected shorelines bordering on the deep (~2 m) portions of the lake. Woody shoreline vegetation, such as *Terminalia amazonica*, *Mangifera indica*, *Cecropia* sp. and *Annona glabra*, extended 1–2 m over the water and often over a thin rim of emergent vegetation, notably *Montricardia arborescens* and a species of *Acrostichum*. *Hydrilla verticillata* formed dense mats of submerged vegetation in a band several meters wide located 1–10 m offshore. Where the *Hydrilla* reached the surface, it could support a juvenile crocodile.

Forty juvenile crocodiles sampled in Gatun Lake fell into two discrete size classes (25–29.5 cm snout–vent length (SVL), 220–380 g and 31–37 cm SVL, 390–710 g). Crocodiles in Gatun Lake hatch near the end of April (Dugan et al., 1981), so these size classes presumably
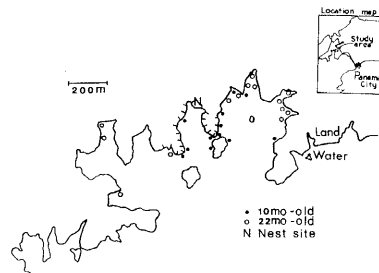
FIG. 1.—Map of the study area. The shoreline tick marks near the nest site indicate the shoreline sectors represented in Fig. 2. All the crocodilians found in this area were juvenile crocodiles, as indicated by this typical census map (data from 30 March 1981).

represented animals 10 and 22 mo old. The monitored 10 mo old animals had SVL's of 26.7–29.3 cm and weights of 270–375 g; the 22 mo old animal had an SVL of 37.0 cm and a weight of 710 g. I presume that the nine 10 mo old animals I telemetered were siblings and probably at least half sibs of the 22 mo old animal.

Each radiotelemetered crocodile was equipped with a transmitter package broadcasting a unique frequency in the 151 MHz range. Modules (AVM Instrument Co.) combined an SM-1 transmitter and a 675 mercury battery with a one-eighth wavelength (~15 cm long) vertical whip antenna. I repackaged each module with an approximately equal volume of styrofoam to yield a final package weighing less than 1 g in water (<10 g in air) and measuring approximately 1 × 1 × 4 cm (minus the antenna). The transmitter packages were attached with two bands of 5 mm diameter surgical tubing split in half and tied around the animals' bodies straddling the forelegs. Before attaching the transmitters to the study crocodiles, I attached similar, as well as heavier and bulkier, transmitters to six other American crocodiles held for observation in deep aquaria. The crocodiles equipped with the packages used in this study exhibited no

noticeable impairment of their natural movements.

On the night of 19 February 1981, I captured, weighed and measured each of the 10 crocodiles visible in the study area, attached transmitters, and immediately released each at its point of capture. During the following month, I located the animals almost every day, at hourly intervals during an 8–10 h period. Water temperature, wind speed and direction, sun or moon visibility and altitude, moon phase, cloud cover, and water level were recorded at the time of each fix. The time of the monitoring period was periodically shifted to obtain 10 data sets for each hour of the day. Thus each individual was located ca. 240 times, a realized total of 2334 fixes. The 66 missing fixes were due to unlocated animals, probably as a result of malfunctioning transmitters. Transmitters on basking animals occasionally overheated, as indicated by dramatically accelerated pulse rates before a transmitter temporarily stopped functioning. I repeatedly searched for undetected animals outside of the normal 0.5–1.5 km reception range, but never found them there. When transmissions were again detected, they always emanated from sites within 50 m of their former locations; on several occasions, I detected a transmitter gradually ceasing or reinitiating transmissions from within the normal reception area. Consequently, I believe that all missed fixes were the result of transmitter failures rather than animals traveling beyond the reception range.

From a centrally anchored boat, I could receive signals from all 10 transmitters. Because the crocodiles limited themselves to a uni-dimensional shoreline habitat, triangulation was rarely necessary to determine an animal's position relative to the nearest vertex of the 50 m grid that I used to record locations. However, to confirm locations, I triangulated each animal's position at least three times during the daily 8–10 h monitoring period. I attempted to keep the boat as far from the shoreline as possible while obtaining readings of the

required accuracy; generally, animals were approached no closer than 100 m. At night I used only a dim shrouded light directed within the boat. If I disrupted the crocodiles' movements at all, my greatest influence probably would have occurred when I entered the study area, but unusual movements were not associated with these times.

The strength of a radiotransmitter's signal is diminished as it passes through dense vegetation or water. However, because the shoreline of the study area was relatively free of dense emergent vegetation, an animal on the surface consistently yielded a strong signal and a very weak signal indicated an animal concealed underwater; signal strength dropped conspicuously as an animal submerged. For 1508 fixes, I noted an especially strong or especially weak signal, and I tabulated the hourly fraction of strong counts as an index of the percentage of crocodiles at the surface.

I prepared a computer model to provide a null hypothesis against which to test the observed spatial distribution of the animals. The computer-generated null hypothesis was used to test the hypothesis that the crocodiles were positioned nonrandomly with respect to their known neighbors. The test was possible because the 240 fixes per animal provided not only good estimates of their home ranges, but also estimates of the amount of time each animal spent in each portion of its range. For a given length of shoreline, a given number of animals, a given home range size, and a given distribution of locations within a home range, the computer model estimated the probability of a given degree of location overlap for crocodiles positioning themselves without reference to their neighbors. I used the empirically determined values for shoreline length, animal number, mean home range size, and location distribution within home ranges. The model assumed habitat homogeneity. Each of the assumptions was conservative. For example, if the habitat had been treated as heterogeneous, one would

have obtained a null hypothesis incorporating crocodile clumping. Compared to such a null hypothesis, the observed distribution of locations might falsely appear over-dispersed. An assumption of homogeneity produces a more rigorous test of over-dispersion. The home range size and distribution assumptions were also conservative; if the observed values had reflected neighbor avoidance, they would have been smaller than the home range sizes of neighborless (i.e., unconstrained) crocodiles. Smaller home range values in the computer model yielded a more conservative test of the neighbor avoidance hypothesis. A few crocodiles without radios undoubtedly used the study area; thus the computer simulation evaluated only the probability of overlap among telemetered animals. The empirical values for neighbor overlap can properly be compared to the computer-generated null hypothesis, but both reflect minimums and are not absolute measurements.

RESULTS

The 13 nocturnal censuses indicated that juvenile crocodiles were located primarily in the vicinity of known nest sites. The older juveniles tended to be further from their presumed hatching site and were often seen further from shore, typically lying on *Hydrilla* mats. In the immediate vicinity of the Buena Vista nest, I occasionally saw a large crocodile, but within the area shown in Fig. 1, I saw no other adults or sub-adults. Almost all 8 mo old juveniles were within 300 m of the nest site; the 22 mo old juveniles had dispersed to a maximum distance of about 700 m.

The radiotelemetered animals moved within relatively small home ranges (Fig. 2). The mean home range of the nine 10 mo old animals was a strip covering 330 m of shoreline. Within these ranges, core areas (where 80% of time was spent) were about 200 m. The 22 mo old animal traveled more; its range included at least 650 m of shoreline.

Of the environmental factors I measured, only moonlight had a significant ef-
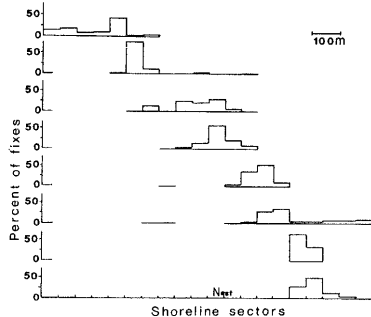
FIG. 2.—Distributions of fixes for the eight adjacent animals (all 10 mo old). The two animals not shown were not continuous with this group. The spatial distributions of fixes for each animal are shown by the percent of its fixes during which the animal occupied the sector indicated (see Fig. 1). Each histogram represents ca. 233 fixes, distributed evenly through the day. Thus the distributions indicate space usage by time.
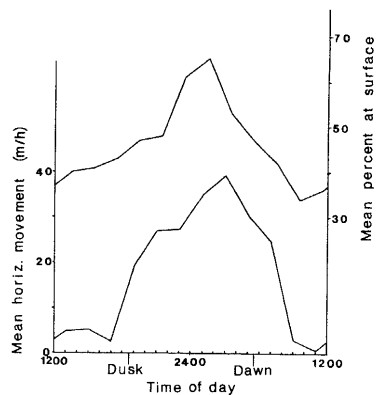

FIG. 3.—Daily pattern of movement. The lower line shows the mean number of meters moved per hour for daytime and moonless nights; the upper line indicates the mean percent-at-surface for each 2 h interval. Note that the horizontal movement values should not be considered absolute. Small or back-and-forth movements would not have been detected.

fect on crocodile movements. During the 8 h for which I have five samples each for moonlit (moon >½ full, >30° in the sky, and not obscured by clouds) and nonmoonlit nights, moonlit horizontal movements were significantly lower (paired *t*-test: $t = 4.48$, df $= 7$, $P < 0.01$) averaging about half the comparable moonless value. To give a consistent measure, Fig. 3 shows means of horizontal movement for moonless nights only. The percent-at-surface values were not noticeably affected by moonlight.

Estimates of home range size are sensitive to error due to insufficient sampling. As one collects fixes, the plotted (cumulative) geographic range of each individual grows until the individual has been recorded from the extremes of its home range (Odum and Kuenzler, 1955). Once this level of sampling has been attained, each additional fix indicates only a previously used area and the animal's cumulative home range estimate remains constant. Thus an asymptote in a cumulative home range size curve is a confir-

mation that sampling has been adequate. Few new locations were recorded for the 10 mo old animals after 85 fixes; subsequent fixes indicated previously used locations (Fig. 4). In contrast, new locations continued to be recorded for the 22 mo old animal; 190 fixes were insufficient to identify all of the areas through which it traveled (Fig. 4). The movement that produced the apparent range extension at fix 193 was immediately followed by the animal returning to its initial location. Thus the apparent range expansion was due to insufficient sampling of a fairly large home range rather than a shift in the location of a relatively small home range. Because no clear asymptote was obtained for the 22 mo old animal, the 650 m value for the size of its home range may be an underestimate.

My use of hourly fixes for determining the home range of a crocodilian was unusual: fixes have generally been obtained daily or at greater intervals (Goodwin and
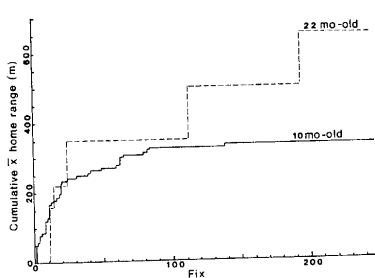
FIG. 4.—Cumulative mean home range estimates. The lower line shows the mean computed home range size after each set of fixes for the 10 mo old crocodiles; the upper line shows the computed home range after each fix for the 22 mo old animal.
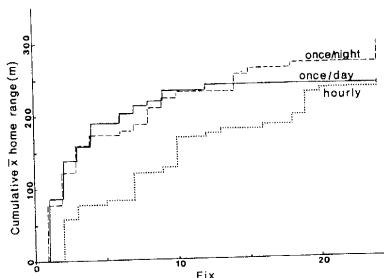

FIG. 5.—Cumulative home range estimates obtained by various sampling schedules for 10 mo old crocodiles. The "hourly" curve shows the first 24 fixes from Fig. 4, redrawn to conform to the different axis scales. The 24 "hourly" fixes were collected during 8–10 h periods spread over three days, whereas the data collection for each of the other two curves required 24 days. The daily and nightly samples shown here denote the closest available samples to noon and midnight on the 24 days when I collected data within 4 h of those times.

Marion, 1979; Joanen and McNease, 1971, 1973; McNease and Joanen, 1975; Taylor et al., 1977). I used subsets of my data for 10 mo old crocodiles to compare once-daily or once-nightly sampling to the schedule I used (Fig. 5). All three schedules gave similar estimates of home range size after 24 fixes, but only the daily sampling procedure yielded an asymptote. The asymptote indicated a mean home range of 240 m.

The distribution of 10 mo old crocodiles along the shoreline and the distribution of their locations within their home ranges (Fig. 2) suggested that the juveniles might be positioning themselves to avoid areas occupied by their neighbors or depleted of resources by their neighbors. This was tested with the computer model described above. To measure the degree of overlap among neighboring crocodiles, the amount of time each crocodile spent in areas variously utilized by its neighbors was tabulated (Fig. 6). The average 10 mo old crocodile spent 37% of its time in areas rarely used (0–10% of their time) by neighbors. The computer simulation obtained this degree of neighbor overlap in only six runs out of 200. Thus the probability of this low a degree of overlap being due to chance is ca. $P = 0.03$ (recognizing the model's assumptions).

DISCUSSION

The nighttime censuses indicated that most juvenile *Crocodylus acutus* in Gatun Lake remained relatively near their nest site for at least 22 mo after hatching. Published data are lacking for *C. acutus* from elsewhere, although Alvarez del Toro (1974) implied that dispersal was modest for juveniles. The distances I observed were similar to those reported for *Alligator mississippiensis* (Chabreck, 1966; Deitz, 1979; Fogarty, 1974) but very different from the estuarine *C. niloticus* (Pooley, 1969) and *C. porosus* (Messel et al., 1980; Webb and Messel, 1978). For example, Webb and Messel (1978) reported movements of up to 38.9 km among 13 mo old *C. porosus*. Juvenile *C. porosus* may disperse more easily because of flowing rivers and tidal currents. However, Webb and Messel reported upstream movements of up to 6.8 km as well, which suggest active dispersal. In their first few months, *C. porosus* may be relatively sedentary, but the *C. porosus* data are not directly comparable to the data for *C.*
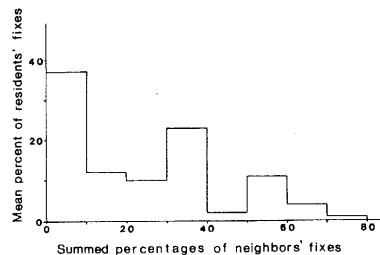
FIG. 6.—Spatial overlap of tracked neighbors. The data in Fig. 2 were used to determine the amount of time each animal resided in sectors variously used by its tracked neighbors. For example, the four sectors at the left in Fig. 2 were used only by the animal indicated at the top of the figure, who spent $14 + 19 + 9 + 10 = 52\%$ of its time in these sectors, which were occupied 0% of the time by neighbors. Similarly, it spent 42% of its time in the fifth section (neighbors 2%), 2% in the sixth (neighbors 77%), and 3% in the seventh (neighbors 26%). Thus the frequency histogram of the upper individual's overlaps would show that $42 + 52 = 94\%$ of its fixes were in sectors occupied by neighbors for 0–10% of their fixes (or time), etc. Eight such histograms, one for each animal, were averaged to produce Fig. 6.

acutus. Messel et al. (1980) suggested that the juvenile *C. porosus* benefited from their movements by encountering better food sources, as the crocodiles tended to congregate in areas where growth was highest. The Gatun Lake crocodiles remained near their nest sites rather than congregating, so one might predict that the heterogeneity in crocodile feeding areas was relatively low in Gatun Lake. Alternatively, the best nest sites also may be the best juvenile feeding areas.

The existence of small home ranges among Gatun Lake juvenile *C. acutus* was also consistent with low habitat heterogeneity. Comparable home range estimates for juvenile crocodiles have not been published, although Deitz (1979) observed similar-sized home ranges among juveniles of the relatively sedentary *Alligator mississippiensis.*

The nocturnal pattern of activity I observed is similar in broad outline to the general crocodilian pattern (Guggisberg, 1972). The maximum value of 65% of the animals at the surface agrees well with the 63–73% estimates for *C. porosus* made by Messel et al. (1980). Alvarez del Toro (1974) stated that *C. acutus* hunt at night, primarily before 2200 h. Peak activity in *Alligator mississippiensis* and *C. niloticus* occurs in the first few hours after dusk (Cloudsley-Thompson, 1964; Deitz, 1979; Woodward and Marion, 1979), rather than later as I observed (Fig. 3). Messel et al. (1980) found no effect of time-of-night for *C. porosus.* I am not aware of any hypothesis that suggests a benefit associated with a crocodilian activity peak after midnight.

Moonlight has been widely cited as a deterrent to hunting by American and Australian crocodilian hunters (Chabreck, 1976; Messel, personal communication). Alvarez del Toro (1974), without citing data, stated that feeding by *C. acutus* is reduced during periods of bright moonlight. Messel et al. (1980) measured moonlight directly and found no effect on *C. porosus* sightings. Woodward and Marion (1979) inferred moonlight levels from moon phase and percent cloud cover and found slightly but significantly more *Alligator mississippiensis* sightings on bright moon nights. The number of sightings, used as an assay by Messel et al. (1980) and Woodward and Marion (1979), would be roughly comparable to my percent-at-surface, for which I found no effect of moonlight. However, moonlight might limit the success of certain crocodilian activities. For example, moonlight could affect a crocodilian's vulnerability to predators, as well as its ability to capture prey. Perhaps one or both of these factors are relatively more sensitive to light in the clear waters of Gatun Lake than in the turbid waters where the other studies were conducted.

In addition to moonlight, Woodward and Marion (1979) found water temperature to be an important factor affecting *Alligator mississippiensis* activity. During my study, the water temperature var-

ied less than 1 C; thus the absence of a water temperature effect is unremarkable.

Cumulative home range sizes have not been reported in other crocodilian studies, although they are a valuable tool for validating a sampling schedule (Odum and Kuenzler, 1955). The daily sampling procedures that have been used to compute crocodilian home ranges could give misleading results. For example, the asymptote for daily sampling in Fig. 5 might lead one to believe that (1) 12 daily fixes were an adequate sample, and (2) 10 mo old crocodiles had home ranges averaging 240 m. These conclusions are inconsistent with those obtained through more thorough sampling (Fig. 4). Alternatively, one could treat daily sampling as a record of daytime rest places. That is, one could correctly conclude that 12 daily samples were adequate for determining the geographic range of daytime rest sites in my 10 mo old crocodiles. In this case, the average crocodile had a 240 m range of daytime rest sites, only 63% of the total range. Daytime sampling would not be useful for determining home ranges, however.

Nightly sampling appeared adequate for home range determinations in 10 mo old crocodiles (Fig. 5), but would require an estimated 6 wk, 4 wk more than was necessary when using an hourly sampling schedule. Juveniles that were expanding their home ranges with age or season might change their home ranges before once-a-night sampling was completed.

The computer analysis of home range overlap suggests that the crocodiles may have been avoiding areas depleted of resources by their neighbors. I observed no situations in which a crocodile actively avoided the presence of another; defense of personal space is thus an unlikely explanation for overdispersion. Deitz (1979) suggested a resource depletion hypothesis to account for daily dispersal away from a communal retreat by hatchling *Alligator mississippiensis*. The presumption of intraspecific competition seems reasonable for the relatively undispersed croco-

diles in Gatun Lake, but direct evidence is lacking.

Resumen

En 19 de febrero de 1980 equipé 10 *Crocodylus acutus* juveniles con radiotransmisores y los solté en el punto donde fueron capturados. Durante el próximo mes obtuve un promedio de 10 determinaciones de posición ("fixes") para cada animal, cada hora del día, por un total de aproximadamente 2400 determinaciones de posición ("fixes"). Durante todo el estudio los animales permanecieron cerca del sitio donde habían eclosionado; la mayoría de los miembros de la postura del año anterior permanecieron a menos de 300 m del nido. Estos animales de 10 meses de edad habitaban un espacio promedio de sólo 330 m de litoral, y más del 80% de sus movimientos ocurrieron dentro de un área focal promedio de menos de 200 m. De manera que estos *C. acutus* eran decididamente más sedentarios que los que han sido observados en otras localidades.

En base a las variaciones en la potencia recibida por las señales de radio se pudo inferir que de 35–45% de los animales se encontraban en la superficie durante el día, aunque sus movimientos horizontales ocurrían raramente de las 0900 a las 1700 h. Los movimientos aumentaron dramáticamente después del anochecer, llegando a su máximo a las 0300 h, y bajando cerca de cero dos horas después del amanecer. Los movimientos durante la noche disminuyeron significativamente durante períodos con brillantes claros de luna, aunque el porcentaje de animales en la superficie no fue afectado notablemente por los niveles de luz durante la noche.

Acknowledgments.—I thank all the researchers of the Smithsonian Tropical Research Institute who graciously aided me with field work. Kraig Adler, Duke Campbell, James Kushlan, Harry Messel, Paul Moler, A. Stanley Rand and Ted Stevens offered suggestions on the manuscript. Kathy Troyer, William Dunson and Paul Moler supplied pertinent unpublished data. Jonathan Shuster wrote the computer program. Argelis Ruíz provided the Resumen. Support and supplies were made available through Dale Madison, the Smithsonian Tropical Research Institute, and the National Science Foundation. A special thanks goes to Stanley Rand, who freely contributed to all aspects of this study.

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