Movements, Home Range, Dispersal and the Separation of Size Classes in Nile Crocodiles[1]

JONATHAN HUTTON

*Department of National Parks and Wildlife Management of Zimbabwe,
P.O. Box 8365, Causeway, Harare, Zimbabwe.*

SYNOPSIS. The movements of 100 crocodiles (0.3–4.3 m) were followed over 3 years by mark-recapture, spotlight survey and radiotelemetry at Ngezi, Zimbabwe. Home ranges were based on frequency of occurrence of animals in 100 m grid squares. Most crocodiles were nocturnal, but adults occasionally moved in daylight. Animals 0.4–2.2 m had home ranges of similar sizes, but dispersed at 1.2 m. Smaller crocodiles were restricted to the river (the only nesting area) whereas all larger animals occupied the lake into which the river flowed. From 2.2 m the range of movement increased until large subadult females (2.7 m) travelled widely without distinct home ranges. Subadults were still largely excluded from the river and the smallest nesting female migrated out of the river after each breeding season. Large breeding females (>2.8 m) had small home ranges near prime nest sites. There appeared to be no difference in the behavior of the sexes up to 2.2 m. There are few data on larger males, but four mature animals (>3.2 m) had distinct home ranges. Home ranges of small juveniles increased in size in the hot season, but for adults the effects of climate and breeding were confused. The different behavior of the various categories of crocodiles resulted in the marked separation of breeding females with their last few season's offspring from immature animals 1.2–2.2 m. Dispersal appears to occur at the same stage in other crocodilians with similar scaling parameters because adults become increasingly intolerant of intermediate-sized animals. It is suggested that size-class separation is part of a general density-dependent regulating mechanism in crocodilian populations.

INTRODUCTION

The distribution and movement of animals must be known in order to understand basic population processes. Although spatial and social behavior associated with reproduction are often conspicuous and generally receive most attention, spatial behavior outside the immediate sphere of reproduction is no less important. Territoriality is "a strategy used by individuals to secure a disproportionate share of each resource of potential significance to genetic success" (Owen-Smith, 1977), but home range strategies (Jewell, 1966) affect life-history processes such as growth and survival. In many crocodilian species an adult can be 3–5 orders of magnitude heavier than a hatchling, and cannibalism may be a fundamental population process (Cott, 1961; Nichols *et al.*, 1976; Polis, 1981; Hutton, 1984). Therefore the way in which size classes are dispersed (placed relative to

one another) throughout the habitat may be crucial.

Dispersal, the movement of animals away from the area in which they spent the initial part of their lives, may also be an important demographic process. Innate dispersal is spontaneous, genetically determined and generally random whereas environmental dispersal is often short and directional resulting from the avoidance of unfavorable habitat or social conditions (Howard, 1960). Innate dispersal may reduce a population's rate of increase (Caughley, 1977) while environmental dispersal is a regulating factor in some vertebrate populations (Bunnell and Tait, 1981).

Despite the potential importance of movement, home range behavior and dispersal to crocodilian life histories, these factors have received careful examination in only one of 22 crocodilian species. From the recapture of marked animals and radiotelemetry, habitat preference, movement and home range behavior have been documented for both immature and adult American alligators *Alligator mississippiensis* Daudin (Chabreck, 1965; Joanen and

McNease, 1972, 1980; McNease and Joanen, 1974; Goodwin and Marion, 1979). Information on other crocodilians is far less complete. For some species short and long-term movements have been recorded through capture-recapture procedures (Gorzula, 1978; Webb and Messel, 1978; Webb et al., 1983). Commonly, this sort of information is combined with data on the relative placement of animals of different sizes to provide information on home ranges and disperal mechanisms (Messel and Vorlicek, 1987; Webb and Messel, 1978). Radiotelemetry has most often been used to give detailed short-term data on local movements within the home ranges of specific size classes (Ouboter and Nanhoe, 1984; Rodda, 1984).

Some aspects of territoriality have been described in Nile crocodiles Crocodilus niloticus Laurenti (Modha, 1967), but there are no data on the spatial and social behavior of younger animals, nor adults out of the breeding season.

Between March 1979 and March 1982 an intensive study was made of the ecology and dynamics of the Nile crocodile population at Lake Ngezi, Zimbabwe (Hutton, 1984, 1986, 1987a, b). This paper reports on both the short and long-term movement patterns of 100 Nile crocodiles of all sizes as recorded by mark-recapture and radiotelemetry. Some additional data from monitoring of the population during the period 1982–1987 are included where appropriate.

The aim of this work was to establish the effect of movement and home range behavior on population dynamics (Hutton, 1984) and more emphasis was placed on the broad pattern of long-term movement than detailed movement within home ranges. The work is unique for its duration and in the number of animals examined. Specifically reported are 1) short-term movement patterns of animals of different sizes, 2) a comparison of recapture and radiotelemetry in the description of long-term movement, 3) the validity of the home range concept to account for the movement of crocodiles of different sizes and reproductive status, 4) dispersal and the ecological separation of size classes, 5) the selective use of total available habitat, 6) seasonal variation in home range behavior. A new method of analyzing home range is presented.

In discussion, I emphasize similarities in the spatial strategies of the large crocodile species for which there are adequate data (the American alligator, Nile crocodile and estuarine crocodile Crocodylus porosus Schnieder) and suggest that size-class separation is part of a density-dependent regulating mechanism in crocodilian populations.

STUDY AREA

Lake Ngezi, an artificial impoundment filled in 1948, lies at 1,220 m above sea level between 30°20'/30°29'S and 18°39'/18°44'E. The area has a hot-rainy season between November and March followed by a cool-dry season until September and a hot-dry season until the start of the rains (Hutton, 1986). Mean minimum air temperatures follow a regular pattern with a trough, in which temperatures may fall to 2°C, in July, rising to a plateau of 15–20°C between October and March. Water temperature follows a similar cycle with a peak of 25–30°C. Rainfall is variable, but most falls between November and February. Annual rainfall averages slightly over 600 mm. Water level is also variable, responding to user requirements, but between the years 1974 and 1983 it stayed at or near its maximum for 7–9 mo before falling to a minimum shortly after the start of the rains. In 1983 and 1984 the country experienced a drought and the water level fell steadily until only the old river bed still had water.

The lake is narrow and irregularly shaped, closely following the course of the river. When full, it covers 5.8 km² (Fig. 1). During the study period the main body of water had gently shelving banks with wide beds of perennial hydrophytes such as Echinochloa stagnina (Retz.) Beauv., Cyperus digitalis Roxb. and Schoenoplectus corymbosus (Roth ex Roem. & Schultz.) Raynal. Over 30% of the lake was less than 2 m deep and supported a dense growth of aquatic macrophytes, notably Ceratophyllum demersum L. The prevailing wind was south-easterly
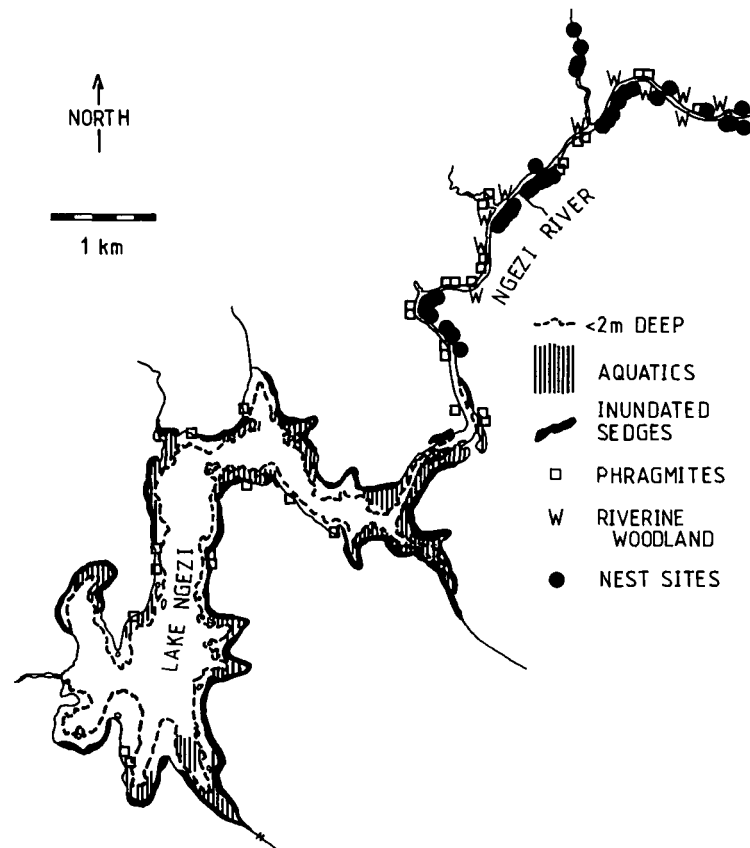
Fig. 1.   Lake Ngezi showing broad vegetation types, water less than 2 m deep and nest sites recorded between 1968 and 1982.

and the long, exposed north-west shore was characterised by rough water, particularly during the cool-dry season. The headwaters of the lake were confined within the steep, raised banks of the Ngezi River. Fringing hydrophytes, such as *Phragmites mauritianus* Kunth, occurred in patches, particularly near sand banks. All crocodiles nested in this area (Fig. 1). Between the main lake and its headwaters in the Ngezi River were extensive shallows in which *Polygonum limbatum* Meisn. and *Polygonum senegalense* Meisn. proliferated (Fig. 1). The shoreline was approximately 32 km, including both banks of the river, and crocodiles occurred at a density of 3.9 km^{-1} and a biomass of 172 kg km^{-1} (Hutton, 1984). Crocodiles occur naturally in the Ngezi River and the population has been fully protected since 1967.

METHODS

Data collection

One hundred crocodiles were captured, measured, sexed, given durable marks from which they could be individually identified, and released (Hutton, 1984; Hutton, 1987c; Hutton et al., 1987; Hutton and Woolhouse, 1989). All measurements given are total lengths. Animals of <1.2 m are termed juveniles, those of 1.2–2.2 m are called intermediates.

A radiotelemetry program, in which 21 animals from 0.8–3.4 m were tagged, tested for biases in resighting data and provided an experimental base for answering specific questions. Two crocodiles were radiotagged in March 1980. Thereafter, transmitters were fitted to animals whenever the opportunity arose. A receiver and portable

directional antenna was used to locate radio-tagged individuals to within a few meters (Hutton, 1984). The term "radiolocation" is used to describe the pin-pointing of an animal by telemetry, the animal not necessarily having been seen, while the use of "sighting" refers strictly to an animal which was only seen. Radiolocations and sightings are "fixes." Fixes were plotted, along with the date and time of each, onto 1:20,000 maps. Sightings (including unmarked and unidentified animals) were recorded on a map for each calendar month. Plotting was accurate to within 10 m. More detailed information, including general demeanor, was recorded chronologically for each animal.

Measurement of home range

A new method for analyzing and presenting movement data (R. B. Martin, unpublished) was found to be appropriate for measuring the home ranges typical of crocodiles. This method is based on the frequency of occurrence of fixes in grid squares, the size of which is chosen to suit the objectives of the study. By constructing contours which enclose a predetermined percentage of fixes, this technique measures the use an animal makes of its habitat. A value for the area enclosed by each contour is calculated as follows:

(a) The frequency of occurrence of squares (S_i) containing 1, 2, 3, . . . , i, . . . , n fixes is calculated where 1 is the lowest number of fixes in any grid square and n the highest,

(b) The total number of fixes (T_i) in the ith class (where 1, 2, 3, . . . , n are the classes) is calculated as $T_i = i \cdot S_i$. For example, if 28 squares each contain 3 fixes then $T_i = 3 \times 28$,

(c) GT is the grand total of fixes.

(d) A cumulative curve of fixes is constructed such that the cumulative value up to any given class, i, is $C_i = \sum_1^i T$.

(e) The cumulative percentage of fixes up to the ith class is $\%_i = 100 \ C_i/_{GT}$.

(f) A contour encloses all squares which contain a cumulative percentage above the contour's value. The 100% contour

can always be constructed but, depending on the distribution of fixes within grid squares, others may not.

The size of the grid squares is critical. Large squares give extremely averaged (smoothed) results while small squares produce individual polygons resembling the original data. In this work, a 100 × 100 m grid was found to give a measure of the variation of activity within a home range.

This method, and all others assessed for use, had two drawbacks. The areas of home ranges were biassed by the number of fixes used in their calculation (though less so in the chosen method than any other). To remove sample size bias, home range areas were compared when fixes were randomly discarded to reduce their number to that of the individual for which fewest fixes were available. It was also found that no measure of the scatter of fixes was obtained. Thus, an animal with a measured "home range" of 0.2 km² may have had a small, localized home range, or it may have been wide-ranging. Only plotting and inspection showed these differences. To quantify the degree to which fixes were aggregated and to which area under the 100% contour (AUC) was reflecting a true home range, mean nearest-neighbour distance (MNND) (Clarke and Evans, 1954; Hammond and McCullagh, 1974) was used as an index of dispersion.

Short-term movements

In order to compare diurnal and nocturnal movement and to show the respective value of day and night-time fixes, a number of crocodiles were radiolocated at three-hourly intervals over five 24 hr periods spaced throughout 1981. To examine more closely the likelihood that a crocodile would change its position during daylight hours, and the distance that it would move, animals of different sizes were radio-tracked twice daily on 25 occasions. The first search was always made between 0700 hr and 0900 hr, the last between 1600 hr and 1800 hr.

Resightings compared with radiolocations

To examine the way in which home range varies when measured from resightings and

radiotelemetry, data from each were used to establish home range characteristics for crocodiles N18 (0.8 m), N203 (1.75 m), N209 (2.25 m) and N80 (3.36 m) over the period that each was radio-tagged. These were the only individuals with a large sample of sightings and radiolocations.

Cumulative fixes and home range size

If crocodiles occupy distinct home ranges, then as fixes accumulate, AUC can be expected to increase until it reaches an asymptote where the home range is fully described, so long as fixes are collected over a period of observation long enough for an animal to traverse its whole living space (Odum and Kuenzler, 1955).

In order to test whether crocodiles have home ranges and to determine the minimum number of fixes necessary to measure them, a relationship between number of fixes and AUC was established for 10 individuals of varying sizes and of differing reproductive status.

Selective use of habitat

During spotlight counts it became obvious that parts of Lake Ngezi were infrequently used by crocodiles. To measure differential use of the total available habitat, fixes for all animals over the study period were combined in a contour analysis.

Crocodile size and reproductive status

Size-related changes in dispersion were evaluated from AUC and MNND for each of 16 female crocodiles in the size range 0.8–3.0 m. To make area data comparable, only 37 randomly chosen fixes were used, the greatest number of fixes for any typical juvenile.

Dispersal and the separation of size classes

The way in which crocodiles of different sizes were placed relative to each other was examined and five size categories of animal which appeared to show differences were identified (<1.2 m, 1.2–2.2 m, 2.2–2.5 m, > 2.5 m non-breeding, > 2.5 m breeding). Movement data from within each category were combined, plotted and compared. A dispersal mechanism was inferred from
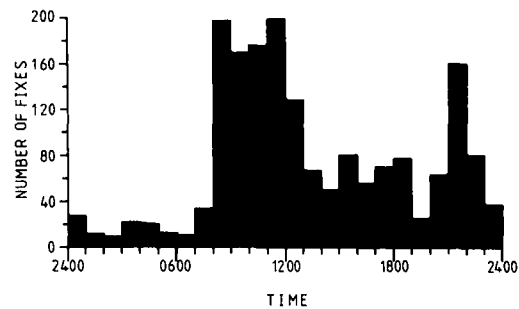

FIG. 2. Temporal distribution of fixes.

individual movements and the relative placement of size classes.

Seasonal variations

The seasons have a fundamental affect on the crocodile's life-history at Ngezi. Growth occurs only in the hot season between 21 October and 15 March (Hutton, 1986). Data on the seasonal movements of juveniles were collected during 1979 and the distance between the two most widely separated fixes of 21 crocodiles during the cool season, and 11 during the hot season, was measured. Seasonal comparisons were also made for animals N77 (2.22 m), N78 (3.10 m), N79 (2.77 m), and N80 (3.36 m) for which there were a large number of fixes in both the hot and cool seasons.

RESULTS

Data collection

For 79 crocodiles with radiotags, the largest number of resightings was 78, but the mean was 25. By contrast, the largest number of radiolocations was 198, the mean 42. To locate the 21 radio-tagged animals, 245 radio-tracking excursions were made on 209 days, most after October 1980. Few spotlight counts or radio-tracking exercises were continued after 2400 hr because a mist formed over the lake making observation difficult. The temporal distribution of fixes is shown in Figure 2.

On 38 occasions, one or more radiotagged individuals were not located, usually due to faulty receiving equipment. Signals were weakened when animals submerged and it is likely that a few of the missing

TABLE 1. *Relationship between crocodile size and the frequency of diurnal movement.*

Croc	Total length (m)	Days sampled	Days moved 20 m	% days moved 20 m
N203	1.6	10	0	0
N208	1.9	10	0	0
N207	1.9	3	0	0
N212	2.2	3	0	0
N209	2.3	11	3	27
N77	2.3	7	1	14
N72	2.5	3	0	0
N73	2.8	3	1	33
N79	2.8	19	7	37
N97	2.9	19	3	30
N78	3.0	11	6	55
N80	3.3	23	5	22

FIG. 3. Home range of N203 as measured by (A) resightings, (B) radiolocations.

crocodiles were in deep water as all were located on a later occasion. Use of burrows as reported by Pooley (1969a) and seen amongst captive animals in Zimbabwe (Hutton, 1984), might have accounted for some of the problems, but no burrows were found in 1984 when the water level fell 7 m.

Short-term movements

Diurnal movements were infrequent among crocodiles <2.5 m. They were more common amongst larger crocodiles, but most moved on less than 40% of days (Table 1).

As measured in intermediate and adult animals throughout the year, nocturnal movements (mean = 660.00 m) were significantly greater than diurnal movements (mean = 73.16) (Mann-Whitney U test, U = 17, n_1 = 15, n_2 = 15, P < 0.001, one tailed test). Home ranges were commonly traversed during the night and crocodiles were rarely seen in exactly the same place from one day to another. As a result, diurnal fixes summarized nocturnal movements and equally well measured the size of home ranges.

Resightings compared with radiolocations

Home ranges estimated from resighting data corresponded well in position with those estimated from telemetry (Fig. 3), but were smaller (Table 2). However, the number of resightings was, in each case,
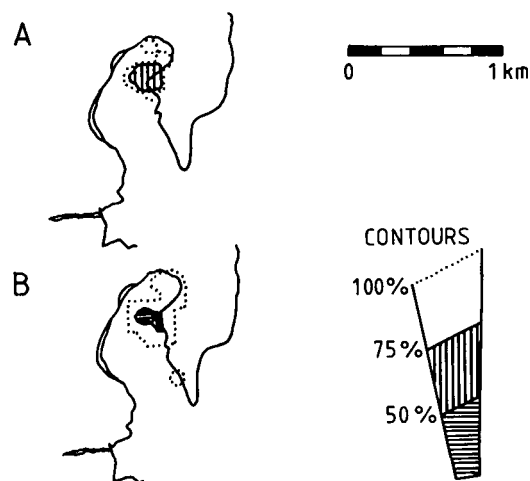
smaller than the number of radiolocations and this was sufficient to explain differences in size.

Cumulative fixes and home range size

When AUC was plotted against cumulative fixes, the curve for 8 of 10 animals approached an asymptote considerably below the total available area, strongly suggesting that these crocodiles were occupying home ranges (Fig. 4).

Home range area and the minimum number of fixes necessary to evaluate it were associated with the size and reproductive status of the individual. In animals <2.2 m (N18, N12, N203, N208) an asymptote was approached at 20–25 fixes. Subsequent small increments were related to the probability of recording unusual movements outside the home range as time progressed. Seasonal home range changes (described later) produced step-like increases in area in individuals 2.2–2.5 m (N77, N209). The two animals for which the area curve did not approach an asymptote were subadult females (N88, N90, both >2.5 m). After 75 fixes the home range of N90 was still increasing.

The curve approached an asymptote at 35–45 fixes in breeding females, more smoothly in N100 than in N78. The step in the curve of N78 was due to an extension of its home range at the end of a nesting

TABLE 2. *Home range size measured from resighting and radiolocation data for crocodiles ranging from 0.8 to 3.4 m (see text).*

Croc	Period	No. sightings	No. radio-locations	Home range area (km²) resightings	Home range area (km²) radiolocations
N18	31/3/81–16/4/81	6	11	0.048	0.064
N203	4/4/81–4/2/82	14	60	0.061	0.120
N209	16/4/81–4/2/82	16	56	0.133	0.262
N80	4/1/81–21/12/81	33	151	0.243	0.799

period rather than to a seasonal change due to climate.

Selective use of habitat

Not unexpectedly, Ngezi crocodiles were largely restricted to the water's edge, though shoreline which had a westerly or north-westerly aspect was sparsely occupied (Fig. 5). The vegetation of these areas was not different from that elsewhere and differential distribution is attributed to factors affecting shelter. The west and northwest shores were characterized by rough water because of the prevailing wind. This shoreline also had fewer inlets, rocks and old termitaria than the most heavily utilized areas. Rocks and termitaria provide shelter, but may also be important basking and feeding sites (Hutton, 1984).

Crocodile size and reproductive status

The area circumscribed by the 100% contour was consistently small among individuals <2.2 m (mean = 0.1052 km², SE = 0.0032, n = 4), quickly rose to a peak among non breeding crocodiles (mean = 0.1978 km², SE = 0.1811, n = 6), but fell sharply again among larger animals (mean = 0.1454 km², SE = 0.0097, n = 6) (Fig. 6). However, these differences were not significant (F = 1.43; df = 2,13; $P > 0.5$). All but two of the animals with areas >0.18 km² were subadult while all but one breeding animal (N97) had home range areas <0.16 km².

Mean nearest-neighbor distance was similarly related to size and reproductive status. For animals <2.2 m, MNND was small (mean = 1.4983, SE = 0.1566, n = 4), a clear increase occurred and a peak was reached among non-breeding females (mean = 9.8326, SE = 3.2013, n = 6), but

as size further increased, MNND fell again (mean = 4.1176, SE = 1.5339, n = 6) (Fig. 6). These differences were significant (F = 13.23; df = 2,13; $P < 0.001$).

Thus, in animals smaller than about 2.2 m home ranges were small and localized. Larger crocodiles ranged increasingly widely and the largest non-breeders had no distinct centre of activity. On attaining maturity females became more sedentary with small home ranges.

There are fewer data on the movement of males because they were poorly represented in the population as a result of temperature-dependent sex determination (Hutton, 1987b). However, in animals <2.2 m there were no obvious differences in behavior between the sexes (Hutton, 1984). Movement data for the three largest males suggest that their home ranges did not overlap, but there is no indication as to whether these areas were exclusive or defended territories.

Dispersal and the separation of size classes

Although AUC and MNND were similar for all animals smaller than about 2.2 m, over 90% of juveniles were found in the Ngezi River whereas animals of roughly 1.2 to 2.2 m were restricted to the lake's main waters (Fig. 7). The home ranges of crocodiles 2.2–2.5 m not only increased in size, but overlapped slightly with those of juveniles. Large subadult females (>2.5 m) were found in similar habitat to slightly smaller animals but, as noted in the previous section, their movements tended to be more wide-ranging (Fig. 8). Breeding females were generally restricted to the Ngezi River, along which all nesting occurred, and only a few individuals ever
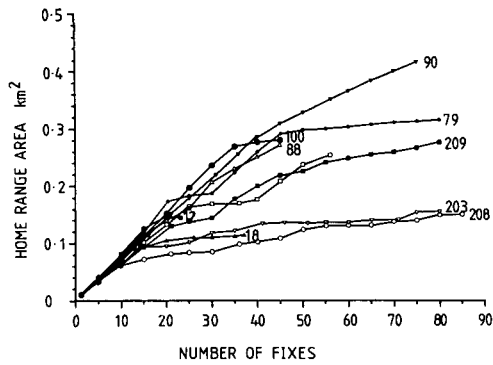
FIG. 4. Relationship between home range area and cumulative fixes for 10 crocodiles of different sizes and reproductive status.
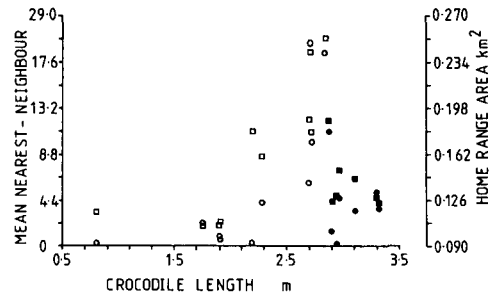

FIG. 6. Variation in home range area and mean nearest-neighbour distance with crocodile size and reproductive status. □, Home range non-breeders; ■, Home range breeders; O, MNND non-breeders; ●, MNND breeders.

moved down into the main waters of the lake (Fig. 9). One of these was notable: At 2.65 m, N91 was the smallest breeding female recorded. During most of the study period she maintained a distinct home range in the lake, and was therefore atypical of her size, but in two years she moved

into the river to nest during September, returning to the lake at the end of the season.

As a result of these locality characteristics, the home ranges of breeding females and juveniles overlapped completely, but they were separate from those of intermediate animals. The most marked sepa-
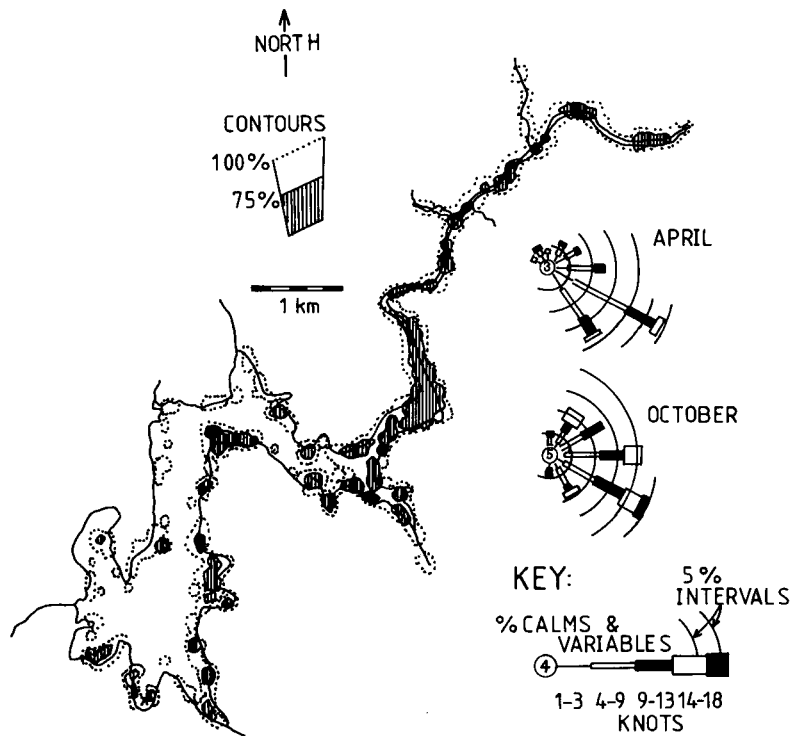

FIG. 5. Direction and strength of prevailing winds and use of total available habitat as indicated by all fixes.
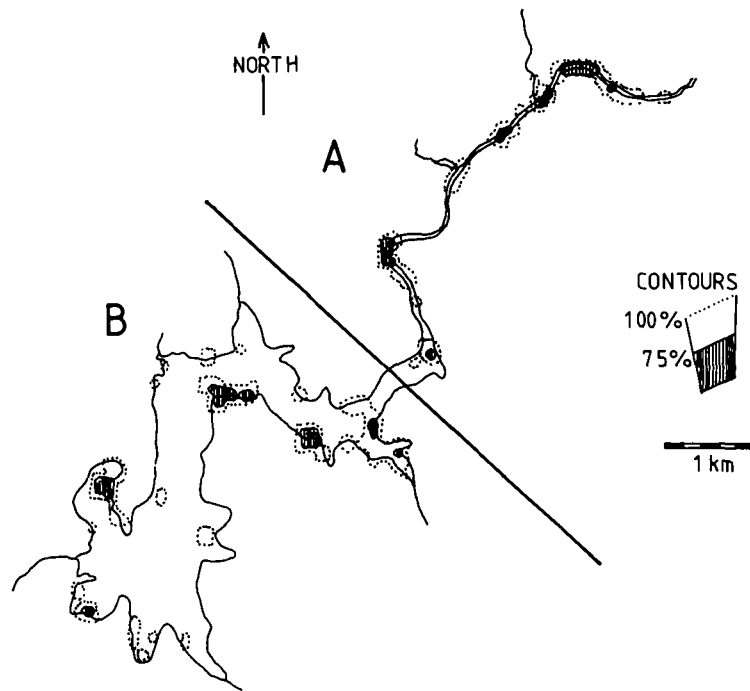
Fig. 7. Ranges of 9 typical juveniles <1.2 m (A) and 7 intermediates 1.2–2.2 m (B).

ration was between animals of 1.2–2.2 m and breeding females together with juveniles (Fig. 10).

Between the years 1979 and 1982, when water level fluctuations were within their average range, all hatchlings established home ranges in the Ngezi River, usually within 6 wk of hatching, and these were maintained until each individual had attained a size of at least 1.0 m. The observed distribution of size classes leads me to believe that this was typical and that a marked change in behavior, consistent with dispersal, occurred at about 1.2 m. One radiotagged juvenile occupied a small, typical home range in the Ngezi River from 1979 until April 1981 when it was about 1.0 m. It then moved a considerable distance downstream toward the main lake and from this time it occupied transient home ranges, up to 2.5 km apart, for periods not exceeding 8 wk. At a size of about 1.1 m it left the Ngezi River and moved into the lake to take up a home range among other crocodiles of intermediate size.

Seasonal variations

Juveniles made larger movements in the hot season. In the cool season, 57% of juveniles ranged along 0.5 km of shoreline and 90% restricted their movements to within 1 km. Even when water level fell below the fringing vegetation, exposing animals to predation, they did not move to seek cover. In the hot season their movements were significantly greater, only 27% of individuals stayed within 0.5 km of river bank, 45% ranged within 1 km while 27% made long movements, up to 4.5 km (cold season mean = 0.520, SE = 0.057; hot season mean = 1.123, SE = 0.367: t = 2.402, df = 33, $P < 0.05$).

The situation with larger crocodiles is less clear. In the cool season of 1981, the home range of N77 (2.22 m) shifted downstream, but its area did not change. By contrast, the home range of N79, a larger subadult female (2.77 m) decreased in size during the cool season, but did not move (Hutton, 1984).
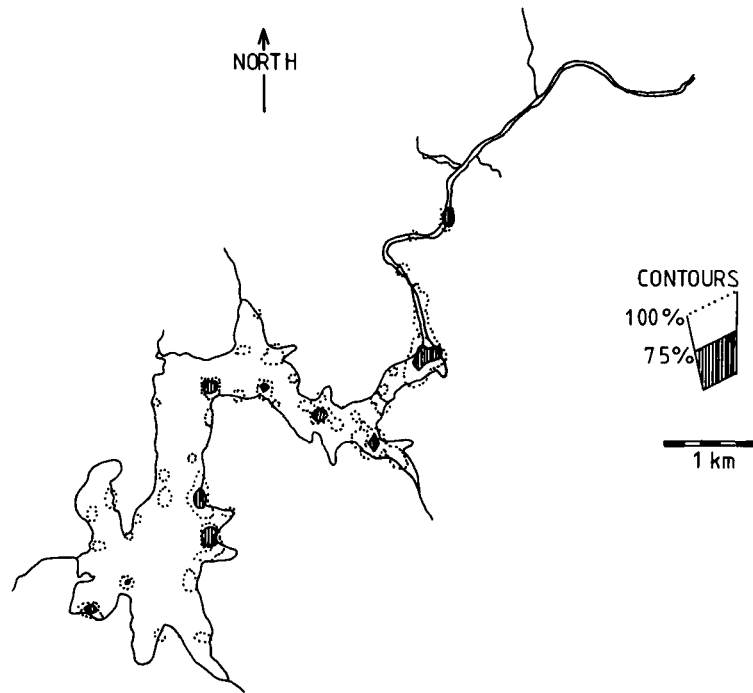
For mature animals, the climatic seasons

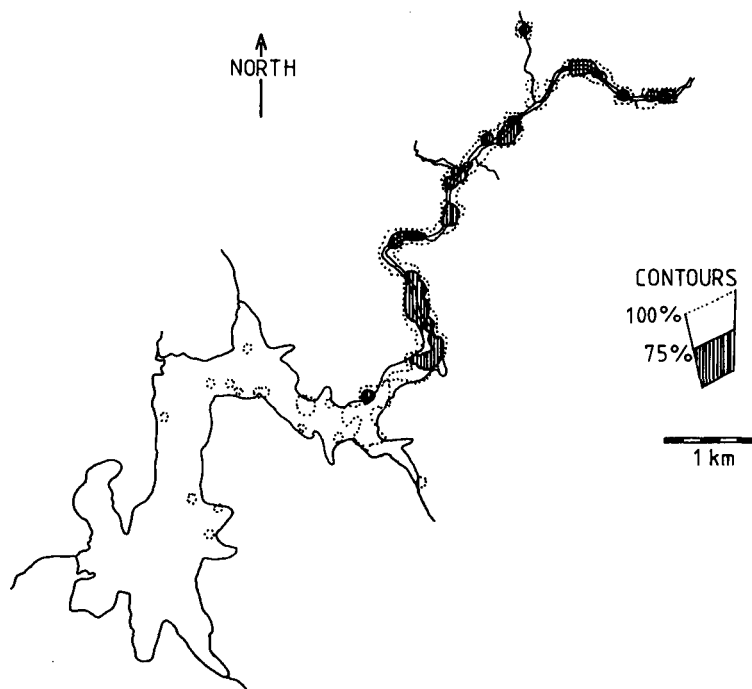FIG. 8.   Total range of 6 subadult females.

FIG. 9.   Total range of 8 breeding females.

are confused by breeding activities. Court-ship and mating take place in July and August of the cool season while nesting occurs largely within the subsequent hot season. In the cool season of 1980 an adult male (N80) was usually to be found in the shallow area at the mouth of the Ngezi River, but in the following hot season its home range moved into the lake. In the cool season of 1981 it was again centered on the river mouth, but it moved upstream rather than downstream in the next hot season. The range of N80 in the cool sea-son corresponded with an important area for courtship and mating, but it is not known whether this influenced the move-ments of the animal.

An illustration of the marked effect of breeding on home range behavior is pro-vided by a female (N78, 3.1 m) which was captured on its nest during October 1980. After release, its movements were confined to the immediate area of its nest until mid-January (the usual time of hatching). After January, its home range was considerably enlarged and remained constant until the next nesting season when it was again restricted to the area of the nest.

DISCUSSION

Techniques

The present study was designed to assess the contribution of movements and dis-persion to the dynamics of a crocodile pop-ulation by examining the broad, long-term spatial behaviour of animals of varying sizes and reproductive status. Rodda's (1984) short-term study of a few juvenile *Croco-dylus acutus* Cuvier gave detailed infor-mation on the proportion of time animals were submerged and the variation in their activity throughout the day. This sort of information is useful in the analysis of sur-vey results and may be essential for a detailed examination of the animal's use of resources. However, information at this level of resolution would have contributed little to the aims of the Ngezi project and would have detracted from other impor-tant aspects of the study (Hutton, 1984). Gross measurement of the range of diurnal and nocturnal movement in relation to
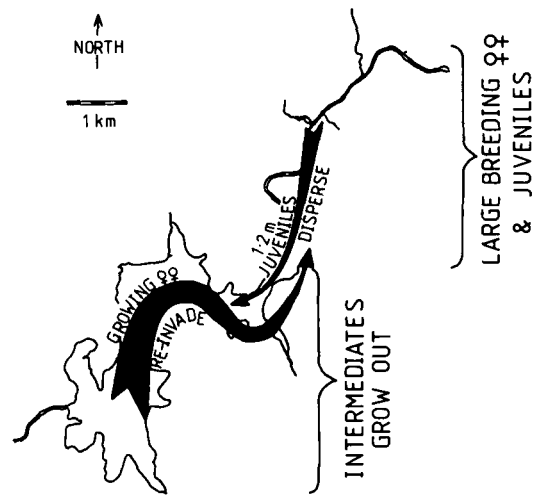

FIG. 10. Summary of the spatial relationships of crocodiles at Ngezi.

crocodile size assisted the interpretation of resighting data. Similarly, where data from resightings and radiotelemetry were com-pared the object was to establish whether these had to be considered separately, or if it was satisfactory to pool information. It is likely that a more detailed study would show, as did that of Rodda (1984), that there are small differences when home range is measured at different times and in different ways. However, the conclu-sions made here, that home ranges derived from resightings corresponded in position with those from radiotelemetry, and that daytime fixes were representative of night-time ranges, were adequate at the required level of resolution.

There are many ways of analyzing and presenting home range data (Anderson, 1982). Methods fall into two general cat-egories: non-statistical techniques as reviewed by Sanderson (1966) and those based on the statistical distribution of activ-ity loci, particularly the arithmetic mean centre of activity, reviewed by Van Winkle (1975). Non-statistical techniques are sub-ject to sample size bias (Jennrich and Turner, 1969) while statistical methods frequently lack biological meaning (Dixon and Chapman, 1980). The chosen method must be appropriate to the type of question being asked, the type of animal and habi-

tat, the quantity and quality of data and the required presentation.

A simple convex polygon method does not give a good measure of home range area and in this study would have presented problems in the interpretation of outlying points and linear ranges such as those in the Ngezi river. This technique also gives no indication of the differential use of space within a home range. Statistical techniques, such as probability ellipses, would have been suitable for some of the linear home ranges, but would have given meaningless area values by including large tracts of habitat not used by crocodiles. They would not have represented the true shape of the home range, nor would they have revealed activity loci within home ranges. The harmonic mean statistical home range technique (Dixon and Chapman, 1980) may have accurately described the shape of home ranges, but would not have indicated true centres of activity. In addition this method is of limited use for comparing areas as their estimation is not direct and the contours of distribution ("isopleths of momental distribution") do not circumscribe any particular probability of occurrence.

The method used in this study appeared, with a 100 × 100 m grid, to produce a summary of movement which closely resembled real home ranges. The comparison of areas under the 100% contour would have given ambiguous results without the use of mean nearest-neighbour distance. Together they characterized the movement behaviour of individuals and allowed the use of statistical tests to examine differences between categories of animals.

Wherever animals have a restricted habitat a line can be drawn around their movement, but their behaviour need not fall within the concept of home range. Plotting of the area bounding an animal's movement as fixes accumulate for that individual can reveal whether movement is restricted to a distinct home range (Odum and Kuenzler, 1955). This approach showed that most crocodiles were restricted in their range and identified those that were

not. Step-like increases in area represented shifts in home range rather than their extension, though this need not always be the case. It is obviously important to look at size and locality data together. The need to have an overview is further illustrated by the observation that the home ranges of all crocodiles smaller than about 2.2 m had similar AUC and MNND characteristics, but those smaller and larger than 1.2 m occupied mutually exclusive habitats. Dispersal was largely inferred from the relative placement of these animals, a conclusion which depends on the pattern of movements having been stable for several years. The most likely disruption would be drought and the subsequent shrinkage of habitat, but water level had been stable for six years prior to the study period.

The method used here to show that crocodiles use only part of the water's edge habitat available to them is better than a simple description of their overall distribution. It benefits from avoiding biases of capture and resighting.

Synthesis

This study shows that movement varies between animals of different sizes and that, for females at least, reproductive status is a contributing factor.

Mapping on a 100 × 100 m grid indicates that all crocodiles smaller than 2.2 m had similar small, localized home ranges of about 0.1 km². However, juveniles were restricted to the Ngezi River while larger animals were all found in the main waters of the lake, mostly on the eastern shoreline. My interpretation of this is that juveniles of about 1.2 m reached a distinct dispersal stage.

Home range behavior changed in size among crocodiles larger than 2.2 m until large subadults effectively abandoned home ranges and ranged widely throughout much of the available habitat, increasingly encroaching on the breeding grounds of the upper reaches of the Ngezi River (Fig. 8). By contrast, though only slightly larger, 8 of 9 mature females maintained small (0.15 km²) home ranges in the upper reaches where they nest. The only excep-

tion was a particularly small animal which lived in the lake for 8 mo of each year, but moved upstream to the river at nesting time. A similar pattern of movement is reported in subadult female estuarine crocodiles (Messel and Vorlicek, 1987) and it seems likely that dominance interactions are responsible for these observations. Under semi-natural conditions, female alligators form a hierarchy (Garrick *et al.*, 1978) as do Nile crocodiles (Pooley, 1982). The behavior of subadults and small breeding females is consistent with status at the bottom of a hierarchy. The movement behavior and resultant size dispersion of crocodiles at Ngezi is summarized in Figure 10.

The ecological separation of juveniles and larger animals was noted among Nile crocodiles by Cott (1961) in Uganda and Zambia, but Graham (1968) believed that any apparent separation in the homogeneous environment provided by Lake Turkana, Kenya, was due to the cryptic diurnal habits of juveniles. Although Ngezi juveniles were more strictly nocturnal than adults, ecological separation has proved to be real. I have noted similar dispersion of crocodiles in parts of the Okavango Delta, Botswana, and it has been reported among crocodiles in South Africa (Pooley, 1982).

For only two other crocodilians of a size range similar to that of the Nile crocodile do we have adequately detailed movement records that permit comparisons. Both the American alligator and the estuarine crocodile have hatchlings of, at most, 0.3 m and adults which can reach over 4 m. There is ample evidence for both species to suggest that their young enter a dispersal stage at about 1.0–1.2 m.

Where studied most thoroughly, the alligator lives in marshland with interspersed natural and artificial open water (Chabreck, 1965; Joanen and McNease, 1972, 1980; McNease and Joanen, 1974; Hunt and Watanabe, 1982). Hatchlings remain close to the nest for their first and often their second year (Chabreck 1965; Joanen and McNease, 1980; Fogarty, 1974; McNease and Joanen, 1974; Garrick and Lang, 1977). By the end of their second

summer Louisiana alligators are about 1.0 m (Chabreck, 1965; Chabreck and Joanen, 1979) and this appears to be the stage at which they begin moving considerable distances (McIlhenny, 1935; Chabreck, 1965; McNease and Joanen, 1974). Juveniles 1–1.8 m range widely, but restrict their movements to the marsh in which adult females maintain home ranges (McNease and Joanen, 1974), and the spatial separation of size classes does not appear to be marked. Adult females attend hatchlings and are aggressive towards juveniles of 0.7–1.35 m, actively driving them away (Hunt and Watanabe, 1982).

The habitat of the estuarine crocodile in northern Australia is more restricted than that of the alligator, the majority of crocodiles being found in or near tidal rivers and creeks, though some breeding does take place in fresh water swamps. Webb and Messel (1978) found little dispersal of yearlings under these conditions, but long range movement became increasingly likely with age. For females at least, the proportion of long distance movers jumped sharply between 0.8 and 1.2 m (Webb and Messel, 1978). Messel and Vorlicek (1987) state that adult estuarine crocodiles usually tolerate conspecifics up to 1.0–1.2 m, but not larger animals. Under these conditions intermediates are excluded from the areas they were able to occupy when they were smaller and take refuge in non-breeding areas which Messel and Vorlicek (1987) term "stockyards." The evidence for this dispersal and the mechanism behind it comes largely from the distribution of size classes.

The marked separation of size classes in the two species of crocodile is probably due to the fact that they tend to live in river systems where nesting habitat and therefore the distribution of adult females is clumped. In alligators the habitat and hence the distribution of females is more homogeneous. Under marshland conditions dispersal is less directional and there is less opportunity for complete separation. It is notable that intermediate alligators tended to show a preference for deep water areas in summer and autumn when nesting was

underway in the marsh, but avoided them in spring when they were occupied by adults during courtship and mating (Joanen and McNease, 1972, 1980; McNease and Joanen, 1974).

In view of the above, it appears that the American alligator, the Nile crocodile and the estuarine crocodile have a common dispersal phase and that the factors which drive dispersal are similar, involving agonistic interactions between adults and growing juveniles. Hunt and Watanabe (1982) suggest that the situation in alligators is a classic parental-offspring conflict (Trivers, 1974) in which young offspring are favored over older ones. The model suggested by Messel and Vorlicek (1987) and the observations at Ngezi support this opinion.

Hunt and Watanabe (1982) suggest that the aggression of adults towards intermediate animals may result in cannibalism. That large crocodiles kill and eat smaller ones is well recorded (Cott, 1961; Pooley, 1969b; Staton and Dixon, 1975; Messel and Vorlicek, 1987) and crocodile remains are often found in stomach contents (Hippel, 1946; Cott, 1961; Graham, 1968), but the role of intraspecific predation has not been investigated in detail. However, this has not discouraged the use of cannibalism in crocodilian population models as a density-dependent regulating mechanism (Nichols et al., 1976). Intraspecific predation among higher vertebrates is by no means rare or perverse behavior (Fox, 1975; Polis, 1981). Indeed, Polis (1981) noted that it is particularly common among animals that show large differences in size between adults and juveniles and that cannibalism among fish may occur when the size ratio of the largest to the smallest individuals is similar to that in most crocodilians. It is reported that intraspecific predation may be a major mortality factor in a variety of vertebrates including fish (De Angelis et al., 1979), birds (Parsons, 1971) and mammals (Kruuk, 1972).

Webb et al. (1977) suggested that a high hatchling survival rate is a feature of depleted populations, implying that the survival of hatchlings is density-dependent. Hatchling crocodilians, of all species so far

investigated, vocalize when distressed, evoking defense reactions from adults (Staton, 1978). In addition, creche formation and maternal protection of newly hatched crocodiles are well documented phenomena, although their expression seems to be variable, even for individuals within the same geographical area (Deitz, 1979; Magnusson, 1980). It is difficult to reconcile this behavior with any suggestion that hatchlings are predated by adults. However, Hunt (1975) reported that in addition to responding to hatchling distress calls, captive Morelet's crocodiles *Crocodylus moreleti* Dumeril, Bribon and Dumeril spontaneously chased other crocodiles away from their hatchlings, implying that it was intermediate animals that would kill hatchlings if given the opportunity. Indeed, as the range of their movement increased, hatchlings disappeared, though no indication was given of the size of the crocodiles presumed to be responsible for the predation. Hunt (1977) indicated that adult Morelet's crocodiles were actively aggressive towards juveniles older than one year, particularly when small hatchlings were present and, as noted earlier, similar behavior was seen among wild alligators (Hunt and Watanabe, 1982). Juvenile Nile crocodiles (>0.8 m) commonly kill and eat hatchlings when they are held together in captivity, even when adequate food is present (Hutton, 1984). It is likely that if the loss of hatchlings through cannibalism is important in the wild, it is due to intermediates and not adults.

Cannibalism certainly occurs among wild Nile crocodiles. Hippel (1946) reported that 11% of the stomachs of "large" crocodiles contained the remains of other crocodiles, but the absence of data on the size and number of the predated animals prevents further analysis. Cott (1961) gives four anecdotal reports of cannibalism, all of large juveniles and intermediates by adults and, in addition, notes that evidence of cannibalism was found in the stomach contents of 17 of 851 animals, only two of which were less than 3.0 m and eight of which were larger than 4.9 m. Pooley (1969b) reports a 2.0 m adult catching and eating an animal of 1.0 m. It would there-

fore appear that, in this species at least, cannibalism, where it occurs, can largely be attributed to adult depredations on animals of dispersal size, and larger.

Messel and Vorlicek (1987) indicate that over 70% of the animals which disperse to "stockyards" may die. During the study period at Ngezi mortality was largely confined to juveniles, whereas intermediates showed survival similar to adults (Hutton, 1984; Hutton and Woolhouse, 1989). However, in the drought of 1983 and 1984, crocodiles from all parts of the lake were forced together in a small area of water which remained in the old river bed. Intermediate animals immediately became more cryptic and by the time the water level rose, about 50% of this segment of the population had disappeared (Hutton and Woolhouse, 1989), probably due to intraspecific predation. This indicates that intermediates suffer high mortality wherever they are unable to avoid adults. Messel and Vorlicek (1987) consider that the loss of intermediates can regulate population growth. Population modelling (and common sense) suggests that density-dependent regulation in crocodilian populations will be more stable and less likely to lead to extinction if it involves subadults rather than younger animals as suggested in the model constructed by Nichols et al. (1976) (Craig and Hutton, unpublished). Intraspecific interactions, which may result in size-class separation in some habitats, certainly provide a suitable mechanism for density-dependent population regulation in crocodilians.

In order to progress with population models capable of predicting the effects of management it is now important for biologists to identify the factors which are actually limiting crocodilian populations.

ACKNOWLEDGMENTS

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