

LONG DISTANCE MOVEMENTS BY *CAIMAN CROCODILUS YACARE*: IMPLICATIONS FOR MANAGEMENT OF THE SPECIES IN THE BRAZILIAN PANTANAL

ZILCA CAMPOS¹, MARCOS COUTINHO², GUILHERME MOURÃO¹, PETER BAYLISS³ AND WILLIAM E. MAGNUSSON⁴

¹EMBRAPA-Pantanal, Corumbá, MS, Brazil

²IBAMA-Ran Campo Grande, MS, Brazil

³CINCRM Casuarina Campus University, Darwin, Australia

⁴INPA-CPEC, Manaus, AM, Brazil

Movement patterns of caimans were studied over a 16-year period in two areas of the Brazilian Pantanal, one dominated by intermittent rivers and another, adjacent region of many isolated lakes. We marked caimans in 100 lakes (1986–2001) and two rivers (1987–1999). We recaptured 163 adult males, 132 adult females and 237 juveniles. In a two-year interval, hatchlings moved only within the lake area or within the river area and the maximum distance moved was 6.0 km (mean=0.5 km, SD=1.0) in the lake area, and 1.25 km (mean=0.6 km, SD=0.3) in the river area. In a period of one year, females and males larger than 40 cm snout-vent length moved similar distances in both areas (max.=9.8 km). We monitored 47 adult caimans by radio-telemetry in the river area for about a year. The size of the area used by telemetered individuals over periods of 30 to 436 days varied from two to 1649 ha. The areas used by five males in sites subjected to experimental hunting were similar to those used by five other males in areas not subjected to hunting. In periods of 1–5 years, females and males larger than 40 cm SVL moved maximum distances of 16 and 18 km, respectively. Five individuals marked as hatchlings in the lake area were recaptured as adults after intervals of 5–15 years. The extensive long-term and short-term movements by caimans mean that individual ranches should not be considered independent management units for sustained use of caimans in the Pantanal.

Key words: crocodilian, dispersal, movement, population management

INTRODUCTION

Crocodylians can move large distances in the short (Bustard & Singh, 1983; Cooper-Preston, 1992) and long term (Webb & Messel, 1978; Bustard & Choudhury, 1979). Movements may be related to reproduction (Tucker *et al.*, 1997; Coutinho *et al.*, 2000), food (Pooley & Gans, 1970; Campos, 2003), seasonal changes in water level (Schaller & Crawshaw, 1982; Ouboter & Nanhoe, 1988), or to avoid predators or pathogens (Lang, 1987). Movement patterns presumably evolved to maximize fitness of individuals under natural circumstances, but where populations are commercially exploited, movement patterns may increase the vulnerability of some segments of the population, and result in mortality patterns very different from those in populations not subject to exploitation by humans. Disturbance due to hunting may influence behaviour and movement patterns (Montague, 1983; Hutton, 1989), and hunting disturbance could lead to individuals migrating from heavily hunted areas (Campos *et al.*, 2003).

When movement patterns among and within habitats vary among demographic segments of the population,

hunting strategies can be adopted that concentrate mortality on particular size or sex classes (e.g. Caughley, 1977; Joanan & Mc'Nease, 1987; Tucker *et al.*, 1997). In general, hunted populations of South American vertebrates operate as source-sink systems, with immigration from lightly hunted areas maintaining stocks in more heavily hunted regions (Bodmer, 1999).

Although short-term studies of movement are useful to determine habitat use by individuals, long-term studies are necessary to determine whether juveniles hatching in lightly hunted areas can be recruited to the size classes subject to hunting in other areas. The monitoring strategy for *Caiman crocodilus crocodilus* in Venezuela recognizes the potential for long-distance movement and quotas are based on regional estimates (Velasco *et al.*, 2003). However, in the Pantanal, monitoring of *C. c. yacare* is based on ranches as management units (Coutinho *et al.*, 1998). If adult caimans regularly move between ranches, or juveniles hatching on one ranch are regularly recruited to adult populations on neighboring ranches, ranches may be too small to function as independent management units.

Populations of *C. c. yacare* were heavily hunted in the Nhecolândia region of the Brazilian Pantanal (Mourão *et al.*, 1996), but hunting pressure was not geographically uniform. Most hunting was concentrated around intermittent rivers because these are easy to ac-

cess, and the pools formed in the dry season have little vegetation in which caimans can hide (Coutinho & Campos, 1996). It is more difficult to access isolated lakes, and caimans in lakes are harder to locate because of emergent vegetation (Mourão *et al.*, 2000). There has been little or no hunting in our study area since 1991. Areas dominated by isolated lakes may contain populations of caimans with dynamics different from those in intermittent-river habitat. Females and clutch sizes tend to be smaller in lake areas (Campos & Magnusson, 1995), and it is generally easier to locate small caimans in lake areas (Campos *et al.*, 1995).

In this study, we investigate the movement patterns of hatchling, juvenile and adult caimans on two adjacent ranches. Campo Dora Ranch (40 000 ha) is in a region of intermittent rivers and, until the 1990s, was heavily hunted (Mourão *et al.*, 1996). Nhumirim Ranch (4300 ha) is in a region of isolated lakes, and was less intensively hunted. Both areas have been intensively studied over the last 20 years (Campos *et al.*, 1995; Coutinho & Campos, 1996; Campos, 2003). We used intensive mark-recapture and radiotelemetry studies to document movements of individuals in the short, medium and long term. Parts of Campo Dora Ranch were subject to experimental hunting in 1995 (Coutinho, 2000), and we used radio-telemetry data to determine whether the experimental hunting influenced the movement of adults that survived the hunt.

MATERIALS AND METHODS

STUDY AREA

The study was conducted on two cattle ranches in the Nhecolândia region of the Brazilian Pantanal. Nhumirim Ranch (18°59'S and 56°39'W) is in an area characterized by isolated lakes surrounded by forest, and Campo Dora Ranch (18°55'S and 56°40'W) is characterized by flooded fields and pools associated with two intermittent rivers. The ranches are contiguous and caimans can move between the lake and river areas.

The climate in the Pantanal is classified as AW (Savanna climate) in the Köppen system. Floods are caused by local rain and/or rain in the headwaters of the rivers. The seasonal changes in the study area are related to two distinct, but related events: seasonal rains and flooding. Most rain falls between December and April (rainy season), with little or no rain between May and November, when the pools dry quickly (dry season). In the study period between 1986 and 2001, rainfall and air temperature were registered at the Nhumirim Ranch Meteorological Station (Soriano, 1997). Between January 1986 and December 1999, monthly rainfall varied from 0 to 123 mm in the dry season and 8.5 to 346.5 mm in the rainy season. Mean air temperature was 22.4°C (SD=1.8) in the cool season (May-Sept.), and 27.1°C (SD=0.8) in the warm season (Oct.-April).

CAPTURE-RECAPTURE STUDY

The capture-recapture study was conducted in the lake area between 1986 and 2001, and in the river area

between 1987 and 1999. Caimans were captured at night, measured and individually marked. Numbered plastic tags were fixed to raised tail scutes, and aluminium tags (National Band & Tag™ 1005-1 for hatchlings, and 1005-3 for adults) inserted in the interdigital membrane of the hind feet. Also, we cut the double and single tail scutes of each caiman in unique combinations. Recapture sessions in the lake area were undertaken monthly between 1986 and 1988, bimonthly in 1989 and once per year in 1990, 1992, 1994, 1997, 1998, 1999, and 2001. In the river area, captures of the caimans were done twice yearly from 1987 to 1994, and monthly from 1995 to 1999. Hatchlings were captured near nests from 1987 to 1999 in both areas. Adult caimans were captured with nooses at night, or seine nets during the day, and females were captured while guarding nests. All caimans were weighed (± 10 g for hatchlings and ± 0.5 kg for larger animals) and snout-vent length (SVL ± 0.1 cm) to the posterior edge of the cloaca, was measured at each capture. We could not confidently determine the sex of caimans with SVL ≤ 40 cm. For this reason, caimans with SVL ≤ 40 cm were recorded as juveniles of undetermined sex. All caimans captured were used to estimate the size structure and sex ratio of populations in each area.

MOVEMENT OF HATCHLING GROUPS IN THE LAKE AREA

In 1996, eight clutches of hatchlings were monitored for periods of up to 11 months. In 1997, six clutches were monitored for periods up to 72 days. In 1999, five clutches were monitored for 120 days. The clutches were located and counted at night on the banks of the lakes, and the presence or absence of an adult (presumed to be the mother) was registered, but, on most occasions, hatchlings were not captured and identified individually.

RADIO-TRACKING STUDY

In the radio-telemetry study, we used two models of radio-transmitter (33 made by Telonics™ and 14 made by Sirtrack™). The Telonics radio-transmitters measured 9.0 cm by 2.3 cm, weighed 80 g and had internal antennas. The Sirtrack transmitters measured 2.0 cm by 2.5 cm, weighed 50 g, and had external 47 cm antennas. All radio-transmitters were encapsulated in resin at the factory.

Most radios were placed between the last double tail crests and sewn to the scutes with nylon monofilament fishing line (Muñoz & Thorbjarnarson, 2000). However, 18 radios (4 Telonics, 14 Sirtrack) were implanted in the peritoneal cavity of caimans. Surgery to implant radios was done in the laboratory, under sterile conditions. The caimans were kept for one hour in a freezer to decrease their body temperature to around 19°C, which immobilized them, and a local anaesthetic (Xylocaine) was used in the region of the implant. All surgical procedures were done respecting ethical procedures for practices with animals recommended by Empresa

Brasileira de Pesquisa Agropecuária (EMBRAPA) veterinarians.

Most caimans with radio-transmitters were not recaptured during the study to avoid disturbance. Caimans were recaptured at the end of the predicted battery life to retrieve the radio transmitters. Tracking was done with Telonics TR2 and TR4 receivers from an ultra-light aircraft, boat, car or on foot. Individuals were monitored weekly. The frequency range of the radio transmitters was 164–166 MHz. The maximum distance of signal reception at ground level was about 800 m.

Radio-tracking of caimans for more than seven months was undertaken only in the river area. Radios were fixed to the tails of 29 caimans and radios were implanted in 18 caimans. In November 1989, radio-transmitters were implanted in one male and three females. In January 1992, radios were fixed to the tails of five males and three females. In August 1993, radio-transmitters were fixed to the tails of three females and eight males. In May 1996, radios were fixed to the tails of 10 males and implanted in peritoneal cavities of seven females. In May 1999, radios were implanted in the peritoneal cavities of five males and two females.

The locations of caimans with radio-transmitters were plotted on a map of the study area. The area used by each caiman was described by a minimum convex polygon (Hayne, 1949), in the Systat 8.0 program. The area covered by the polygon was estimated by the number of pixels covering each area in Adobe Photoshop 4.0 images. The size of the pixels was determined from known areas of 25 km² and 100 km². Only caimans that were tracked for 30 days or more were used in the analyses.

CAIMANS RADIO-TRACKED IN AREAS WITH AND WITHOUT HUNTING

In August 1995, four blocks of 24 km² were delimited in the river area. The distances between blocks were around 4 km. Two blocks were not hunted (controls) and controlled harvesting was undertaken in the other blocks. In the hunted blocks, 648 adult caimans (SVL > 80 cm) were killed (Coutinho, 2000). Between May 1996 and May 1997, 10 adult males (SVL ≥ 90 cm) were radio-tracked. Two or three caimans were tracked in each block, for a total of five caimans in control blocks and five caimans in hunted blocks.

INDEX OF DISTANCE MOVED

The maximum distance moved by caimans monitored by radio-telemetry was calculated as the maximum straight-line distance between positions that the caiman was recorded. To maintain independence of the capture-recapture data, only the first and last captures of each individual were used. The distances moved between captures were measured on a LANDSAT satellite image of the study area, at a scale of 1:100,000.

CONDITION INDEX

The individual condition of the caimans with radio-transmitters was estimated as the residual of the linear

regression between log body mass (logM – kg) and log snout-vent length (logM = 10.25 + 2.906 × logSVL; $r^2 = 0.95$; $n = 47$; $P < 0.001$).

RESULTS

CAPTURE-RECAPTURE

We marked 2576 caimans in the lake area and 3042 caimans in the river area between 1986 and 2001. In the 16 years of the study, 532 caimans (9.5%) were recaptured (237 hatchlings, 163 males and 132 females) over varying time intervals. The size structure of the populations varied between the lake and river areas (Fig. 1). The proportion of caimans with SVL ≤ 40 cm was 72% in the lake area and 13% in the river area.

Of the 237 hatchlings, 67% remained in the lake in which they were captured for up to two years, and 33% moved to other lakes. In six reproductive seasons, 197 hatchlings less than one year old were recaptured. Of these, 186 moved distances up to 6.0 km (mean = 0.5 km, SD = 1.0) between lakes in the lake area. Eleven hatchlings in the river area moved < 1.2 km (mean = 0.6 km, SD = 0.3) and remained in the river area. No individuals were recorded moving from the lake to the river area, or vice versa, during the first two years of life (Fig. 2). Although 197 hatchlings were recaptured within the first year of life, most did not move independently. Fig. 2 shows only the 34 independent movements. Animals that moved to and from the same places were not considered to have moved independently, and group movements are represented by single arrows.

In the reproductive seasons of 1996, 1997 and 1999, we monitored the movement of eight, six and five hatchling groups, respectively, that remained together with females in the lake area. These hatchlings were not captured at each survey, so we can only assume that most individuals remained in their original groups. However, it is extremely unlikely that a hatchling group

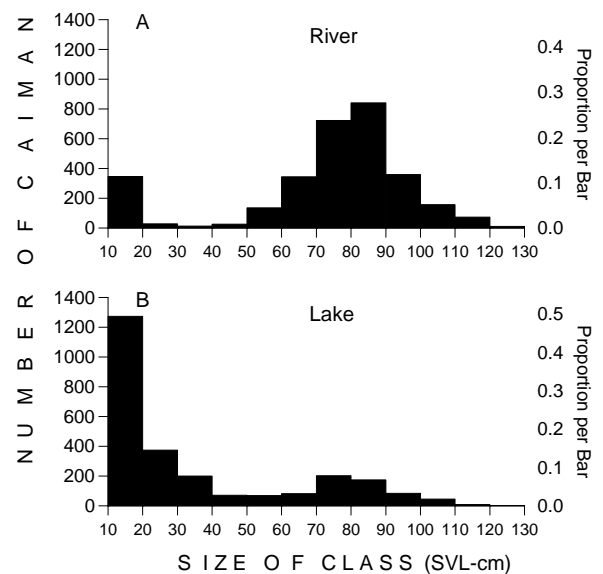


FIG 1. Sizes of caimans captured in the river area (A) and the lake area (B).

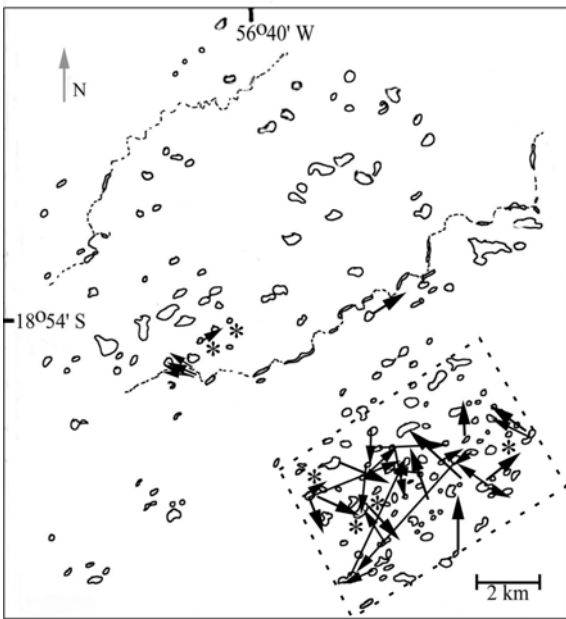


FIG 2. Movements of hatchlings (SVL \leq 40 cm) during intervals of up to two years, between lakes (arrows) and recaptured in the same lake (asterisks). If all hatchlings in a groups were captured and recaptured at the same places, they are represented only as a single arrow. The straight broken lines indicate the boundary between the two ranches, which corresponds to the boundary between the lake area (south of the southern limit) and the river area (north of the southern limit).

moved and was replaced by another hatchling group of similar size in the same place. In 1996, hatchling groups remained together in the same lake for 74–330 days. In 1997, hatchling groups could be encountered for 72 days. Individuals in one of the clutches moved to another lake 500 m from where they hatched in an interval of 30 days, and the other clutches remained in the lakes where they were first recorded. In 1999, we were able to follow hatchlings for 120 days. One of the clutches moved from one lake to another 500 m away, and the others remained in the original lakes.

The maximum distances between captures recorded for males and females with SVL \geq 40 cm during periods up to 364 days were similar (males: max.=9.5 km, mean=1.33, SD=1.97, females: max.=9.8 km, mean=1.6 km, SD=2.05). About 30% of the variance in distance moved, D (m), by caimans could be accounted for by a multiple regression including interval between captures (I , in days), snout-vent length (SVL, in cm) and water level (L , in cm) ($D = -4868 + 1.27 \times I + 49.82 \times \text{SVL} + 22.58 \times L$; $R^2 = 0.32$, $F_{3,47} = 7.23$, $P < 0.001$). SVL ($P \leq 0.001$) and mean water level in the period between captures ($P = 0.002$) contributed significantly to the model, but interval between captures did not ($P = 0.487$).

The majority of caimans were recaptured at intervals of 1–5 years. In these periods, some animals were recaptured within the same ranch, but many moved between the river and lake areas (Fig. 3). Individuals recaptured in the same place may have undertaken more extensive movements, but this cannot be determined from capture-

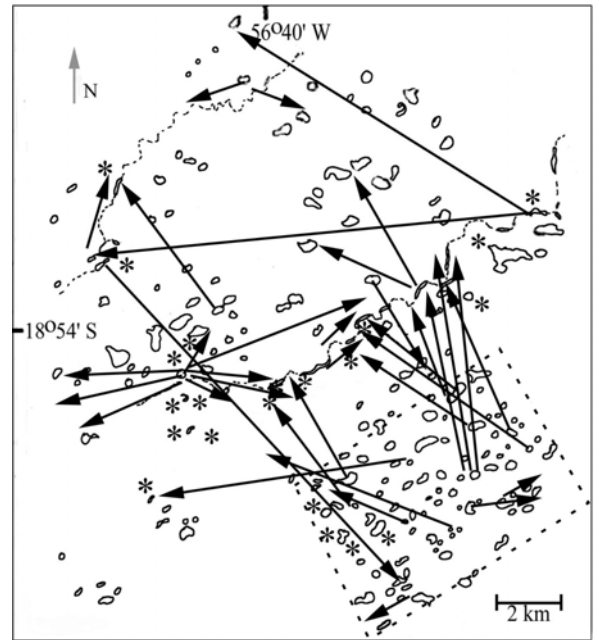


FIG 3. Movement of caimans recaptured after intervals of 1–5 years in lake and river areas. Seven caimans found dead at hunting sites are indicated with crosses. Asterisks indicate locations of hunting sites. The straight broken line indicates the boundary between the two ranches, which corresponds to the boundary between the lake area (south of the line) and the river area (north of the line).

recapture data. Most movements were within or towards the river area. Only four of 16 individuals marked in the lake area were recaptured in the lake area. Only one of 19 individuals marked in the river area that were recaptured moved to the lake area. Most individuals that were recaptured moved to the river area ($n = 12$) or remained there ($n = 18$). The maximum distance between captures in < 5 years was 18 km (mean=5.0 km, SD=4.3).

The mean distances moved during 1–5 years by males and females were similar and not significantly different ($t_{66} = 0.318$, $P = 0.751$); males moved an average distance of 2.3 km (SD=3.2) and females moved a mean of 2.1 km (SD=3.4). About 30% of the variance in distances (D , m) moved by caimans in 1–5 years could be predicted by a multiple regression including interval between captures, I (days), SVL (cm) and water level (L , cm): $D = -6756 - 2.92 \times I + 55.3 \times \text{SVL} - 73.6 \times L$ ($R^2 = 0.29$, $F_{3,38} = 5.19$, $P = 0.004$). SVL ($P = 0.038$) and interval between captures ($P = 0.004$) contributed significantly to the model, but the evidence for an effect of water level was equivocal ($P = 0.079$).

Twenty-one caimans were recaptured after periods ≥ 5 years. The maximum interval between recaptures was 14 years. The relationships between distance moved (D , in km) and log SVL (cm) at first capture for the 21 caimans were described by the following equation: $D = 25.9 - 5.4 \times \log \text{SVL}$ ($R^2 = 0.61$, $F_{1,19} = 29.5$, $P = 0.001$). Although the log-linear equation described most of the data well, the area predicted to be used by large individuals (0 ha) was unrealistic (Fig. 4). Radio-telemetry

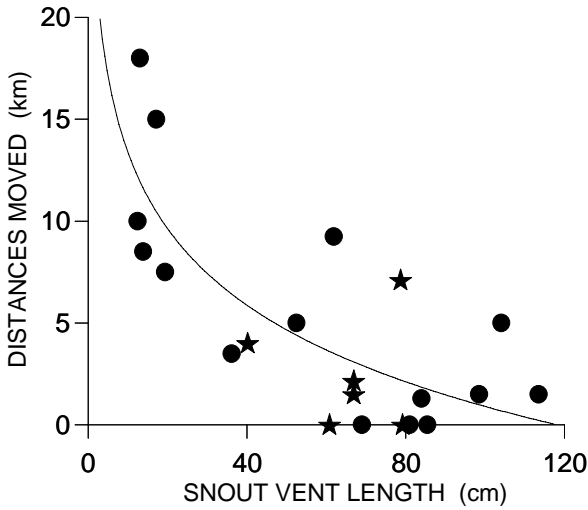


FIG. 4. Relationship between distances moved and snout-vent length at first capture for 21 male (circles) and female (stars) caimans, captured over periods of 5–15 years.

data (see above) indicates that the mean linear distance covered by large individuals over periods in excess of one year is about 4.6 km. Based on Fig. 4, the area used by individuals approaches this value at a snout-vent length of about 52 cm, suggesting that juveniles establish fixed home ranges at about this size.

As in the medium-term movements, most of the long-term movements were from the lake area to the river area (Fig. 5). Four of the five males that were marked in the first year of life in the lake area were recaptured as adults in the river area 6–9 years later, 8–18

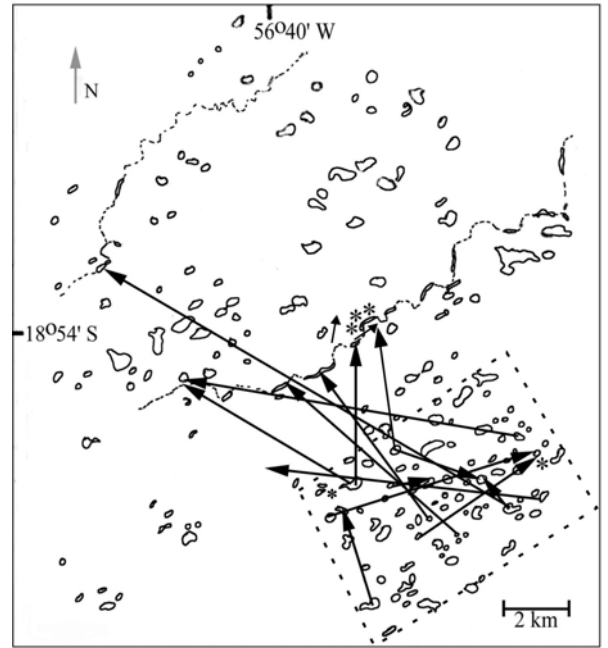


FIG. 5. Movements of 21 caimans recaptured after periods of 5–15 years. Asterisks indicate caimans that were recaptured at the site at which they were first captured. The broken line indicates the boundary between the two ranches which corresponds to the boundary between the lake area (south of the line) and the river area (north of the line).

km from where they were marked (Table 1). One individual was recaptured in the lake area at 10 years of age, 7.5 km from where it was marked as a hatchling.

TABLE 1. Sizes of the caimans recaptured over intervals of 5 and 15 years and maximum distances between capture points in the river (R) and in lake areas (L).

Sex	Date of capture	Capture habitat	SVL (cm)	Mass (kg)	Date of recapture	Recapture habitat	SVL (cm)	Mass (kg)	Interval (days)	Distance (km)
M	15/04/89	L	12.5	0.046	17/03/97	R	80.0	11.0	2892	10.0
M	28/07/88	L	13.1	0.044	26/08/96	R	83.0	7.0	2948	18.0
M	22/11/87	L	17.2	0.087	02/09/96	R	90.5	17.0	2835	15.0
M	17/04/92	L	13.9	0.054	14/07/97	R	71.5	7.7	1915	8.5
M	06/12/89	L	36.1	1.10	19/11/99	L	80.0	12.0	3633	3.5
M	04/12/87	L	52.5	3.5	13/02/98	R	105.0	26.0	3719	5.0
M	03/12/87	L	61.9	5.0	02/11/97	R	104.0	32.0	3620	9.25
M	27/09/89	L	69.0	7.5	19/11/99	L	82.5	12.0	3701	0.0
M	20/10/94	R	81.0	11.5	29/09/99	R	107.0	38.0	1805	0.0
M	08/11/94	R	84.0	15.0	29/09/99	R	106.0	31.0	1825	1.3
M	08/11/94	R	98.5	25.0	07/10/99	R	101.0	22.0	1795	1.5
M	20/10/94	R	85.5	14.0	26/09/99	R	108.0	-	1801	0.0
M	05/10/89	L	104.1	27.0	10/09/99	R	110.0	28.5	3625	5.0
M	06/01/88	L	113.5	31.0	06/08/93	L	114.0	-	2005	1.5
F	10/12/89	L	19.4	0.114	19/11/99	L	72.0	9.0	3628	7.5
F	20/10/94	R	60.8	6.0	30/09/99	R	79.0	11.0	1805	0.0
F	02/12/87	L	66.9	6.0	05/08/93	L	79.0	9.0	2068	1.5
F	21/02/87	L	66.9	6.0	07/08/93	L	79.0	9.0	2356	2.15
F	21/11/87	L	40.2	1.4	27/01/01	L	85.0	-	5136	4.0
F	05/10/89	L	79.2	14.0	29/01/01	L	84.0	-	4129	0.0
F	19/09/89	L	78.7	11.0	07/11/94	R	79.0	13.0	1873	7.1

EFFECT OF MOVEMENT ON VULNERABILITY TO HUNTING

Local hunters informed us that carcasses were generally left near the site of capture, and hunting sites were identified from carcasses and skeletons left on the banks of rivers and lakes. Four hunting sites were in the lake area and 18 in the river area. Between 1989 and 1990, we found plastic numbered tags that we used to mark caimans at the hunting sites. The caimans had been marked in the lake area 515–1065 days (mean=794 days, SD=229) before being found at river hunting sites. All caimans killed were males and their sizes at original capture were greater than 60 cm SVL (Table 2). The distances moved by the caimans from their initial capture sites to where they were killed by hunters varied from five to 11 km (mean=8.0 km, SD=2.4).

RADIO-TELEMETRY

The pattern of water level fluctuations in the river channel was generally similar in 1992–2001, with low levels between August and December. The months between August and December were dry in all years, but in other months, water level varied between years. The monthly movement rate (MR) of the caimans with radio-transmitters was not related to water level (L) ($MR=74.267-0.566 \times L$, $R^2=0.107$, $n=26$, $P=0.103$). The mean movement rate of the caimans was only 46.7 ± 66.9 m/day. There was no significant difference between movement rates of males and females (Kruskal Wallis test; $KS=7.8$, $P=0.253$, $SD=6$). The body condition of the caimans with radios was not related to monthly movement rate ($r^2=0.008$, $P=0.686$, $n=22$).

The area used by 47 caimans (Table 3) tracked for up to 436 days in the river area varied from 2 to 1650 ha (mean=153, SD=299). About 25% of the variance in the size of the area used (A – ha) was accounted for by the multiple regression, which included snout-vent length of the caiman (SVL – cm), log interval (logI – days), and sex of the caiman (S, dummy variable coded 0,1) ($A=582-2.299 \times SVL+198.6 \times \log I+4.774 \times S$, $R^2=0.254$; $F_{3,42}=4.89$, $P=0.005$). However, only time of tracking ($P \leq 0.001$) contributed significantly to the model. There was little evidence of an effect of SVL ($P=0.549$) or sex ($P=0.965$).

Although there is a large scatter of points, both LOWESS regression (Fig. 6 – broken line) and log-linear regression (Fig. 6 – solid line) indicate that estimates of area used increased slowly after about 225 days. One individual covered a large area (1649 ha) in 246 days, and was an outlier in the analyses. However, removal of this individual had little effect on the position of the lines, and did not affect the statistical conclusions. The mean of the maximum distances between records for caimans tracked for more than 225 days was 4.6 km (min.=1.0, max.=9.8).

During the period of experimental hunting, 10 males were monitored in the experimental blocks in the river area over periods of 249–436 days (Table 4). The area

used by the 10 caimans varied from 50 to 777 ha (mean=348, SD=255). However, the mean area used by the five caimans in the hunted blocks not was significantly different from the mean area used by five caimans in the control blocks (ANOVA, $F_{2,7}=2.32$, $P=0.171$).

DISCUSSION

Little is known about dispersal in wild populations of vertebrates (Horn, 1984), and one reason is the difficulty of marking young individuals and recapturing them as adults. This difficulty is especially great for crocodylians, which have long life spans and can move great distances. The individual *Caiman crocodilus yacare* in this study moved not only inside the lake and river areas, but also between them. We were able to record movements of some individuals from soon after hatching to adulthood, but only by marking more than 5000 animals and maintaining capture effort over 15 years.

The distances moved by hatchling *C. c. yacare* varied little between the first and second years of life, when they tended to remain near nests. In the first year of life, some individuals moved distances of up to 6 km in the lake area and up to 1 km in the river area. However, we have no evidence of hatchlings moving from the lake to the river area, or vice versa, during the first two years of life.

Hatchlings in the lake area remained together with an adult for up to 11 months. In the northern Pantanal, the majority of hatchling *C. c. yacare* remained within 200 m of their nests over a period of six months, and were attended by females (Cintra, 1989). Da Silveira *et al.* (1997) reported that clutches of *C. c. crocodilus* are also relatively sedentary in the first months of life.

In this study, individual *C. c. yacare* moved extensively throughout the year. Although there was a significant relationship between water level and distance moved by animals recaptured over periods of up to one year, the effect of water level was not apparent in the data for animals monitored by radio-telemetry. In the dry period, caimans remained concentrated in the remaining pools. However, they regularly moved between pools (Campos *et al.*, 2003). Why caimans move between pools in groups is unknown, but may be related to

TABLE 2. Sizes of caimans marked in the lake area and found dead at hunting sites in the river area, and distance from where they were marked.

Date of capture	SVL (cm)	Mass (kg)	Date of death	Interval (days)	Distances (km)
24/03/87	60.0	-	24/02/90	1065	11.0
13/03/87	92.4	13.0	13/01/90	1035	6.1
24/04/87	80.0	-	23/12/89	970	9.5
05/12/87	101.0	27.0	08/12/89	733	9.25
31/07/87	104.3	24.0	31/01/89	545	5.5
20/08/87	59.0	5.0	20/01/89	515	5.0
02/01/88	64.2	5.4	08/12/89	700	9.5

TABLE 3. Sizes and distances moved by caimans tracked by radio-telemetry.

SVL (cm)	Mass (kg)	Body condition	Sex	Interval (days)	Area used (ha)	Maximum distance moved (km)
95.2	27.0	0.303	M	114	42.0	1.75
82.4	16.0	0.202	F	123	22.3	1.35
71.1	10.0	0.163	F	246	1649	9.80
83.4	16.0	0.167	F	239	32.2	1.00
80.0	12.5	0.042	F	144	7.0	0.30
96.0	20.0	-0.021	M	144	19.0	1.00
103.0	22.0	-0.132	M	216	728.2	7.50
99.0	22.0	-0.016	M	140	63.0	2.75
71.0	9.0	0.062	F	126	42.3	0.50
74.0	10.0	0.046	F	125	6.0	0.00
115.0	37.5	0.079	M	159	50.0	1.50
85.0	16.0	0.111	M	116	96.2	1.90
102.0	24.0	-0.016	M	60	8.120	2.40
108.0	32.0	0.104	M	75	48.4	1.75
76.5	10.0	-0.051	F	157	17.1	1.65
72.5	8.5	-0.056	F	47	14.0	2.25
80.5	12.0	-0.017	F	102	36.5	2.75
68.0	9.0	0.188	F	83	261.6	7.50
84.0	14.0	0.012	F	185	41.5	6.75
79.0	11.5	-0.005	F	169	168.4	5.00
87.5	18.0	0.144	F	82	172.5	2.50
74.0	9.0	-0.059	F	48	2.0	0.75
105.0	24.0	-0.101	M	96	15.4	6.75
99.0	21.0	-0.062	M	397	90.0	5.00
111.0	28.5	-0.091	M	399	86.2	3.70
99.5	25.0	0.097	M	398	50.0	2.50
117.0	36.0	-0.012	M	395	417.0	3.50
108.0	26.0	-0.103	M	249	426.0	2.70
97.0	20.0	-0.052	M	335	210.6	2.50
93.5	18.5	-0.022	M	249	378.4	5.00
114.0	35.0	0.036	M	436	727	7.50
102.0	22.5	-0.081	M	335	777	8.75
112.5	32.5	0.001	M	397	313	3.75
58.0	4.0	-0.158	M	37	11.5	0.00
111.0	28.0	-0.109	M	36	11.5	0.50
99.0	22.0	-0.016	M	62	11.5	0.00
74.0	8.0	-0.177	F	42	11.5	0.00
89.0	12.0	-0.311	M	39	11.5	0.00
60.0	5.0	-0.034	F	35	11.5	0.00
75.0	8.5	-0.155	F	44	3.0	0.00
87.5	14.0	-0.107	F	38	3.0	0.00
80.0	11.0	-0.086	F	38	3.0	0.00
82.5	12.0	-0.089	F	38	3.0	0.00
79.5	14.0	0.173	F	38	72.2	2.50
78.5	11.0	-0.031	F	42	3.0	0.00
85.0	14.0	-0.022	F	38	3.0	0.00
63.5	6.0	-0.017	M	57	11.5	0.00

reproductive behaviour or feeding habits (Coutinho *et al.*, 2000; Campos, 2003).

There was large individual variation in movement patterns for both sexes in *C. c. yacare*. Some apparently moved short distances or returned to the same water

body after many years, and others were recorded to move great distances in short periods. Caimans undertook extensive movements in both the lake and river areas. The distributions of the distances moved by males and females were similar in the short and long

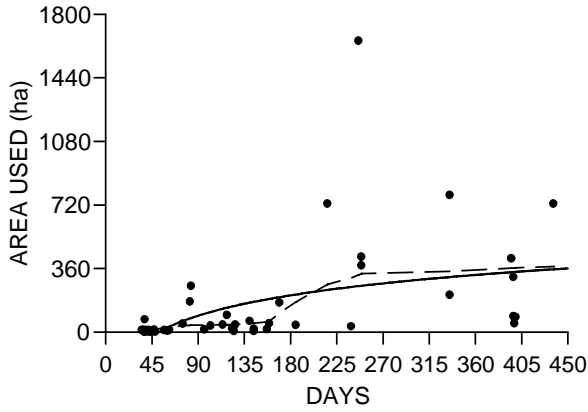


FIG. 6. Areas used by 46 caimans with radio transmitters in the river area in relation to the period the caimans were monitored. The line broken line is a LOWESS regression (tension = 0.5), and the solid line represents a least-squares linear-log regression.

terms. In periods of up to one year, caiman moved distances of up to 9.8 km. In the northern Pantanal, the maximum distance moved in the dry season by *C. c. yacare* in an interval of six months was 9.4 km (Schaller & Crawshaw, 1982). However, Ouboter & Nanhoe (1988) found that most individual *C. c. crocodilus* in their study area in Suriname were sedentary and the largest distance moved in one year was 3 km. In our study, male caimans were recorded moving distances of up to 18 km, and females up to 14 km, in the long term. Movements over distances greater than these would have taken caimans out of the study area, so our data probably underestimate the degree of movement.

Although hatchling caimans tended to remain together close to the nesting site during the first two years after hatching, individuals of $SVL > 40$ cm moved extensively within and between habitats. For individuals with $SVL > 40$ cm, smaller individuals were recorded moving larger distances than larger individuals, and small individuals may have moved greater distances than those recorded, as more extensive movements would have taken them out of the study area. Distances moved in the long term by caimans with $SVL > 52$ cm were similar to distances moved by larger individuals in the short term, indicating that individuals may establish relatively fixed home ranges at about this size.

The pattern of movement of some species of vertebrates is related to density (Hansson, 1991), and increase in disturbance could cause increased movement. However, the reduction in population density and the disturbance caused by hunting in the experimental blocks did not result in differences in the area used by the five males monitored by radio telemetry within hunted blocks in relation to the five males monitored in areas without hunting.

Our study area was around 50,000 ha, involved two ranches, and apparently was too small to study dispersal of caimans. The caimans moved from the lake area to the river area and, within the river area, moved from one river to another. This probably contributes to the low recapture rate of the caimans in the study area. However,

TABLE 4. Sizes of male caimans used to investigate movement in hunted and unhunted areas.

SVL (cm)	Mass (kg)	Interval (days)	Distance (km)	Area used (ha)	Hunted area
99.0	21.0	397	5.0	90.0	No
111.0	28.5	399	3.7	86.2	No
99.5	25.0	398	2.5	50.0	No
97.0	20.0	335	2.5	210.6	No
114.0	35.0	436	7.5	727.0	No
93.5	18.5	249	5.0	378.4	Yes
117.0	36.0	395	3.5	417.0	Yes
108.0	26.0	249	2.5	210.6	Yes
102.0	22.5	335	8.75	777.0	Yes
112.5	32.5	397	3.75	313.0	Yes

movement over large distances between habitats can be an advantage in sustained-use programmes, if populations of caimans in areas that are not hunted can sustain recruitment to populations in hunted areas. In the controlled harvest programme in Venezuela, monitoring is done over units much larger than individual ranches and quotas are determined on a regional basis (Velasco *et al.*, 2003). In contrast, individual ranches are monitoring units in the egg-collection program in the Pantanal (Coutinho *et al.*, 1998). The results of this study indicate that ranches are not large enough to be considered independent management units in the Pantanal, and that movement between ranches should be considered when allocating quotas to individual ranches.

It has been suggested that hunted populations of South American vertebrates operate as source-sink systems, with immigration from lightly hunted areas maintaining stocks in more heavily hunted regions (Bodmer, 1999). Information from hunters, and the distribution of hunting sites, indicates that hunting was more intensive in the river area than the lake area. This could be because the caimans tend to be larger in the river area, because there is less available water in the dry season and the caimans become more concentrated in the river area, because of the difficulty of hunting in the heavily vegetated lakes, or a combination of these factors.

Based on the size distribution of the populations, the number of hatchlings produced is much greater in the lake area than in the river area, despite the smaller average size of the females (Campos & Magnusson, 1995). However, movement of caimans from the lake area to the river area is frequent; most of the caimans marked in the lake area that were recaptured over periods of ≥ 5 yrs moved to the river area. Four of the five males that were marked as hatchlings in the lake area were recaptured as adults in the river area 6–9 years later, 8–18 km from where they were marked. Other individuals marked as hatchlings may have dispersed larger distances, but these would have moved out of the study area.

The combination of light hunting, extensive reproduction and frequent dispersal probably result in the lake area being a source for the hunted population. In con-

trast, intensive hunting and low reproductive rate probably mean that the river population is a sink, and would not have been able to sustain the intensive hunting of the 1980s (Mourão *et al.*, 1996), if it had been isolated from the lake area. Some other hunted populations of crocodylians also appear to represent source-sink systems, with most reproductive individuals in areas that are not readily accessible to hunters (e.g. *Alligator mississippiensis* – Joanen & Mc'Nease, 1987; Elsey & Kinler, 2004; *Melanosuchus niger* – Da Silveira, 2001).

Whatever the specific roles of Nhumirim and Campo Dora Ranches in the dynamics of local populations of caimans, this study has shown that individual *Caiman crocodilus yacare* undertake extensive movements seasonally, annually and over the life span of individuals. These movements cover areas much larger than the average size of ranches in the Pantanal, so individual ranches should not be considered autonomous units in management plans for the Pantanal caimans.

ACKNOWLEDGMENTS

This study represents part of a PhD thesis by Zilca Campos presented to the Universidade Federal de Minas Gerais, under the supervision of Gustavo Fonseca, and was financed by EMBRAPA Pantanal, WWF-USA, Fundação O Boticário and Conservation International do Brasil. We thank Luís Gomes da Silva (owner Campo Dora farm), Francisco (*in memoriam*), Procópio, José Augusto, Vândir, Luís, Henrique, Sebastião and Joãozinho for help in the capture of caimans, Jeuilson, and Zairo for help in radio-tracking. Graeme Caughley (*in memoriam*), Clarence Abercrombie and Ronis da Silveira participated in radio tracking in the river area.

REFERENCES

- Bodmer, R. E. (1999). Uso sustentable de los ungulados amazónicos: implicaciones par las areas protegidas comunales. In *Manejo y Conservación de Fauna Silvestre en América Latina*, 51-58. Fang, T. G., Montenegro, O. L. & Bodmer, R. E. (Eds). New York: Columbia University Press.
- Bustard, H. R. & Choudhury, B. C. (1979). Long distance movement by a saltwater crocodile (*Crocodylus porosus*). *British Journal of Herpetology* **6**, 87-92.
- Bustard, H. R. & Singh, L. A. K. (1983). Movement of wild gharial, *Gavialis gangeticus* (Gemini) in the River Mahanadi, Orissa, (India). *British Journal of Herpetology* **6**, 287-291.
- Campos, Z. (2003). *Caiman crocodilus yacare*. Food-related movement. *Herpetological Review* **34**, 141-141.
- Campos, Z., Coutinho, M. & Magnusson, M. (2003). Terrestrial activity of caiman in the Pantanal, Brazil. *Copeia* **2003**, 628-634.
- Campos, Z. & Magnusson, W. (1995). Relationship between rainfall, nesting habitat and fecundity of *Caiman crocodilus yacare* in the Pantanal, Brazil. *Journal of Tropical Ecology* **11**, 351-358.
- Campos, Z., Mourão, G., Coutinho, M. & Abercrombie, C. (1995). Night-light counts, size structure, and sex ratio in wild populations of yacare caiman (*Caiman crocodilus yacare*) in the Brazilian Pantanal. *Vida Silvestre Neotropical* **4**, 46-50.
- Caughley, G. (1977). *Analysis of Vertebrate Populations*. London: John Wiley & Sons.
- Cintra, R. (1989). Maternal care and daily pattern of behavior in a family of caimans, *Caiman yacare* in the Brazilian Pantanal. *Journal of Herpetology* **23**, 320-322.
- Cooper-Preston, H. (1992). *Geographic Variation in the Population Dynamics of Crocodylus johnstoni (Kreffft) in Three Rivers in the Northern Territory, Australia*. Ph.D. dissertation, University of New England, Armidale, Australia.
- Coutinho, M. (2000). *Population Ecology and the Conservation and Management of Caiman yacare in the Pantanal, Brazil*. Ph.D. dissertation, University of Queensland, Brisbane, Australia.
- Coutinho, M. & Campos, Z. (1996). Effect of habitat and seasonality on the densities of caiman in Southern Pantanal – Brazil. *Journal Tropical Ecology* **12**, 741-747.
- Coutinho, M., Campos, Z., Bampi, I. & Dal'Ava, F. (1998). Preliminary report for the management system of yacare caiman in the Pantanal: a proposal for future research and the development of a monitoring system for wild population subjected to nest harvests. *Ciência e Cultura* **50**, 60-64.
- Coutinho, M., Campos, Z., Cardoso, F., Martinelli, P. & Castro, A. (2000). Reproductive biology and its implication for management of caiman *Caiman yacare* in the Pantanal wetland, Brazil. In *Crocodylian Biology and Evolution*, 229-243. Gordon, G., Seebacher, F. & Franklin, C. E. (Eds). Chipping Norton, Australia: Surrey Beatty & Sons.
- Da Silveira, R. (2001). Monitoramento, crescimento e caça de jacaré-açu (*Melanosuchus niger*) e de jacaré-tinga (*Caiman crocodilus crocodilus*). Ph.D. dissertation INPA/UA, Manaus, Brazil.
- Da Silveira, R., Magnusson, W. E. & Campos, Z. (1997). Monitoring of distribution, abundance and breeding areas of *Caiman crocodilus crocodilus* and *Melanosuchus niger* in the Anavilhanas archipelago, Central Amazonia, Brazil. *Journal of Herpetology* **31**, 514-520.
- Elsley, R. & Kinler, N. (2004). Louisiana's alligator program: adapting management as populations recover and risk of unsustainable use decreases. In *Crocodyles*, 92-101. Proceedings of the 17th Working Meeting of the Crocodyles Specialist Group of the Species Survival Commission of IUCN. Darwin: IUCN.
- Hansson, L. (1991). Dispersal and connectivity in metapopulations. In *Metapopulation Dynamics: Empirical and Theoretical Investigations*, 89-103. Gilpin, M. E. & Hanski, I. (Eds). London: Academic Press.
- Hayne, D. W. (1949). Calculation of size of home range. *Journal of Mammalogy* **30**, 1-18.

- Horn, H. S. (1984). Some theories about dispersal. In *Dispersal and Migration*, 55-62. Lidicker, Jr, W. Z. & Caldewell, R. C. (Eds). USA: Hutchinson Ross Publishing Company.
- Hutton, J. (1989). Movements, home range, dispersal and separation of size classes in Nile crocodiles. *Animal Zoology* **29**, 1033-1049.
- Joanen, T. & Mc'Nease, L. (1987). The management of alligators in Louisiana, USA. In *Wildlife Management: Crocodiles and Alligators*, 33-42. Webb, G. W., Manolis, S. C. & Whitehead, P. J. (Eds). Chipping Norton, Australia: Surrey Beatty & Sons.
- Lang, J. (1987). Crocodilian behaviour: implications for management. In *Wildlife Management: Crocodiles and Alligators*, 273-294. Webb, G. W., Manolis, S. C. & Whitehead, P. J. (Eds). Chipping Norton, Australia: Surrey Beatty & Sons.
- Montague, J. J. (1983). Influence of water level, hunting pressure, and habitat type on crocodile abundance in the Fly River drainage, Papua New Guinea. *Biological Conservation* **26**, 309-339.
- Mourão, G. M., Campos, Z., Coutinho, M. & Abercrombie, C. (1996). Size structure of illegal harvested and surviving caiman (*Caiman crocodilus yacare*) in the Pantanal, Brazil. *Biological Conservation* **75**, 261-265.
- Mourão, G., Coutinho, M., Mauro, R., Campos, Z., Tomás, W. & Magnusson, W. (2000). Aerial surveys of caiman, marsh deer and pampas deer in the Pantanal Wetland of Brazil. *Biological Conservation* **92**, 175-183.
- Munõz, M. C. & Thorbjarnason, J. (2000). Movement of captive-released Orinoco crocodiles (*Crocodylus intermedius*) in the Capanaparo river, Venezuela. *Journal of Herpetology* **34**, 397-403.
- Ouboter, P. E. & Nanhoë, L. M. R. (1988). Habitat selection and migration of *Caiman crocodilus crocodilus* in a swamp and swamp-forest habitat in Northern Suriname. *Journal of Herpetology* **2**, 283-294.
- Pooley, A. C. & Gans, C. (1976). The Nile crocodile. *Scientific American* **234**, 114-124.
- Schaller, G. B. & Crawshaw, P. G. (1982). Fishing behavior of Paraguayan Caiman (*Caiman crocodilus*). *Copeia* **1982**, 66-72.
- Soriano, B. A. (1997). *Boletim Agrometeorológico: 1989-1996*. Corumbá, MS, Brazil: Empresa Brasileira de Pesquisa Agropecuária - CPA Pantanal.
- Tucker, A. D., Limpus, C. J., McCallum, H. I. & McDonald, K. R. (1997). Movement and dispersal of the Australian freshwater crocodile (*Crocodylus johnstoni*) in the Lynd River, Queensland. *Wildlife Research* **24**, 379-396.
- Velasco, A., Colomina, G., De Sola, R. & Villarroel, G. (2003). Effects of harvests on wild populations of *Caiman crocodilus crocodilus* in Venezuela. *Interciencia* **28**, 544-548.
- Webb, G. J. W. & Messel, H. (1978). Movement and dispersal patterns of *Crocodylus porosus* in some rivers of Arnhem Land, Northern Australia. *Australian Wildlife Research* **5**, 263-283.

Accepted: 1.6.05