Copeia, 2003(3), pp. 628–634

Terrestrial Activity of Caiman in the Pantanal, Brazil

ZILCA CAMPOS, MARCOS COUTINHO, AND WILLIAM E. MAGNUSSON

Coordinated terrestrial movement has not previously been reported in crocodilians. However, between 1989 and 1999, 94% of 525 *Caiman crocodilus yacare* found on land in the Pantanal were in coordinated groups (n = 73) walking head to tail and forming nearly straight lines. Caimans left pools and initiated terrestrial movements spontaneously and in response to disturbance by researchers and hunters. The sex ratio of the groups was biased toward males (0.8 ± 0.24) and was similar to that found in aquatic habitats in the study area. However, two groups consisted only of females. When caimans left pools subjected to disturbances, such as hunting and capture for research, they walked head to tail in lines. Caimans that left pools in response to disturbance buried in mud near pools or in leaf litter in forest.

Movimento terrestre coordenado não tem sido registrado em crocodilianos. No entanto, entre 1989 e 1999, 94% de 525 *Caiman crocodilus yacare* encontrados em terra no Panatanal estavam em grupos coordenados (n = 73) andando um atrás do outro, em linhas quase retas. Os jacarés saíram das poças e iniciaram movimentos terrestres espontaneamente, e em resposta às perturbações por pesquisadores e caçadores. A razão sexual dos grupos foi tendenciosa para machos (0,8 ± 0,24), e foi semelhante daquela encontrada em ambientes aquáticos na área de estudo. No entanto, dois grupos consistiram apenas de fêmeas. Quando os jacarés saíram de poças sujeitas a perturbações, como caça clandestina e captura para pesquisa, eles andaram em linhas um atrás do outro e depois se enterraram na lama perto das poças ou em serrapilheira na floresta.

CROCODILIANS are mainly active in water, but terrestrial movement is common in crocodilians that live in areas that dry periodically (Lang, 1987). Under conditions of water stress, some species of crocodilians aestivate for several months in mud or holes (e.g., *Crocodylus niloticus*—Guggisberg, 1972; *Caiman crocodilus crocodilus*—Staton and Dixon, 1975; *Crocodylus palustris*—Whitaker and Whitaker, 1984).

The movement of several individuals between pools has been recorded for some species of crocodilians (Lang, 1987), and there are records of many individuals moving between pools in a short period (V. Vyas, Crocodile Specialist Group News Letter, World Conserv. Union [IUCN] Species Surv. Comm., 2001). However, direct observations of coordinated group activities in crocodilians are limited to interactions during feeding. Group fishing has been observed in *C. niloticus* in Africa (Pooley and Gans, 1976), *Caiman crocodilus crocodilus* in Venezuela (Thorbjarnarson, 1993) and *Caiman crocodilus yacare* in the Brazilian Pantanal wetland (Schaller and Crawshaw, 1982). There are no published direct observations of coordinated terrestrial movement in groups by crocodilians.

Terrestrial movements between pools may be induced by human disturbance. Effects of disturbance have been reported for many species of crocodilians (e.g., Webb and Messel, 1979; Montague, 1983; Pacheco, 1996). Crocodiles learn to avoid humans after capture (Bustard, 1968). Hutton (1989) reported that hunted crocodiles (*C. niloticus*) were more timid than crocodiles in areas without hunting, and Montague (1983) reported that individuals of *C. porosus* and *C. novaeguineae* in hunted populations moved greater distances than individuals in populations that were not hunted.

We report on coordinated terrestrial movements in groups of caimans (*C. crocodilus yacare*) and their terrestrial hiding places, in the Brazilian Pantanal wetland, under natural conditions and after disturbance by humans.

MATERIALS AND METHODS

Observations of terrestrial activity were made at Campo Dora Ranch, an area with intermittent rivers, and Nhumirim Ranch, an area with many isolated lakes, in the Pantanal wetland of the Nhecolândia region, Brazil, between 1989 and 1999 (Campos, 1993). The area is subject to a strong dry season (August to November) and a rainy season (December to March). Caimans congregate in the few sites containing water of a suitable depth in the dry season, and

this results in extremely high densities (Coutinho and Campos, 1996).

The sex ratio of the population of caimans in the study area was estimated from 2332 caimans captured in the lake area and 3168 caimans captured in the river area between 1986 and 1999. The majority of caimans engaged in terrestrial movement were located from an ultralight aircraft or a car in surveys that were carried out during all times of day between 0600 h and 2400 h. One adult female in a group with 10 other caimans was located because she was carrying a radio transmitter.

Caimans were considered to be in groups when two or more individuals separated by 5 m or less traveled overland, one behind the other, in the same direction. When caimans left pools in response to disturbance, or to bask, they initially faced in many different directions and were generally several to dozens of meters apart. Had they continued uncoordinated terrestrial movement, the probability that any of the groups would have randomly formed a straight line with individuals near each other was very small. Caimans in groups and solitary caimans were counted, measured, marked, and their sex noted. Snout–vent length (SVL in centimeters) was measured from the tip of the snout to the posterior border of the cloaca.

Caimans responded to disturbance caused by researchers during capture sessions, such as sounds of cars, boats, and human voices, by initiating terrestrial movements. Disturbance occurred in early morning, late afternoon, and night. The pools that caimans abandoned were generally less than 100 m in the greatest dimension, less than 1 m deep, and contained high densities of caimans. Nevertheless, it was much more difficult to capture individual caimans in the water than on land. We considered movements on land by caimans during or within 30 min after such disturbance to have been induced. Caimans that had not been subject to disturbance by researchers or other people were considered to have shown spontaneous behavior.

Data gathered on individuals within groups are not independent in relation to hypotheses about the behavior of caimans in the population as a whole. As we have no evidence of communication among groups, each caiman group was considered as an independent test of hypotheses related to group structure. To calculate an overall probability for multiple tests of the same hypothesis, we used Fishers log-probability test (Winer, 1971).

Regression randomization tests were carried out in the RT program (Manly, 1991). These tests use conventional *F*-tests, but compare the observed value of *F* to the distribution of *F* when the relationship among the variables is randomized by permutation of the values of one of the variables. For each test, 1000 randomizations were used to produce the distribution expected under the null hypothesis. Summary statistics are reported as mean ± 1 standard deviation.

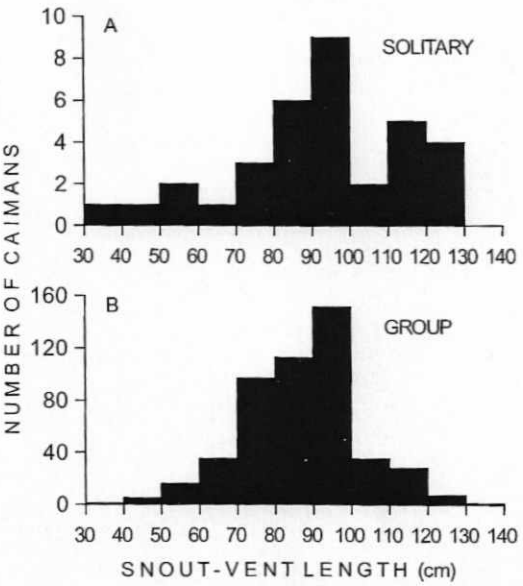

Fig. 1. Distribution of sizes of caimans captured moving (A) solitarily (n = 34 individuals) and (B) in groups (n = 491 individuals) in the Pantanal, Brazil, between 1989 and 1999.

This study was undertaken under IBAMA permit 017/02. All field manipulations were undertaken under the guidance of EMBRAPA veterinarians and followed ethical guidelines. Captured animals were released at the capture site.

Results

Composition and sex ratio of groups.—We encountered 73 groups of caimans and 34 solitary individuals moving over land in the study area between 1989 and 1999. The largest group had 50 individuals. The distribution of sizes of caimans moving in groups was significantly different (Kolmogorov-Smirnov test, P = 0.047) from that of caimans found alone on land. The mean size of solitary caimans was larger than that of caimans in groups (Fig. 1). The caimans found in groups had SVLs between 35 cm and 135 cm. However, only 7% of individuals in groups were larger than 110 cm SVL (85.8 ± 15.4 cm). Solitary caimans had SVLs ranging from 36.3–121 cm (90.4 ± 22.3 cm) and 21% were larger than 110 cm SVL (Appendix 1).

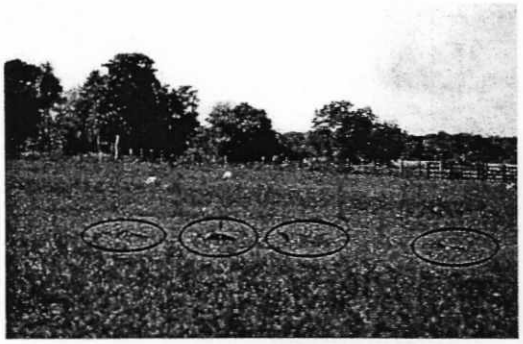

Fig. 2. Caimans (circled) in a group undergoing terrestrial movement across a paddock in the Pantanal.

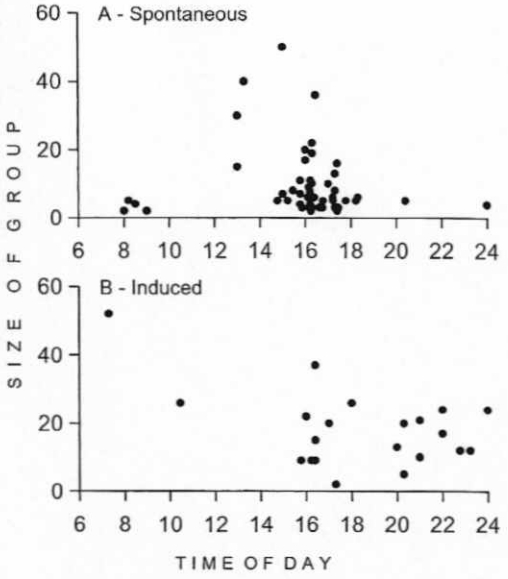

Fig. 3. Frequency of encounter of groups at different times of day. (A) Groups in spontaneous movement, (B) groups induced to leave the pools by human disturbance.

Caimans in groups walked nose to tail in a line (Fig. 2). In only five of the 14 times that sizes were registered for spontaneous groups, the largest caiman was at the front of the line, but positions of caimans of different sizes in lines were extremely variable. Overall, there was no significant relationship between size and position in the line (14 regression randomization tests, Fisher's log-probability test, $P > 0.5$).

There was no significant difference (Kruskal Wallis test = 16.5, $n = 22$, $P = 0.351$) between sizes of caimans in spontaneous groups (SVL = 87.0 ± 18.4 cm)and caimans in induced groups (SVL = 85.6 ± 13.9 cm). Terrestrial activity by groups of caimans was recorded in both the lake area and the river area. However, most groups (90%) were found in the river area, near the pools with the greatest concentrations of caimans in the dry season. Individuals were not marked, so some individuals may have participated in more than one group.

There was no significant difference between sex ratios in spontaneous groups and in induced groups (Kruskal Wallis test = 8.9, $n = 10$, $P = 0.54$). The mean sex ratio of the caimans in groups (0.80 ± 0.29 males) was significantly greater than 0.5 (one sample t-test: $t_{32} = 6.1$, $P < 0.001$). However, the sex ratio of the caimans caught in pools was also biased toward males (0.57 males in the lake area and 0.65 males in the river area).

The majority of the groups in spontaneous movement were found in the afternoon (1500–1800 h; Fig. 3A), but induced movement was recorded approximately equally in the afternoon and at night (Fig. 3B). Few spontaneous groups were found at night, but this may be because most capture efforts were at night, which leads to disturbance of the caimans and the assumption that movement was induced. On five days, groups of caimans moving spontaneously were encountered between 0830 h and 1400 h. Those days were cloudy and rainy. Solitary caimans ($n = 22$) were found active on land during the day and night, except for the period between 1200 h and 1400 h.

Disturbance caused by capture apparently induced individuals to leave pools. They left in lines and moved into fields or forest. Of the 127 caimans that were captured after leaving pools (Table 1), 78% moved into forest and buried under litter, and 22% buried in mud. Of the 127 that left pools, 22 had been captured previously, but only two of the 118 individuals captured in water were recaptures.

Discussion

Terrestrial movement in groups has not been recorded for other species of crocodilians, but most *C. crocodilus yacare* moving overland in the Pantanal were in groups. Movement in groups occurred under natural conditions and in response to disturbance caused by researchers. Hatchling crocodilians remain together for a year or more, and this may reduce risk of predation (Lang, 1987). However, terrestrial feeding is unlikely and whether traveling in groups reduces predation on adult caimans is unknown.

Animals can learn movement patterns from other individuals or their own experience (Swingland, 1984). For example, shoaling fish

TABLE 1. EFFECT OF CAPTURE DISTURBANCE IN SIX POOLS IN THE RIVER AREA. The caimans responded to disturbance by burying in mud or moving to the forest and burying under leaf litter.

Date	Number of caimans counted in pool	Total number captured	Number captured in water	Number captured in forest	Number captured buried in mud	Number recaptured in water	Number recaptured in forest or mud	Total recapture rate
25 IX 1999	100	17	12	5	0	2	2	23.5
27 IX 1999	1000	45	40	5	0	0	1	2.2
29 IX 1999	400	40	30	10	0	0	4	10.0
07 X 1999	100	20	19	1	0	0	1	5.0
08 X 1999	200	63	11	52	0	0	6	9.5
19 X 1999	300	60	6	26	28	0	8	13.3

and flocking birds learn about potential food sources from observation of other individuals (Krebs, et. al., 1972; Pitcher et al., 1982). In the case of caimans, nothing is known about the role of experience in the organization of groups. There was no clear size hierarchy among caimans in groups. Few small caimans (< 40 cm) were found moving on land in groups or alone, and a greater proportion of caimans with SVL > 110 cm moved alone. Solitary terrestrial movement may be more risky for small caimans because of predators or lack of experience, and caimans with SVL < 40 cm generally remain near nests where they are accompanied by an adult (Campos, 2002).

The sex ratio of terrestrial groups was biased toward males, as was the sex ratio in the aquatic environments in the study area. However, two all-female groups were found in terrestrial movement in the river area. Therefore, the presence of males is not necessary to induce group formation.

Response to disturbance may involve changes in physiology and behavior (Lang, 1987). Also, learning by crocodiles can reduce capture rates (Webb and Messel, 1979). In response to attempts at capture by researchers, caimans left the pools and buried under leaf litter in forests, or in mud around the lakes. Of 127 caimans that were captured after leaving pools and burying themselves, 17.5% were already marked. This contrasts with a low recapture rate in pools and suggests that caimans learned to avoid capture by leaving pools.

Disturbance induced individuals to move terrestrially in groups, during the day and the night. Local hunters reported that, in the 1980s, caimans that left pools in response to disturbance were killed on land. Caiman hunting is currently less intensive in the Pantanal than it was in the 1980s (Mourão et al., 1996). However, this behavior may make caimans vulnerable if intensive hunting resumes. The behavior of burying in mud and in forest may influence estimates of population density from direct counts, such as those used in the Venezuelan management program (Thorbjarnarson, 1991). Also, terrestrial movement may affect the number of caimans subject to harvest in isolated pools.

Terrestrial movement in groups opens the possibility of mass capture in scientific studies, or harvest programs, but may be detrimental to stocks of caimans subjected to illegal hunting. In any case, as in other aspects of behavior (Lang, 1987), the social implications of terrestrial movement in crocodilians seem to be greater than has previously been appreciated.

ACKNOWLEDGMENTS

This study represents part of a doctoral dissertation by ZC submitted to the Federal University of Minas Gerais, under the supervision of Gustavo Fonseca and WEM, and was financed by EMBRAPA-Pantanal, WWF-USA, Fundação O Boticário, and Conservation International. The license for capture and manipulation of the animals (017/02) was given by the Brazilian Enviromental Agency (IBAMA). We thank Francisco (in memoriam), Procópio, Luís, José Augusto, Vandir, and Henrique for indispensable help in the capture of caimans.

LITERATURE CITED

BUSTARD, H. R. 1968. Rapid learning in wild crocodiles. *Crocodylus porosus*. Herpetologica 24:173–175.

CAMPOS, Z. 1993. Effect of habitat on survival of eggs and sex ratio of hatchlings of *Caiman crocodilus yacare* in the Pantanal, Brazil. J. Herpetol. 27:127–132.

———. 2002. Comportamento de termorregulação, movimento, área de uso e suas implicações para o manejo do jacaré-do-Pantanal (*Caiman crocodilus yacare*). Unpubl. Ph.D. diss., Univ. Federal of Minas Gerais, Minas Gerais, Brazil.

COUTINHO, M., AND Z. CAMPOS. 1996. Effect of habitat and seasonality on the densities of caiman in southern Pantanal, Brazil. J. Trop. Ecol. 12:741–747.

GUGGISBERG, C. A. W. 1972. Crocodiles—their natural history, folklore and conservation. Davies and Charles, Newton Abbot, Devon, U.K.

HUTTON, J. 1989. Movements, home range, dispersal and the separation of size classes in Nile crocodiles. Am. Zool. 29:1033–1050.

KREBS, J. R., M. H. MACROBERTS, AND J. M. CULLEN. 1972. Flocking and feeding in great tit *Parus major*: an experimental study. Ibis 114:507–30.

LANG, J. W. 1987. Crocodilian behaviour: implications for management, p. 301–317. *In:* Wildlife management: crocodiles and alligators. G. J. W. Webb, S. C. Manolis, and P. J. Whitehead (eds.). Surrey Beatty and Sons, Sydney, New South Wales, Australia.

MANLY, B. F. 1991. Randomization, bootstrap and Monte Carlo methods in biology. Chapman and Hall, London.

MONTAGUE, J. J. 1983. Influence of water level, hunting pressure, and habitat type on crocodile abundance in the Fly River drainage, Papua New Guinea. Biol. Conserv. 26:309–339.

MOURÃO, G. M., Z. CAMPOS, M. COUTINHO, AND C. ABERCROMBIE. 1996. Size structure of illegal harvested and surviving caiman (*Caiman crocodilus yacare*) in the Pantanal—Brazil. *Ibid.* 75:261–265.

PACHECO, L. F. 1996. Wariness of caiman populations and its effect on abundance estimates. J. Herpetol. 30:123–126.

PITCHER, T. J., A. MAGURRAN, AND I. J. WINFIELD. 1982. Fish in larger shoals find food faster. Behav. Ecol. Sociobiol. 10:149–151.

POOLEY, A. C., AND C. GANS. 1976. The Nile crocodile. Sci. Am. 234:114–124.

SCHALLER, G. B., AND P. G. CRAWSHAW. 1982. Fishing behaviour of Paraguayan caiman (*Caiman crocodilus*). Copeia 1982:66–72.

STATON, M. A., AND J. R. DIXON. 1975. Studies on the dry season biology of *Caiman crocodilus crocodilus* from the Venezuelan llanos. Mem. Soc. Cienc. Nat. La Salle 35:237–266.

SWINGLAND, I. R. 1984. Intraspecific differences in movement, p. 102–115. *In:* The ecology of animal movement, I. R. Swingland and P. J. Greenwood (eds.). Univ. of Oxford Press, Oxford.

THORBJARNARSON, J. B. 1991. An analysis of the spectacled caiman (*Caiman crocodilus*) harvest program in the Venezuela, p. 217–235. *In:* Neotropical wildlife use and conservation. J. Robinson and K. Redford (eds.). Univ. of Chicago Press, Chicago.

———. 1993. Fishing behavior of spectacled caiman in the Venezuelan Llanos. Copeia 1993:1166–1171.

WEBB, G., AND H. MESSEL. 1979. Wariness in *Crocodylus porosus* (Reptilia: Crocodilidae). Aust. Wildl. Res. 6: 227–234.

WHITAKER, R., AND Z. WHITAKER. 1984. Reproductive biology of the mugger (*Crocodylus palustris*). J. Bombay Nat. Hist. Soc. 81:297–317.

WINER, B. J. 1971. Statistical principles in experimental design. McGraw-Hill Kogashuka, Tokyo.

(ZC, MC) EMBRAPA-PANTANAL, CP 109, 79320-900 CORUMBÁ MS, BRAZIL; AND (WEM) INSTITUTO NACIONAL DE PESQUISAS DA AMAZÔNIA (INPA)–COORDENAÇÃO DE PESQUISAS EM ECOLOGIA, CP 478, 69011-970 MANAUS AM, BRAZIL. E-mail: (ZC) zilca@cpap.embrapa.br; (MC) coutinho@cpap.embrapa.br; and (WEM) bill@inpa.gov.br. Send reprint requests to ZC. Submitted: 22 Sept. 2002. Accepted: 14 March 2003. Section editor: C. Guyer.

APPENDIX 1. NUMBER AND SIZES OF INDIVIDUALS MOVING IN GROUPS THAT LEFT POOLS SPONTANEOUSLY IN GROUPS THAT WERE INDUCED TO LEAVE POOLS BY HUMAN DISTURBANCE (I).

Type of movement	Number of caimans counted	Number of caimans captured	Sex ratio	SVL minimum	SVL maximum	SVL mean ±
S	2	2	—	35.0	78.0	56.5 ±
S	2	2	—	—	—	—
S	2	2	—	72.0	76.0	74.0 ±
S	2	2	—	70.0	119.0	94.5 ±
S	2	2	—	—	—	—
S	2	2	1.000	65.0	85.0	75.0 ±
S	2	2	1.000	60.0	65.0	62.5 ±
S	3	3	1.000	120.0	123.0	121.0 ±
S	3	0	—	—	—	—
S	4	4	0.000	50.5	89.0	68.5 ±
S	4	0	—	—	—	—
S	4	0	0.250	—	—	—
S	4	0	—	—	—	—
S	4	4	1.000	95.0	95.0	95.0
S	4	4	—	70.0	85.0	77.5 ±
S	5	5	—	85.0	95.0	93.0 ±
S	5	5	0.800	81.0	106.0	93.1 ±
S	5	5	1.000	74.0	81.0	77.6 ±
S	6	6	1.000	97.0	120.0	110.0 ±
S	6	6	0.830	50.0	104.0	82.9 ±
S	6	4	1.000	85.0	112.0	97.4 ±
S	6	6	—	70.0	95.0	85.8 ±
S	7	4	0.714	51.0	135.0	75.4 ±
S	8	8	—	95.0	95.0	95.0
S	8	8	1.000	91.0	111.5	101.6 ±
S	8	1	—	74.0	—	—
S	9	9	1.000	84.0	121.5	105.0 ±
S	10	1	—	—	—	—
S	10	0	—	—	—	—
S	10	10	0.700	61.5	115.0	89.1 ±
S	12	0	—	—	—	—
S	13	13	0.461	75.0	111.0	90.2 ±
S	15	13	—	—	—	—
S	16	12	1.000	50.0	104.0	82.7 ±
S	17	0	—	—	—	—
S	19	16	0.810	53.0	103.0	78.8 ±
S	20	0	—	—	—	—
S	22	22	0.670	70.0	95.0	81.8 ±
S	30	0	—	—	—	—
S	36	16	0.687	72.0	91.0	77.0 ±
S	40	0	—	—	—	—
S	50	0	—	—	—	—
I	2	2	—	95.0	95.0	95.0
I	5	4	0.750	60.5	112.5	86.4 ±
I	9	6	0.670	40.0	94.0	69.3 ±
I	9	7	1.000	72.0	114.0	94.9 ±
I	9	9	0.111	87.0	119.0	106.8 ±
I	10	8	—	70.0	95.0	88.1 ±

APPENDIX 1. CONTINUED.

Type of movement	Number of caimans counted	Number of caimans captured	Sex ratio	SVL minimum	SVL maximum	SVL mean ± SD
I	11	11	0.730	62.0	118.0	88.8 ± 20.3
I	11	10	0.700	62.0	118.0	86.1 ± 19.2
I	13	10	1.000	45.0	95.0	78.2 ± 18.6
I	15	0	—	—	—	—
I	17	17	0.650	57.0	90.0	81.6 ± 10.2
I	20	0	—	—	—	—
I	20	0	—	—	—	—
I	20	0	—	—	—	—
I	22	22	—	51.0	95.0	87.8 ± 13.7
I	24	24	0.833	58.5	94.0	73.0 ± 10.2
I	24	13	0.690	50.0	90.0	73.9 ± 12.8
I	26	21	0.940	70.0	90.0	87.4 ± 6.0
I	26	26	0.700	60.0	96.5	79.3 ± 8.9
I	37	37	—	95.0	100.0	92.8 ± 6.2
I	52	52	0.890	70.0	116.0	89.9 ± 12.5