

Habitat Selection and Migration of *Caiman crocodilus crocodilus* in a Swamp and Swamp-Forest Habitat in Northern Suriname

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ABSTRACT.— In Suriname swamp-bordered river parts usually have higher caiman (*Caiman crocodilus*) densities than forest-bordered river parts. In the Coesewijne River area, caimans showed a preference for shallow water. Most juveniles and subadults were found in a section with much aquatic vegetation, Zeekoe Creek. This tributary drains a large grass-swamp, which is an important nesting area. It is shown that the high caiman density was mainly caused by the high number of juveniles born in the area.

Caimans over three years of age were generally equally distributed between the main river and the tributary although some seasonal differences were apparent. With receding water levels these caimans left the tributary, or they moved to deeper parts; with rising water levels many caimans entered the creek and finally dispersed into the inundated swamp. At the start of the dry season about 52% of the subadult and adult caimans and 68% of the second year caimans returned to the location they were found before the rainy season. Caimans were rather sedentary; the longest distance between two recordings was 3 km.

Recently our knowledge on the life history of *Caiman crocodilus* has increased significantly by studies of Alvarez del Toro (1974), Rivero Blanco (1974), Staton and Dixon (1975, 1977), Gorzula (1978), Crawshaw and Schaller (1980), Ayarzagüena (1983) and Magnusson (1985). Most of these studies were conducted in savanna habitat, whereas most of the range of *C. crocodilus* consists of forests and swamps. This study was performed in swamp and swamp-forest habitat in Suriname. This country is especially suited for caiman research, since all three species inhabiting Suriname, were not hunted commercially until 1978 and have good populations (Medem, 1973; Hoogmoed, pers. comm.). In 1978 and 1979 hide hunting occurred on a small scale in western Suriname and in the Coesewijne River. According to the State Forest Service (LBB) between 1500 and 2000 caimans were killed in the Coesewijne (also see Anon., 1979; LBB/Stinasu, 1979). The status of *C. crocodilus* in this river was investigated in the first three months of 1981 and the population was reported depleted (Glastra, 1983). In 1982, 1983 and 1984 we continued ecological research into *C. crocodilus* in the

Coesewijne. In this paper we report on habitat selection and migration. Results concerning breeding biology and population dynamics are dealt with elsewhere.

STUDY AREA

The study area covered part of the Coesewijne River, a rather narrow river, 190 km in length, draining a vast savanna, swamp-forest and swamp area in the coastal lowlands of central Suriname (Fig. 1). This area has four seasons: The long rainy season (May to July/August), the long dry season (July/August to November), the short rainy season (December and January) and the short dry season (February to April). During the long dry season most tributaries of the Coesewijne completely dry out and in the largest of them, Zeekoe Creek, water recedes to a level between 20 and 70 cm. In the short rainy season some areas may become flooded; in the long rainy season nearly all land is inundated. In 1983 the long rainy season actually started in March/April and the short dry season was not noticeable. The difference in water level between the long rainy season and the long dry season was 170 cm in 1982 and 182 cm in 1983.

Research was concentrated in an area around the first 2 km of the Zeekoe Creek and 5 km upstream and downstream on

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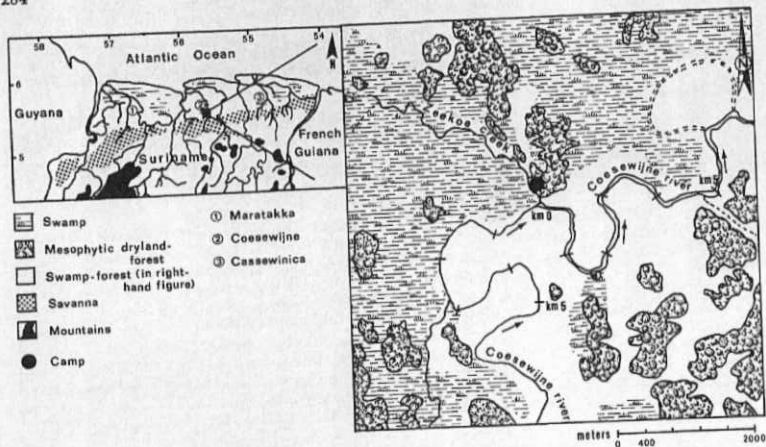


FIG. 1. Map of northern Suriname and the study area.

the main river. This part of the river is in its middle reaches, about 130 km from the coast, but still within the area of tidal influence during the dry season (the difference between low and high tide is about 20 cm; the water is fresh all year round). In the rainy season no tidal influence can be observed. In the five downstream kilometers of the study area the river is bordered by fringing xerophytic swamp-forest of *Crudia glaberrima* and *Macrobium acaciifolium*, with grass- and fern-swamps with scattered *Pterocarpus*-bushes beyond (Teunissen, 1978). In the study area's two kilometers which are most upstream, the river is bordered by the same kind of swamp-forest, but in the first three upstream kilometers (from the confluence with Zeekoe Creek) swamp-forest is only present on the right hand shore, the left hand shore is a large grass-swamp of *Lagenocarpus guianensis* and *Rhynchospora gigantea* (Teunissen, 1978). Zeekoe Creek drains the northern part of this swamp. On higher ground one can find mesophytic dryland-forest (Fig. 1).

Zeekoe Creek was navigable for 2 km only (during the long dry season of 1982 for 1 km), due to the growth of bushes and

Montrichardia arborescens in the creek. It is the only tributary of the Coesewijne with dense aquatic vegetation, mainly of *Nymphaea rudgeana*. Most tributaries and the river itself lack aquatic vegetation. The Coesewijne differs from most small coastal rivers by the absence of a dense growth of *Montrichardia* in shallow water and on the banks, bushes of this Araceae only occurring in certain spots, especially in river bends.

Coesewijne is one of the rivers most abounding with fish (Mohadin, pers. comm.). The most abundant larger species are the piscivorous *Hoplias malabaricus*, *Hoplerhynchus unitaeniatus* and *Serrasalmo spilopleura* and *Aequidens potaroensis*. Most fish species breed during the long rainy season in the inundated swamps and swamp-forests (e.g., Vari, 1982; pers. obs.). Local fishermen reported reduction in fish populations shortly after the killing of about 2000 caimans in the long dry season of 1978 and 1979 (Glastra, 1983; Ramfalli, pers. comm.).

METHODS

The study area was visited during the following periods: 1982: 16-19 September,

5-29 October, 17 November-6 December; 1983: 6-26 January, 14 March-11 April, 4-12 May, 2-19 July, 3-5 August, 6-9 September, 19 September-13 October; 1984: 26-30 September.

During each visit night counts were performed, in many cases in combination with size estimates. Usually the study area was covered in three successive nights. We selected nights without much moonlight, wind and rain to obtain good figures (also see Gorzula and Paolillo, 1984). Caimans were located by the reflection of their eyes in the beam of a 6-volt headlight. In order to check the representativeness of the study area for the rest of the Coesewijne, night counts were also performed outside the study area, up to 18 km upstream and 22 km downstream of the confluence with Zeekoe Creek.

Caimans were captured at night (between 1900 and 2300 h local time) using a noose of iron-wire at the end of a 3 to 4 m aluminum tube. A 10 m dug-out with a 6 hp outboard motor was used for transportation. Caimans under 110 cm total length were often more easily captured by hand. Caimans larger than 150 cm total length were marked, measured and released ashore, smaller caimans were handled inside the boat and released at the point of capture. Handling usually lasted less than 10 minutes.

Marking following Chabreck (1963), Whitaker (1978) and Glastra (1983) and was done by cutting one or two triangles out of one or more dorsal scutes of the single tail crest with a tinsnipper. Only the first (proximal) six scutes were used, because the loss of part of the tail is known to occur frequently in some populations. In all but the first year juveniles, marks remained clearly visible for the total period of 12 months. Marks in hatchlings usually had to be renewed upon recapture.

Sex was determined by probing for the penis with the little finger inside the cloaca (Brazaitis, 1968). This was only possible with caimans exceeding 80 to 90 cm total length. Smaller caimans were sexed by pressing beneath the pubis at the vent with one or two fingers, bending the tail upwards at the same time. The penis should

protrude if the specimen is a male (Chabreck, 1963). In contrast to *Alligator mississippiensis* (see Joanen and McNease, 1978) the difference between penis and clitoris was clearly visible in this population of *C. crocodilus*, even in hatchlings, but specimens over one or two months of age were sometimes reluctant to protrude anything. Age up to the fourth year could be determined by the size of a specimen (see Ouboter and Nanhoe, 1984, in press).

Eleven caimans (4 males and 7 females with a total length between 75 cm and 152 cm) were outfitted with radio-transmitters (Wildlife Materials) operating on the 151 MHz band. Two large transmitters operated perfectly, but six out of nine small transmitters malfunctioned, probably due to water leakage at the antenna base. Transmitters were attached by elastic harness and alpha-cyanoacrylate glue on the back between the shoulders. Transmitter range was reduced to about 3% of the range given by the manufacturer (9-13 km), mainly because the antennae were submerged most of the time, due to the transmitter's point of attachment.

Transmitters were monitored using a miniature receiver (Wildlife Materials) and a null-peak antenna system (Cushcraft). With every census transmitters were tracked several times (usually in day-time). Positions were determined by triangulation. The two large transmitters were occasionally monitored for 12 h periods.

Water levels were measured in Zeekoe Creek and these data were compared with an official measuring point 79 km downstream in order to provide complete data on water levels for the study period (Fig. 2A).

Surveys were performed on two other Surinam coastal rivers, the Maratakka River (western Suriname) and the Cassewina Creek (eastern Suriname) (Fig. 1), in order to compare data from the Coesewijne area with data from other rivers.

RESULTS

Habitat Selection.—Habitat selection was determined using the number of caimans counted (Fig. 2B) and captured (Table 1) in

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TABLE 1. Numbers of caimans captured according to age and locality of capture. *—distribution of age-class significantly different from randomness.

Age	Downstream swamp-forest bordered (5 km)	Upstream swamp-forest bordered (3 km)	Zeekoe Creek swamp bordered (2 km)	χ^2
0-1	30	43	110	178.34*
1-2	58	9	50	89.84*
2-3	36	14	36	21.13*
3-4	17	12	11	1.35
>4	16	6	12	5.25
Total	157	84	219	142.30*

TABLE 2. Differences between the four parts of the study area.

	Downstream	Upstream 0-3 km	Upstream 3-5 km	Zeekoe Creek
River width	40-50 m	30-40 m	25-35 m	3-20 m
Water depth	4.0-6.0 m	3.0-5.0 m	2.7-4.7 m	0.2-3.0 m
Inlets in shore-line	many	some	some	many
Exposure of shore	often exposed	exposed	rarely exposed	exposed
Shore vegetation	swamp-forest	swamp/swamp-forest	swamp-forest	swamp
Aquatic vegetation	none	none	none	extensive

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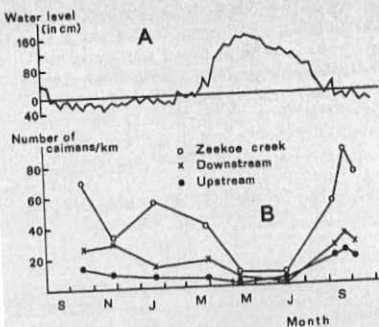


FIG. 2. A: Water level with regard to Coesewijne shore level (at km 0). B: Number of caimans counted in three different parts of the study area.

different parts of the study area. Some differences between these parts are listed in Table 2.

The number of caimans differed markedly between Zeekoe Creek and the upstream and downstream parts of the river (Fig. 2B). In spite of large fluctuations in numbers counted in different times of the year, the highest density was always observed in Zeekoe Creek and the lowest usually in the upstream river part. A higher number of caimans downstream than upstream probably applied to the greater part of the Coesewijne, as shown by night counts outside the study area (Table 3). Comparing the first three upstream kilometers of the Coesewijne (having swamp-forest on one shore and swamp on the other shore) with Zeekoe Creek and the downstream portion of the Coesewijne, shows that the differences in total density are even more pronounced and highly significant for most age classes (Table 1). It is obvious that the first three age-classes in particular are responsible for the differences in densities. These age-classes were overrepresented in Zeekoe Creek. Hatchlings were less abundant than expected in the downstream part of the study area and the same holds true for second year caimans in the upstream part. The number of fourth year and older caimans did not differ significantly between the three areas. When comparing only the downstream and upstream

river parts, there was no significant difference for the total number of caimans (χ^2 -test; $\chi^2 = 0.8$, $P > 0.3$) and for most age-groups, apart from hatchlings and second year caimans. This applies to the part bordering the open swamp. Farther upstream caimans are clearly less abundant than in the downstream river part (see Table 3).

It is difficult to determine which habitat qualities most influence the number of caimans. Certain microdistributional preferences could give an indication. Although there are no exact figures, direct observations indicate a preference for shallow water and a gradual sloping shore with many inlets. High numbers of caimans were seen on some of the mudbanks in the inner bends of the river and at the mouth of tributaries. Within Zeekoe Creek distribution was mainly determined by the water level. In dry circumstances caimans moved to deeper parts of the creek or to the river, when water level rose they sought shallow places and ultimately dispersed into the swamps.

The main differences between the densely populated Zeekoe Creek and the main river are the aquatic vegetation and the shallow water (Table 2). We think that these factors, as well as shelter provided by inlets, are important in the habitat selection of *C. crocodilus*.

The shore vegetation may be important too. Zeekoe Creek as well as the first 3 km of the upstream river part are bordered by swamps, but there is a great difference: unlike Zeekoe Creek, the shore along the upstream part is high and steep during the

dry season and does not provide many opportunities for concealment. Some additional data are provided by the results of surveys on the Maratakka and the Cassewinica. For most of their length these creeks are bordered by a dense growth of *Montrichardia*. The shore vegetation is mesophytic dryland- and marsh-forest in both the Maratakka and the downstream part of the Cassewinica. The upstream part of the Cassewinica is bordered by swamps. We calculated the following densities (caimans/km) for these areas in December and January: Maratakka: 1.7; Cassewinica downstream: 1.7; Cassewinica upstream: 25.3 (for comparison Coesewijne in January downstream: 13.6; upstream: 6.6). It seems that river parts with a dry shore all year round have low caiman densities and river parts bordered by or near swamp areas have high densities.

Migration.—Migration data were obtained by radio fixes, recaptured specimens, counts and direct observations of movement in Zeekoe Creek. Unfortunately the distances travelled by caimans cannot be visualized in a simple graphic way, mainly because captures and recaptures were made in seven different periods, but also because migration is dependent on season, part of the study area and age of the caimans concerned.

As long as the water did not rise above shore level, migration in the main river was very restricted. Juveniles and sub-

adults were usually recaptured at exactly the same point or less than 100 m away from it and 95% of all river caimans were recaptured within 1000 m of the original point of capture. However, adults seemed to have a rather large home range. One female of 152 cm total length, outfitted with a radio-transmitter, used a river length of 1 km in one year and occupied a minimum home range (only the river) of 35 ha in the dry season (Fig. 3A). The minimum home range of another female of 135 cm was much smaller, 11.25 ha in the dry season, using only 250 m of the river (Fig. 3B).

Migration in Zeekoe Creek was much greater. As soon as the water level fell below 30 to 50 cm, most caimans over 90 cm total length aggregated in deep parts of the creek (between 1.3 and 2.0 km upstream) or they left the creek altogether. This movement was demonstrable in one caiman only, recognizable by its large size (Table 4, no. 184, 07-10), but night counts provided additional circumstantial evidence. Fig. 2B shows that numbers fell drastically in Zeekoe Creek in November, but that numbers in the downstream part of the river increased at the same time. Apparently most caimans leaving the creek moved downstream. During this period no caimans exceeding 90 cm were seen in the first 1.3 km of Zeekoe Creek.

For migration in the opposite direction, with rising water, much more data are available. Circumstantial evidence was

TABLE 3. Caiman density (caimans/km) inside and outside the study area in different months, as determined by night counts.

	Oct	Nov	Jan	Mar	Jul	Oct
Upstream study area	13.2	9.2	6.6	5.0	1.8	15.2
Upstream outside study area	14.2	12.7	8.7	3.4	—	12.5
Downstream study area	25.6	26.6	13.6	16.2	1.4	24.8
Downstream outside study area	25.8	24.8	18.5	14.6	1.4	24.6

TABLE 4. Minimum distance travelled (over 200 m) by caimans in the study area. Locations are given as kilometers from the confluence of Zeekoe Creek and the Coesewijne River (see Fig. 1). For locations in the Coesewijne River, D indicates downstream and U upstream from the confluence with Zeekoe Creek. When flooding inundated an area the minimum distance is a straight line measurement between the two locations. An asterisk (*) indicates those measurements.

No.	Age (years)	Sex	From		To		Number of days	Minimum distance
			Date	Location	Date	Location		
Zeekoe Creek								
67	2	—	20-10-82	0.5-0.6	25-10-82	0.9-1.0	5	300 m
70	3	—	21-10-82	0.2	11-01-83	0.5	82	300 m
76	1	—	21-10-82	0.9-1.0	13-07-83	1.2	265	200 m
157	3	—	12-01-83	0.6	13-01-83	0.8	1	200 m
157	3	—	13-01-83	0.8	19-01-83	1.2	6	400 m
217	3	—	28-03-83	0.5	30-03-83	0.9-1.0	2	400 m
243	1	—	03-04-83	0.9-1.0	13-07-83	0.5	101	400 m
249	1	—	08-05-83	1.6-1.8	26-09-83	1.2-1.3	141	300 m
298	4	♀	25-09-83	0.9-1.0	26-09-83	1.2	1	200 m
66	3	—	20-10-82	0.5-0.6	11-01-83	0.9-1.0	83	300 m
Zeekoe Creek								
Coesewijne								
66	—	—	11-01-83	0.8-1.0	06-10-83	D 0-1	268	800 m
4	1	—	10-10-82	0.9-1.0	10-10-83	U 3-4	365	2800 m*
63	2	—	23-01-83	0-0.2	30-09-83	D 2-3	250	2000 m
175	1	—	20-03-83	1.2-1.3	21-09-83	U 1-2	185	1000 m*
178	3	—	21-01-83	1.2-1.5	06-10-83	D 0-1	258	1200 m
219	1	—	28-03-83	1.8-2.0	07-10-83	U 2-3	193	2900 m*
232	2	—	06-05-83	1.2	28-09-83	D 1-2	145	2000 m*
184	>4	♂	07-10-82	0.9-1.0	10-01-83	U 0-1	95	900 m
Coesewijne								
Zeekoe Creek								
184	>4	♂	10-01-83	U 0-1	22-01-83	1.2-1.3	12	1200 m
11	>4	♀	10-10-82	D 1-2	28-03-83	2.0-2.1	169	3000 m
190	3	—	23-01-83	U 1-2	08-10-83	0.5-0.7	258	900 m*
252	>4	♂	09-05-83	D 0-1	08-10-83	1.5	152	1500 m
268	4	♂	11-07-83	U 0-1	09-10-83	1.8-2.0	90	1800 m
Coesewijne								
Coesewijne								
122	>4	♂	21-11-82	D 0-1	08-01-83	D 2-3	48	1000 m
134	4	♀	23-11-82	U 3-4	05-10-83	U 5-6	316	1000 m
151	1	—	20-01-83	D 2-3	07-10-83	U 2-3	260	2700 m*
152	>4	♀	15-03-83	U 4.2	23-03-83	U 4.8	8	600 m
152	—	—	23-03-83	U 4.8	08-04-83	U 4.1	16	700 m
152	—	—	05-07-83	U 4.1	15-07-83	U 3.8	10	300 m
152	—	—	15-07-83	U 3.8	24-09-83	U 4.4	71	600 m
259	2	—	10-05-83	U 3-4	29-09-83	D 2-3	141	2200 m*
275	3	—	22-09-83	U 1-2	10-10-83	U 2-3	18	1800 m

provided by the night counts of January 1983 (Fig. 2B); with increasing numbers of caimans in Zeekoe Creek, the numbers in the downstream part of the study area fell. Movement up the creek was performed in such a short period (11-13 January), that aggregations of caimans were formed in front of narrow parts of the creek. Three caimans were proven to move upstream during rising water in January and March 1983 (Table 4, no. 157, 217, 184) and three others seemed to have moved upstream in

the same period too (Table 4, no. 70, 66, 11).

At the start of the long rainy season (in May), with rapidly rising water levels, caimans dispersed into the swamps and swamp-forests. Most of them (64%) were found in the area bordering the river or creek part they occupied during the rest of the year; 36% had moved to another place. It is likely that some of the last ones, adults in particular, travelled over long distances. Unfortunately, very few data are

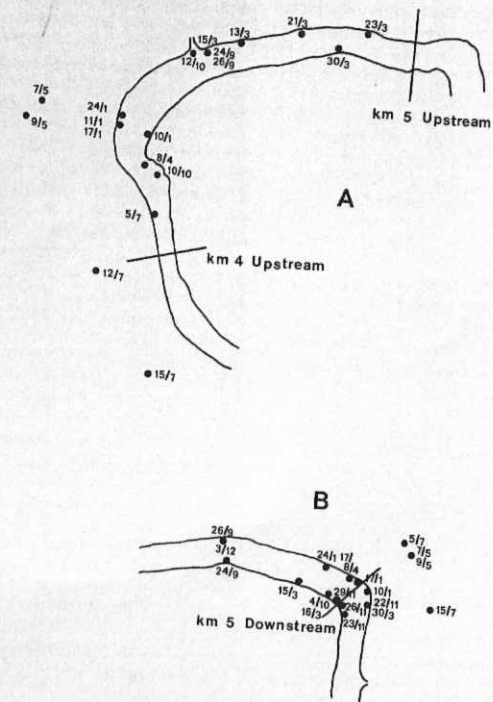


FIG. 3. Localities of two caimans as determined by radio-telemetry. Dots are fixes at each encounter. Dates between 22 November 1982 and 12 October 1983. A: a 152 cm female; B: a 135 cm female.

available on adult movement during the long rainy season. The two females, outfitted with radio-transmitters, travelled little and could always be tracked somewhere in the swamp-forest bordering the river part they inhabited most of the year (Fig. 3).

Most long range movement (exceeding 500 m) of first and second year caimans took place near the end of the long rainy season (Table 4, no. 4, 63, 175, 219, 232, 151, 259). Distances travelled were sometimes considerable: 2.9, 2.8 and 2.7 km were recorded for three first year juveniles (Table 4, no. 219, 4, 151, resp.). Most of them left Zeekoe Creek during the long rainy

season and were found in the main river at the beginning of the long dry season. There, the juveniles at the start of their second year, usually joined pods of hatchlings. Their brothers and sisters remained in or returned to exactly the same spot as they were found in the year before (68% of them), often associated with hatchlings-of-the-year too (see Ouboter and Nanhoe, 1984, 1987). Of the subadults and adults about 52% returned to the location they were found in before or in the rainy season.

With receding water level, not only did some juveniles leave the swamps at the side of the river, but also many older caimans.

This is demonstrated by counts. Usually the density in the upstream part of the river bordering the open swamp (0-3 km) is much lower than in the downstream part (unpublished data). Only at the start of the dry season this situation is reversed (6-8 September 1983: upstream 24.0 caimans/km, downstream 22.4 caimans/km; 27-30 September 1984: upstream 19.7 caimans/km, downstream 11.0 caimans/km).

DISCUSSION

The term habitat selection is often used to indicate the differential abundance of animals. We use this term here, because a better one is not available. Actually it is incorrect if used in this context, because it suggests an animal's possibility to choose its place in a certain habitat dependent on abiotic and biotic influences. For mobile animals this possibility could exist and in studies on the habitat selection of lizards the term has been useful (see e.g., Heatwole, 1977). The differences in the number of caimans in the three parts of the area studied here, are among other things influenced by "real" habitat selection. Larger caimans sometimes swim considerable distances (see Migration) and mature females will have to select a nesting site. The number of first and second year caimans in a certain habitat, however, is probably not determined by their own habitat selection. The high number of caimans from the first three age-classes in Zeekoe Creek is caused by the high number of nesting sites in this area (Ouboter and Nanhoe, 1987); therefore, by nesting-habitat selection of the reproductive females. It seems likely that nesting sites are selected on the basis of egg survival, but possibly also on the basis of the female's well-being, as suggested for *Crocodylus porosus*, a species also nesting in swamp areas (Webb et al., 1983d). A good habitat for the hatchlings is probably not an important criterion for the selection of a nesting site. In *Crocodylus acutus*, nests are sometimes situated in areas with deep, turbulent water and after hatching the young are removed to another area by the adult (Ogden, 1978). The same probably happened sometimes in the Coesewijne

population. Some pods were removed to other localities within a day's time (see Ouboter and Nanhoe, 1987). We assume that almost all nests were made in the open swamp areas around Zeekoe Creek and that pods found in the main river were brought there by one of the parents (probably the mother). More pods were observed in the upstream part of the study area than in the downstream part. Again habitat selection by the mother seems to play a role. Why the upstream area is preferred, is not known; it could have something to do with the open swamp bordering the river on one side.

Another factor influencing the number of (young) caimans in a certain habitat is differential mortality. The low number of second year caimans in the river (especially upstream) was probably caused by high hatching mortality: of 37 hatchlings marked in the river only one was recaptured after a year. In a Zeekoe Creek pod of 19 hatchlings, at least 16 survived one year later (Ouboter and Nanhoe, 1984, in press).

Although the high number of juveniles in the creek cannot be attributed directly to "real" habitat selection of this group, the Zeekoe Creek habitat seems to be very suitable. It provides shallow water, an abundance of insects, which are the main food items of juveniles (Ouboter and Nanhoe, 1984), and shelter between the aquatic vegetation. As already stated above hatching mortality is low in Zeekoe Creek.

It is difficult to compare our data with other studies on habitat selection in crocodylians. With the exception of the study by Magnusson (1985), the other extensive ones were performed in quite different habitats; on *Crocodylus johnstoni* in river pools (Webb et al., 1983c) and on *A. mississippiensis* in large permanent wet marshes. Here adult females remained in the marsh all year round (which is impossible in the Coesewijne area), except in the four-teen day period of courtship, when they visited open water (Joanen and McNease, 1970). Adult males preferred open water (Joanen and McNease, 1973) and immature alligators areas with aquatic vegetation (McNease and Joanen, 1975; Taylor et al.,

1976). Preference for areas with aquatic vegetation by juveniles and subadult specimens was also obvious in the Coesewijne population of *C. crocodylus* (Zeekoe Creek) and is reported for other populations too (e.g., Alvarez del Toro, 1974; Ayarzagüena, 1983). In the Coesewijne area Glastra (1983) counted 96% of the hatchlings (erroneously called second year juveniles by him) in grass strips along the downstream part of the river (outside our study area) and in tributaries, and larger adults in significantly higher numbers in the main river. Our observations indicate that adults can be found in tributaries in densities as high as in the main stream, but that this is highly dependent on water level and social factors; the highest number occurred there in March at the beginning of the long rainy season (see Migration). In the larger rivers, lakes and canals of Amazonia *C. crocodylus* (juveniles, subadults as well as adults) was predominantly found in shallow and grassy areas (Magnusson, 1985). This is in agreement with the preference we found for shallow water and for swamp bordered river parts.

It is not completely clear why in the upstream part of the river (also outside the study area) caiman density was lower than in the downstream part (Table 3). Maybe it is related to relatively steep shores and less shallow water upstream (factors which are difficult to quantify). In addition the upstream area has less marshland and therefore probably fewer nesting sites. Unfortunately no exact figures on fish abundance are available in order to compare these two river parts (and Zeekoe Creek), but the restriction of commercial fishing to the downstream river part could indicate greater fish abundance there.

The large fluctuations in the numbers counted in different times of the year (Fig. 2B) cannot be explained by migration alone. As long as water level was not rising above shore level migration was restricted. Consequently the total number of caimans in the river and tributaries had to remain almost stable (apart from some gain and loss due to birth and mortality). However, the numbers counted (and captured) are influenced by the number of submerged spec-

imens as well. Inactive specimens remain submerged for most of the time (unpublished data). Thus, it seems that the rate of activity fluctuates and is highest at the start of the long dry season (September) when food is very abundant, and much lower during the short rainy and short dry seasons (December to April).

In *C. crocodylus* of the Coesewijne area, migration is mainly determined by changes in the water level. They follow receding water level and as far as we know no specimens remain in isolated pools as is the case in *Crocodylus johnstoni* (Webb et al., 1983c) and *C. crocodylus* in savanna areas (Staton and Dixon, 1975; Gorzula, 1978). Specimens of the species mentioned above have to burrow when these pools dry up (Alvarez del Toro, 1974; Staton and Dixon, 1975; Ayarzagüena, 1983) or have to migrate to permanent water over land. These terrestrial migrations have been reported for both species (Staton and Dixon, 1975; Gorzula, 1978; Webb and Gans, 1982) and usually seem to be accompanied by an excellent homing ability. Gorzula (1978) performed homing experiments and observed homing in 83% of the specimens. One caiman homed a total distance of 2.4 km in ten days, mainly over land. *Crocodylus johnstoni* was even observed to return to the pool of capture over a distance of 30 km (Webb et al., 1983b). Murphy (1981) demonstrated that *A. mississippiensis* is able to orientate itself on celestial bodies. This ability probably exists in other crocodylians as well. Homing has not yet been demonstrated in populations of crocodylians in which the need seems to be less. The fact that 68% of the first and second year caimans and 52% of the older caimans in the Coesewijne population returned to the exact location they were found in before the rainy season, makes it likely that their homing ability is well developed too. In *Crocodylus johnstoni* these percentages are higher (Webb et al., 1983a): 72.8% returned to the same pool, 83.4% to within 1 km of the same pool. There is no reason, however, why all specimens should return to a fixed spot. In maturing adults (fourth year caimans) habitat selection probably changes slightly since many leave Zeekoe

Creek (see Habitat Selection) and we have the impression that they move more as well. According to Neill (1971) maturing *A. mississippiensis* have to find their place among the other adults and so they have to move a lot. Schaller and Crawshaw (1982) reported on *C. c. yacare* that on average sub-adults moved the longest distances.

With rising water levels caimans enter the creek and finally disperse into the swamps. Dispersal during periods of inundation is reported for many crocodylians (e.g., *C. crocodylus* (Staton and Dixon, 1975; Crawshaw and Schaller, 1980; Ayarzagüena, 1983), *A. mississippiensis* (Chabreck, 1965), *Crocodylus niloticus* (Cott, 1961), *Crocodylus johnstoni* (Webb et al., 1983c), *Crocodylus porosus* (Webb and Messel, 1978)). These migrations could have several causes. One of the most important ones probably is, that crocodylians prefer shallow water for resting and hunting and consequently they have to disperse to follow the shore-line. The inundated areas usually are swamps, which are very productive in all kinds of (semi-)aquatic organisms, especially insects, the main food of young crocodylians. Fishes are dispersed, but probably easier to catch in the swamps than in the rivers. Thus food availability may be a second reason. A third reason probably only applies to species which normally make a mound-type nest. These nests are often constructed in swamps during the rainy season. These are completely surrounded by water. It is likely that these spots are chosen in order to reduce egg predation (see Webb et al., 1983d and Ouboter and Nanhoe, 1987).

Juveniles were generally very sedentary. The long distances travelled by some of them, were probably all at the end of the rainy season, when they were forced to move in a certain direction by the topography of the terrain and the receding water. Immobility of juvenile crocodylians is known for other species as well. In *Crocodylus acutus* in Gatun Lake (Panama) juveniles with an age of about 10 months used an area of 300 m along the shore, 22 months old juveniles an area of about 600 m (Rodda, 1984).

Distances travelled by subadult and adult

caimans in the Coesewijne population were small compared to other populations and other crocodylians. Schaller and Crawshaw (1982) presented figures on *C. c. yacare*. Of all caimans resighted 71% had moved more than 1 km. The three longest distances travelled were 7.0, 7.3 and 9.4 km by an adult male, a subadult female and a subadult male, respectively. Few animals travelled more than 4 km. These results were for the dry season. For *A. mississippiensis* the average minimum daily distance travelled, ranged from 92–150 m in immature alligators (average minimum home range 97.8 ha) studied by Taylor et al. (1976) to 734 m in adult males (minimum home range 183 to 5083 ha) (Joanen and McNease, 1973). One adult male covered a distance of 53 km in five months. Only nesting females were rather sedentary, with an average daily distance travelled of 14 to 34 m (minimum home range 2.6 to 16.6 ha) (Joanen and McNease, 1970). *Gavialis gangeticus* is reported to occupy a home range of 10.4 to 19.2 km of river and to have travelled a maximum distance of 44.4 km (Bustard and Singh, 1983). Even more extensive movements probably occur in *Crocodylus porosus* (Webb and Messel, 1978). Bustard and Singh (1983) suggested that long range movement occurs in the absence of large numbers of conspecifics, so it could be a characteristic of depleted populations. Movement is probably also associated with habitat (probably more movement in large rivers and coastal habitat than in swamps) and adult size.

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