Notes on nesting and parental care in *Caiman crocodilus crocodilus* in northern Suriname and an analysis of crocodilian nesting habitats

Paul E. Ouboter, Lurly M.R. Nanhoe

Department of Animal Ecology, Catholic University of Nijmegen, 6525 ED Nijmegen, The Netherlands and Rijksmuseum van Natuurlijke Historie, Postbus 9517, 2300 RA Leiden, The Netherlands.

Present address: Indira Gandhiweg 268 (km 14), District Wanica, Suriname. *

Abstract. *Caiman c. crocodilus* constructed nests on small elevations in swamps during the long rainy season (May-July). Eggs were buried just beneath ground level and in addition covered by a small mound of dry leaves. This nest type is intermediate between the hole-type and the mound-type nest. Hatching occurred from the beginning until midway into the long dry season. One of two egg-containing nests studied was destroyed by predators. In the other nest 18 of 28 eggs hatched, which coincides with estimates based on pod sizes and estimated mean clutch sizes. Hatchlings stayed together (sometimes associated with second year caimans) for up to 18 months. Most of these pods were attended by an adult caiman for about seven months, until the beginning of the long rainy season. The sex ratio of newborn young was 0.5, but some pods seemed to consist of one sex only (sex ratio being 0 or 1). These results are compared with data on other populations of *C. crocodilus* and other crocodilians. In general there is a correlation between the nest type used and the nesting season; hole-nesting species nest in the dry season, whereas mound-nesting species usually nest in the rainy season. Nesting in the dry season by mound-nesting species occurs and possibly can be explained by avoidance of competition with sympatric mound-nesting species.

Introduction

During the last decade, data on the nesting of *Caiman crocodilus* have increased significantly (e.g. Alvarez del Toro, 1974; Rivero Blanco, 1974; Staton and Dixon, 1977; Crawshaw and Schaller, 1980). However, most of these data were obtained in savanna pools, whereas the species over most of its range occurs mainly in rivers and creeks in forest and swamp areas. During a study of the migration and population dynamics of *C. crocodilus* in northern Suriname (Ouboter and Nanhoe, in press), we collected additional data on the nesting and parental care of this species in swamp and swamp-forest habitats. In these habitats, nests were very difficult to locate and data that could only be obtained at the nests themselves are scarce. However, our limited

observations disclose some differences from data in other studies. In contrast to the situation in savanna pools, pods (groups of juveniles which stay together for several months) were easy to observe in the habitat we studied. Hence we can present new information on these pods and additional data on possible parental care.

Study area

The main study area covered part of the Coesewijne river, a rather narrow river with a length of 190 km, draining a vast savanna, swamp-forest and swamp area in the coastal lowlands of central Suriname (see Fig. 1 in Ouboter and Nanhoe, in press). This area has four seasons: The long rainy season (May to July/August), the long dry season
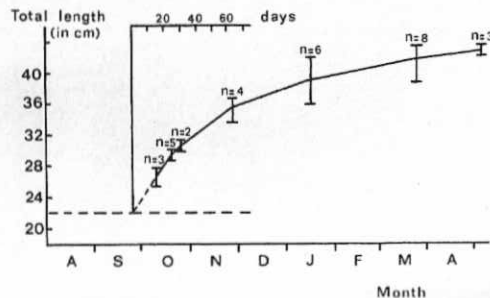

Figure 1. Average growth curve and size range for the hatchlings of pod no. 1, which was used to determine the age of other hatchlings caught.

(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 branch-creeks of the Coesewijne river become completely dry and in the largest of them, Zeekoe creek, the water level drops to 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.

Observations were concentrated in an area around the first 2 km of Zeekoe creek and 5 km upstream and downstream on the main river. Along most of its length the Coesewijne is bordered by xerophytic swamp-forest and downstream by grass- and fern-swamps (Teunissen, 1978). Zeekoe creek drains a large grass-swamp. On elevated areas one can find mesophytic dryland forest. Zeekoe creek is the only branch-creek of the Coesewijne with dense aquatic vegetation, mainly of *Nymphaea rudgeana*. Most

branch-creeks and the river itself lack aquatic vegetation. More details on the Coesewijne area are presented in Ouboter and Nanhoe (in press).

Additional data were collected on the Maratakka (western coastal Suriname), a river bordered by mesophytic dryland and marsh-forest, in the upstream part of Cassewinica creek (eastern coastal Suriname) which is bordered by swamps, and in pools situated in cultivated areas near Lelydorp and Domburg (central coastal Suriname).

Methods

The Coesewijne area was visited on ten occasions between September 1982 and October 1983. Most visits lasted for four weeks, but some took only a few days. The Maratakka was visited for three days in December 1982; the Cassewinica for six days in February 1983 and again for three days in June 1983. A pool near Lelydorp was visited regularly, the one near Domburg only once in February 1983.

For transportation 10 m dug-outs with an outboard motor were used. At night caimans were located by the reflection of their eyes in the beam of a 6-volt headlight. Juveniles were captured by hand, marked, measured and sexed.

Caimans were marked 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 hatchlings, marks usually had to be remade upon recapture; in older caimans, marks remained clearly visible for the total period of 12 months.

Sex was determined 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 these populations of *C. crocodilus*, even in hatchlings, but specimens over one or two months of age were sometimes reluctant to protrude anything.

In the Coesewijne population the age of hatchlings was determined by means of the average growth figures for one pod (the pod for which we obtained most data) (Fig. 1). This pod (no. 1) probably consisted of males only. In crocodilians, growth seems to be equal in males and females up to a length of about 1 m (see e.g. Chabreck and Joanen, 1979; Webb et al., 1983a). Thus, we think that the unisexual composition of this pod does not influence the growth curve. The curve presented (Fig. 1) was used directly to determine the age of hatchlings that were caught for the first time still within the long dry season (most eggs hatched at the start of this season). For older hatchlings, the date of hatching was estimated by constructing a line parallel to the growth curve of Fig. 1 (assuming that growth was dependent on the season and independent of the date of hatching within one season).

During the long rainy season all potential nest sites were searched. Nests were opened and eggs counted, after which the nests were closed again as neatly as possible.

One egg from each nest was opened to determine the species concerned (*Paleosuchus palpebrosus* lives in the area too) and the stage of embryonic development.

Results

Nesting season

In the Coesewijne population, pods of newborn caimans were found between mid September and mid November in 1982. In 1983, the first pod already was seen at the end of August and most pods were probably born before the beginning of October. The calculated dates of hatching of all pods found, are shown in Table 1.

Table 1. Age and date of birth of 14 pods in the study area, calculated with the help of Fig. 1 (see Methods). For pods nos. 6 and 12 the number of specimens first encountered was so low that data from a later catch with more specimens are included as well. Locality is indicated as kilometers from the confluence of Zeekoe creek and the main river; C - Zeekoe creek; U - Coesewijne upstream; D - Coesewijne downstream.

Pod no.	Locality	Date first found	Mean size of hatchlings	Age (days)	Calculated date of hatching
1	C 0.9-1.0	10-10-1982	26.5 ± 1.1	15	25-09-1982
2	U 2-3	27-10-1982	25.7 ± 1.0	12	15-10-1982
3	D 2-3	20-11-1982	23.3 ± 0.2	4	16-11-1982
4	C 1.2-1.3	19-01-1983	29.6 ± 1.2	–	03-11-1982
5	C 1.4-1.5	22-01-1983	45.6	–	03-09-1982
6	C 1.8-2.0	28-03-1983	31.1	–	09-11-1982
	C 1.8-2.0	08-05-1983	42.9 ± 2.5	–	25-09-1982
7	D 1-2	20-09-1983	30.4 ± 1.4	30	20-08-1983
8	U 1-2	21-09-1983	25.6 ± 1.1	12	09-09-1983
9	C 0.9-1.0	25-09-1983	30.5 ± 0.7	30	25-08-1983
10	C 0.4	26-09-1983	30.6 ± 0.8	30	26-08-1983
11	C 1.2	26-09-1983	25.6 ± 0.8	12	14-09-1983
12	C 1.9-2.0	27-09-1983	28.4 ± 1.7	22	05-09-1983
	C 1.9-2.0	09-10-1983	29.9 ± 1.3	28	12-09-1983
13	C 1.9-2.0	09-10-1983	25.5 ± 0.7	12	27-09-1983
14	U 2-3	07-10-1983	32.1 ± 0.8	40	28-08-1983

Assuming that growth rate is the same, the time of hatching in other rivers can be determined by the length of first and second year juveniles caught. In the Maratakka (western Suriname) only one second year caiman could be found. Its size (60.8 cm) corresponded well with the size of 15 months old juveniles of Coesewijne (Fig. 2). In first and second year juveniles from Cassewinica creek (eastern Suriname) there was more variation in size (Fig. 2), but on the whole their size was not significantly different from 5 and 17 months old juveniles of Coesewijne (Wilcoxon-Mann-Whitney R-test (Zijp, 1974), first year juveniles: $19 < R < 26$, $P > 0.05$; second year juveniles: $R = 72.5$, $P > 0.05$). So, in all three rivers examined, hatching occurred between the
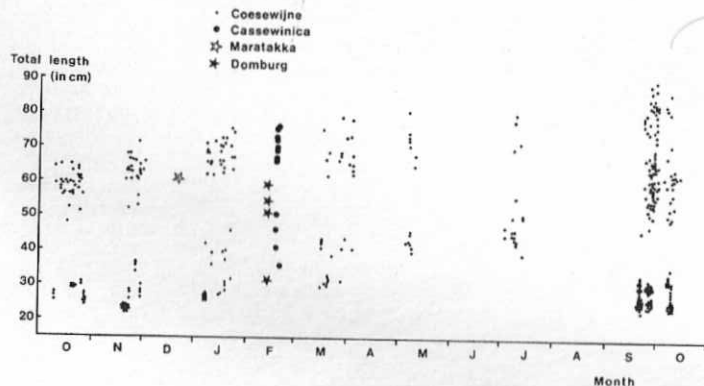
Figure 2. Size of first and second year juveniles caught during the study period.

end of August and mid November, i.e. from the beginning till halfway into the long dry season. In 1983, most young hatched considerably earlier than in 1982. This is most likely to be correlated with the early start of the long rainy season in 1983, during which the water level started to rise quickly at least one month earlier than in 1982 (unpublished data). Nesting probably starts after the rise of the water above a certain level. Taking into account the incubation period determined by Alvarez del Toro (1974: 75-80 days) and Staton and Dixon (1977: 73 days), all clutches were laid in the long rainy season (with the water level exceeding 140 cm above shore level). This agrees well with the period in which we found active or recently destroyed nests (see Nesting).

The situation in pools was sometimes quite different. In a pool near Lelydorp (central coastal Suriname) four recently born hatchlings were seen in September (agreeing with the Coesewijne hatching season). Three juveniles caught, out of a pod of eight, in a pool near Domburg (central coastal Suriname), however, differed significantly from first year juveniles of Coesewijne (Wilcoxon-Mann-Whitney R-test, $R = 6$, $P < 0.005$), but were too small for second year juveniles ($R = 6$, $P < 0.005$) (Fig. 2). The same pool was also inhabitated by at least two much smaller juveniles. One of these was caught and was comparable in size with Coesewijne hatchlings.

Nesting

Nest construction was never observed and, due to difficult terrain, only few nests were found. On June 25 two nests were found along the Cassewinica creek (eastern Suriname), one of which was already destroyed and one active (containing 14 eggs). Of

three nests discovered along Zeekoe creek in July, one was freshly constructed but empty, another was already destroyed and only the third contained eggs (28).

In spite of an intensive search of all forest islands that remained dry during the long rainy season, as well as of the wet swamps, no nests could be found there. All five nests discovered were in the swamp, but on small (2 to 5 m²) elevations, which were usually located along small creeks. Their vegetation mainly consisted of *Montrichardia arborescens*, but owing to their elevated position some other bushes and even trees grew on these islets. These islets probably were formed by a silting process between the *Montrichardia*-stems. They were ideal nesting sites to limit egg predation by terrestrial animals, since the land was inundated for kilometers in all directions. Nests were partly shaded. The egg-chambers were just below ground level and the eggs were covered by small piles of dry leaves (of 20 to 30 cm in height), which the females apparently gathered in the small clearings between the bushes. The substratum below the nests mainly consisted of dead leaves too. In all nests discovered, the ground and the plant material surrounding the eggs or the remains of the eggs was already laced together by growing rootlets. The height of the eggs above the mean rainy season water level was 30-80 cm.

Hatching and nesting success

Direct data on hatching could only be obtained at the Zeekoe creek nest. On July 6, when it was discovered, two eggs out of 28 had decayed and another one, containing a viable embryo, was removed by us. When checking the nest on August 4, an unidentified animal had been digging a hole, but had only damaged the uppermost egg, so 24 eggs remained. Of these 17 hatched successfully, six were found to have decayed, and one had hatched but the hatchling did not leave the nest and died. When found (on September 7) the dead hatchling had not yet decomposed and only a small part of it had been eaten by the ants that inhabited the nest. Apparently hatching took place only a few days earlier. All of the egg shells in the nest were intact, except for the holes through which the young had escaped. The hatchlings left the nest not at the top, but through a sloping passage, leading down to the water. No hatchlings were discovered near the nest.

Thus, of 28 eggs, 17 (61%) hatched successfully, or assuming that the egg taken by us would have hatched, 18 (64%). Data from this single observation, can be checked against the number of hatchlings in a pod soon after hatching; this ranges from 6 to 32 (mean 18 ± 7, $n = 11$) (Tab. 2). Assuming an average clutch size identical to that of the Venezuelan population studied by Staton and Dixon (1977), i.e. 28.6 eggs, these values too indicate a hatching success of 64%.

Our data on the percentage of nests from which young hatched are meagre. Of the three nests found in the Coesewijne population only one hatched (33%), or excluding the empty nest 50%.

Assuming that sexually mature females nest every year, the proportion of nests that

Table 2. Size and sexual composition of 14 pods in the study area and the presence of an adult caiman and/or second year caimans near the pods. Pods nos. 4, 5 and 6 were found after the long dry season, so that the association with an adult caiman and/or second year caimans could not be ascertained. Data on second year juveniles near pods nos. 12 and 13 are combined, because these pods were together in the same crèche.

Pod no.	Breeding season	Adult caiman seen near pod	Number of second year caimans seen near pod	Males	Females	Sex unknown	Number examined
1	1982	+	2	13	0	12	25
2	1982	+	–	6	1	6	13
3	1982	+	–	8	7	1	16
4	1982	(–)	(–)	0	3	5	8
5	1982	(–)	(–)	0	0	1	1
6	1982	(–)	(–)	10	0	4	14
7	1983	+	–	9	5	0	14
8	1983	–	1	12	10	0	22
9	1983	+	6	11	2	5	18
10	1983	+	–	7	2	1	10
11	1983	+	–	0	14	0	14
12	1983	+	15	2	4	0	6
13	1983	+		7	13	0	20
14	1983	–	3	5	3	0	8

produced live young can also be calculated using the number of pods and the number of mature females. In the 1982 nesting season six pods were counted on about 48 adults of five years and older (these are sized over 120 cm and are probably sexually mature (see Rivero Blanco, 1974 and Staton and Dixon, 1977)). Assuming a sex ratio of 0.5 (see Ouboter and Nanhoe, in prep.; sex ratio expressed as proportion of males), this results in a proportion of successful nests of 6/24 or 25%. But not all females nested every year; two females outfitted with radio-transmitters (see Ouboter and Nanhoe, in press) occupied habitats during the nesting season most unlikely for nesting. So, the figure of 25% successful nests is too low. Gorzula (1978) suggested that females nest every two years. Application to the Coesewijne population, predicts a proportion of successful nests of 50% and an overall hatching success of 32% (= 50% of 64%).

Parental care and formation of hatchling groups

We could not make any observations on nest attendance. On two visits (day and night) no adult was seen near the active nest along Cassewinica creek and only once in four day-time visits and four night-time visits an adult was seen near the active Zeekoe creek nest. This caiman disappeared immediately when approached.

At the active Zeekoe creek nest, no signs of nest opening by one of the parents were visible after hatching. The passage through which the young escaped was very narrow (about 3 cm wide). It is unlikely that it was made by one of the parents.

Out of 11 newborn pods (1982 and 1983 breeding season) at least nine were usually accompanied by an adult caiman of 120 to 140 cm total length (Tab. 2). These always

dived before they could be captured, but their length indicated that they probably were females. Some disappeared completely on approach, but most remained close by as their hatchlings were handled, sometimes submerging for some minutes and surfacing again in another spot nearby. On three occasions the accompanying adult displayed in response to the hatchling's distress call, swimming rapidly in our direction and beating on the water with its tail. They never attacked, however. The adults could be seen near their pods until the beginning of the long rainy season, i.e. for a period of five to seven months. During the long rainy season, observations were difficult to make, due to dispersal of the caimans (Ouboter and Nanhoe, in press). One adult attending a pod that only consisted of second year juveniles (about nine) was observed during the 1982 breeding season. However, several hatchling groups were accompanied by a small group of second year caimans. This association was observed in six out of eleven pods (Tab. 2). At least four of the six second year juveniles that were found with pod no. 9 were marked in the same part of the creek the year before and were members of pod no. 1. The second year juveniles associated with the pod nos. 12 and 13 were members of pod no. 6, which also inhabited the same part of the creek. On the other hand, some juveniles travelled for long distances during the long rainy season (Ouboter and Nanhoe, in press) and the three second year caimans associated with pod no. 14 came from pod no. 1 (min. distance 2800 m), pod no. 3 (min. distance 2700 m) and pod no. 6 (min. distance 2900 m).

Transportation of the young by an adult, which is reported for *Crocodylus niloticus* (Cott, 1971; Pooley, 1974; Pooley and Gans, 1976) and *A. mississippiensis* (Kushlan, 1973), was never observed in *C. crocodilus*, but probably occurred frequently in the Coesewijne population. That is, some pods crossed the river or pods of a few weeks old suddenly appeared in an area where we had not seen them before. We think that these movements of whole pods over rather large distances are only possible when an adult carries the young on its back or in its mouth. The observed movements are listed below: Pod no. 3 crossed the river at least two times, once between November 1982 and January 1983 and a second time between January 15 and 20. Pod no. 8 crossed the river and moved another 200 m downstream between September 8 and 21, 1983. No juveniles were found near the Zeekoe creek nest which had hatched a few days before we visited it. On September 6, 1983 pod no. 10 (age about 30 days) appeared in a place in Zeekoe creek where it had not been before, and on October 7, 1983 pod no. 14 (age about 40 days) appeared at the entrance of a branch-creek where it had not been before.

Most pods remained in or were brought to Zeekoe creek, which seems to be an ideal nursery site because of shallow water, shelter provided by aquatic vegetation and rich insect life. Consequently the distribution of hatchling groups between river and branch-creeks was not random (χ^2-test, $\chi^2 = 178.34$, $P < 0.001$) (see Ouboter and Nanhoe, in press).

Crocodilian hatchlings keep contact with each other, and probably with the attending adult as well, by grunting (Cott, 1961; Campbell, 1973; Herzog and Burghardt,

1977; Crawshaw and Schaller, 1980; Magnusson, 1980; Medem, 1981). In the Coesewijne population the young of some pods were quite silent, while others grunted continuously. Movement was always in the direction of other grunting young, even when potential enemies had to be passed on the way to the source of the sound(s).

In hatchlings of the *C. crocodilus* population studied, the penis could clearly be distinguished from the clitoris by its larger size; however, by the age of two to three months sexing was hampered as most males were reluctant to protrude the penis. Due to our inexperience, a great number of hatchlings could not be sexed in 1982. Figures for 1983 are much better, showing a sex ratio of 0.5 (53 males and 53 females). This is a combined figure; separate pods may show very different sex ratios (Tab. 2). Two pods of the 1982 breeding season (pod nos. 1 and 6) probably consisted of males only and all 14 hatchlings of pod no. 11 were females.

Discussion

In the three rivers studied, the nesting period of *C. crocodilus* coincides with part of the long rainy season (May-July) and most young hatch at the start of the long dry season (August-October). This is in agreement with data provided by Medem (1983) for Galibi (eastern coastal Suriname) and Uitkijk (central coastal Suriname). In both Guyana (Beebe, 1917) and French Guiana (Medem, 1983) the nesting period seems to be the same as in Suriname. Medem (1983) reported slightly longer periods for Guyana: nesting from the end of April till August/September and hatching from July till November. In the Venezuelan part of the Guianas the young hatch in October and November (Gorzula, 1978). Outside the Guianas nesting occurs in the rainy season too. In the Venezuelan Llanos from August till October (Staton and Dixon, 1977) and in the Pantanal (southwestern Brazil) in January (Crawshaw and Schaller, 1980).

The breeding biology of *C. crocodilus* seems to be correlated with water levels. Apart from species occupying areas with a relatively cold period, this probably holds true for most crocodilians. Ferguson (1985) could not find consistent trends between breeding times and water levels across all species. However, if one distinguishes two nesting time strategies and two nest-types, a correlation becomes clear (Tab. 3). One group of crocodilians nests when water levels are receding or low and the young hatch when water levels are rising. According to Cott (1961), this has the advantage that nests are not likely to be flooded, that the young hatch in the vicinity of water, that dispersal is easy and that food, i.e. insects, is abundant. Especially the first point seems important as all hole-nesting crocodilians exhibit this strategy (Tab. 3). They usually nest on dry sand-banks or on the shore of a river or lake. These sites are not available during periods of high water or are extremely vulnerable to flooding, so that the best period for nesting is with receding or low water during the dry season. In most areas of the world the precipitation cycle is such that, with this nesting strategy, the young hatch with rising water levels, with the coincident advantages mentioned by Cott. However, we could think of some disadvantages as well; for instance, in some areas newborn

Table 3. Nest type, nesting season and hatching season of crocodilians. Data between brackets indicate data presented in an indistinct way, data doubted by recent authors, or observations made in captivity. References are: 1) Chowdhury et al., 1983; 2) Bustard, 1984; 3) Alvarez del Toro, 1974; 4) Ogden, 1978; 5) Medem, 1981; 6) Webb et al., 1983b; 7) Longman, 1925; 8) Cott, 1961; 9) Modha, 1967; 10) Pooley, 1969; 11) Whitaker and Whitaker, 1976; 12) Wayialingham, 1880; 13) Prakash, 1971; 14) Varona, 1966; 15) Smith, 1931; 16) Yangprapakorn et al., 1971; 17) Schmidt, 1919; 18) Witte, 1927; 19) Jelden, 1981; 20) Jelden, 1984; 21) Webb et al., 1977; 22) Webb et al., 1983c; 23) Joanen, 1969; 24) Goodwin and Marion, 1978; 25) Neill, 1971; 26) This study; 27) Staton and Dixon, 1977; 28) Crawshaw and Schaller, 1980; 29) Freiberg and Carvalho, 1965; 30) Hagmann, 1902; 31) Medem, 1983; 32) Medem, 1971; 33) Magnusson et al., 1985; 34) Magnusson, pers. comm.; 35) Greer, 1970.

Species	Nest			Nesting season Water level			Hatching season Water level		
	Hole-type	Inter-mediate	Mound-type	Receding Low	Rising	High	Receding Low	Rising	High
Gavialis gangeticus	12			12				12	
Crocodylus acutus	3,4,5	4	3,4,5	3,4,5				3,4,5	
intermedius	5		5	5				5	
johnstoni	6		(7)	6				6	
niloticus	8,9,10					10		8	10
palustris	11	12,13		11,13				11,13	
rhombifer	14								
siamensis	15								
cataphractus			(16) 17,18		(15,16)				(16)
novaeguineae			19,20	19,20				19,20	
porosus			20,21,22			20,21,22	22		
moreletii			3	(3)					
Osteolaemus tetraspis			17						
Alligator mississippiensis			23,24			(17) 23,24			23,24
sinensis		26	25						
Caiman crocodilus			27,28 29			26,27,28	26		
latirostris									
Melanosuchus niger			30,31	5,30,31			5,30	5,31	
Paleosuchus palpebrosus			5,32						
trigonatus			5,33,34	34					
Tomistoma schlegeli			35						

young will have fewer opportunities to rest in shallow places and consequently it will be more difficult to remain together as pod (also see p. 344). In the region occupied by the Coesewijne population of C. crocodilus insect food is just as or even more abundant at the beginning of the dry season than during the rainy season (pers. obs.). The only departure from the rule that hole-nesting species nest with receding or low water is Crocodylus niloticus in Southern Africa (Pooley, 1969). Here the dry season coincides with the coldest period of the year, when temperatures are too low for successful incubation of crocodile eggs.

The second nesting strategy is described for C. crocodilus (Rivero Blanco, 1974; Staton and Dixon, 1977; Crawshaw and Schaller, 1980) and for Crocodylus porosus (Webb et al., 1977, 1983c), but probably occurs in some other species as well. In this case, nesting starts in the rainy season and the young hatch at the end of this season or at the beginning of the dry season. Crawshaw and Schaller (1980) mention the following advantages: 1) on account of large parts of the area being flooded, females are able to select nest sites where the chances of egg predation are reduced, 2) hatchlings can avoid intraspecific competition for food during the first months of their lives, 3) in the rainy season humidity is high and temperatures vary little, which has a positive influence on hatching success. These advantages also apply to the Coesewijne population, although the second is inconsequential. A completely different set of reasons for nesting in the rainy season has been suggested by Staton and Dixon (1977); reasons mainly related to disadvantages for the female to follow the first mentioned strategy, which is thought to enhance the survival of the young: 1) for hatchlings to emerge during the rainy season, nest building and incubation must occur during the dry season. In the Venezuelan situation the female would have to guard the nest at a time when she finds neither shade nor water for cooling or protection, and 2) she would have to construct the nest of dry materials. Even if these arguments are realistic for the Venezuelan habitat studied, the advantages suggested by Crawshaw and Schaller (1980) (see above) could apply just as well (egg predation after receding water levels (see advantage 1 mentioned by Crawshaw and Schaller) is indeed mentioned by Staton and Dixon (1977)) and these probably have a more general validity. At any rate, Staton and Dixon's (1977) arguments do not apply to the Coesewijne population; here shade, water and fresh nest material are available near all known nest sites throughout the year.

Most species that exhibit the second nesting strategy, construct mound-type nests (Tab. 3). These nests are probably more vulnerable to desiccation and excessive heat than hole-type nests and consequently more suitable for nesting during the wet season, during which temperatures tend to be lower. In addition nesting material is more readily available during this season (Magnusson, pers. comm.). In contrast to the hole-nesting species, which follow the first nesting strategy almost without exception, mound-nesting species show more variation in nesting strategy (see Tab. 3). A mound-nesting species will probably have less difficulties finding a nest site in a wet spot (shade) during the dry season, than for a hole-nesting species to find a spot that is not

likely to flood during the rainy season. Consequently mound-nesting species will be able to adapt more readily to local circumstances. A possible reason why some mound-nesting species nest in the dry season could be avoidance of competition with sympatric (syntopic) crocodilian species; competition for nest sites and competition of hatchlings for food and shelter. Unfortunately too few data are available on sympatry and nesting season of the crocodilians concerned, to support this idea with clear observations. The data available are presented in Table 3 for the sympatric pairs: *Crocodylus porosus* / *Crocodylus novaeguineae*, *Crocodylus moreletii* / *C. crocodilus*, *C. crocodilus* / *Melanosuchus niger*, *C. crocodilus* / *Paleosuchus palpebrosus*.

So far, no explanation has been given for the juveniles of aberrant size in the pool near Domburg. This pool is surrounded by cultivated land and not subjected to seasonal flooding. Here the breeding season may not be strongly fixed by the seasons and breeding could occur all year round. Assuming the same growth rate as for specimens in the Coesewijne area, the larger Domburg juveniles will have been about four months older than Coesewijne juveniles and consequently must have hatched in May, at the start of the long rainy season. Another possibility is that growth rate is slower in small pools, due to insufficient food (compare slow growth rate in savanna pools observed by Gorzula (1978)). Another indication in this direction is that the smallest specimen of the oldest pod at Domburg was rather lean. The presence of a pod of much smaller hatchlings in the same pool could support either explanation.

Mound-type nests are constructed by at least 13 species of crocodilians, whereas 8 species construct hole-type nests (Tab. 3). Opinions differ about the origin of these two different nest types and about the rigidity of crocodilian nesting habits. Neill (1971) claimed that actually only the mound-type nest exists and that even crocodilians nesting in sand use this to shape a mound; this suggestion cannot be taken seriously. Wermuth (1953) argued that all transitions between hole-type and mound-type nests exist, so that the nest type lacks phylogenetic significance. Greer (1970) disagreed, claiming the nest type to be phylogenetically fixed for a certain species. One year later he suggested that nest type correlated with habitat too (Greer, 1971). Campbell (1972) confirmed a correlation with the habitat, but he mentioned several cases in which species departed from their usual nesting habits. His view was partly supported by observations of Ogden (1978) who observed that *Crocodylus acutus* constructed both hole-type and mound-type nests, as well as intermediate ones, but who denied a correlation with the habitat. He reported that young females used hole-type nests or made a small mound, whereas older females constructed large mound-nests. Webb et al. (1983b) agreed with Greer (1970, 1971) that the nest type used by a certain species is fixed, although correlated with the habitat; mound-nesting characterizes crocodilians which nest during wet seasons or in wet environments (see our discussion on nesting-season/nest-type relations on p. 341. They argued that the cases of species that use both nest types are poorly documented, or, in the case of *Crocodylus acutus*, the nest pile does not resemble the mound-nests constructed by other species. However, both Alvarez del Toro (1974) and Medem (1981) mentioned low "real" mound-type nests for *Crocodylus*

acutus and Medem (1981) also documented a mound-type nest for *Crocodylus intermedius*.

C. crocodilus is always reported to construct mound-type nests (e.g. Staton and Dixon, 1977; Crawshaw and Schaller, 1980; Medem, 1981). However, the nests we found in the Coesewijne and Cassewinica populations were clearly intermediate between the mound-type and the hole-type. There was probably insufficient material available for a big pile. In a real hole-type nest on the other hand, the eggs would be too close to the water level, increasing the chance of flooding. So, caimans using this kind of nest site are probably forced to use the intermediate nest type described. On the basis of these observations we agree with Campbell (1972) that the behaviour of some crocodilians is sufficiently flexible to permit the construction of different nest types depending on the kind of habitat. However, the nest type which is usually made may have a phylogenetic significance.

We have data on the proportion of eggs which hatched (which was 64%) for one nest only, and the figure for the proportion of nests that produced live young (50%) is based on the observations from two active nests. The other methods used to calculate these proportions (number of young in a newborn pod and number of pods on the number of reproductive females) seem to support the figures obtained. Although these methods are based on many assumptions, the figures obtained are well within the range known for other crocodilians, but rather high compared to other populations of *C. crocodilus*. Staton and Dixon (1977) reported an average proportion of successful nests of 15.8% and Crawshaw and Schaller (1980) an overall hatching success of 20.1%. In both cases the main cause for these low figures was predation. In the Coesewijne population predation is probably limited by nesting on the swamp nest sites described.

In most crocodilians the female opens the nest, usually in response to the hatchlings calling within the eggs (Beebe, 1917; Cott, 1961, 1971; Modha, 1967; Pooley and Gans, 1976; Pooley, 1977; Webb et al., 1983b; Bustard, 1984) and in one case even the male was observed to free the hatchlings from the nest and the still unhatched juveniles from the eggs (Alvarez del Toro, 1969). When the walls of the egg-chamber are hard, nest opening is essential for the survival of the hatchlings (Cott, 1961; Magnusson, 1980). In the case of less compact nests, for instance the grass nests of *A. mississippiensis*, many young manage to escape from the nest by themselves (Joanen, 1969). The nests of the Coesewijne and Cassewinica populations lacked hard egg-chambers, but the material surrounding the eggs was laced together by a network of growing rootlets, so that freeing themselves without outside help must have been hard work for the hatchlings. Crawshaw and Schaller (1980) suggested the same for *C. c. yacare* nests, where roots also contributed to the compactness of the nest-piles. The hatchlings from the Zeekoe creek nest hatched (i.e. emerged from the eggs) by themselves, as all egg shells remained in the nest and the shells were intact, except for the holes through which the young escaped (see Crawshaw and Schaller, 1980). They probably even escaped from the nest unaided. It is unlikely that the mother would have been able to make the narrow passage through which they escaped.

According to all reports on adults attending a crèche (usually assumed to be one of

the parents), the adult leaves the young after a few weeks in Crocodilinae (Cott, 1961; Modha, 1967; Pooley and Gans, 1976; Webb et al., 1977). Gharials (*Gavialis gangeticus*) stay with their pods for at least some weeks, but the exact duration of attendance is unknown (Bustard, 1980). In the Alligatorinae, longer periods of attendance have been reported. *A. mississippiensis* stays with its pod for more than a year (Chabreck, 1965). In *C. crocodilus* attendance on a pod varies from two weeks to four months mentioned by Staton and Dixon (1977), to 18 months observed in the Coesewijne population and in the Venezuelan population studied by Gorzula (1978). It is not certain if the duration of attendance depends on the subfamily concerned, as suggested above. Another possibility is a relation with the hatching season. Newborn hatchlings will have more difficulty remaining together during the rainy season when water levels are high.

It is not known whether long periods of attendance in *C. crocodilus* are usual or exceptional. If the first and second year juveniles which are members of the same crèche have the same mother and she is the one attending, then 18 months is the usual period of attendance. This would also mean that at least some females nest in two successive years. The fact that one crèche was partly made up of second year juveniles originating from three different pods, suggests another possibility. We believe that the association of first and second year caimans is advantageous for the latter (maybe also for the former), because they obtain protection from the presence of the hatchlings' attending adult in this way. The distress call of a crocodilian does not only arouse the response of the attending adult, but of other conspecifics as well (e.g. Neill, 1971; Gorzula, 1978; pers. obs.). This makes it likely that the attending adult also will defend the second year caimans in its crèche against predators. This tendency of young to seek the protection of a group and a (probably related) adult may occur in more species of crocodilians. Webb et al. (1977), studying *Crocodylus porosus*, recovered a hatchling after 55 days in another group of hatchlings 5.6 km upstream. Strangely enough, reports on crèches with both first and second year crocodilians are rare. This association has been mentioned for *C. crocodilus* in Guyana (Beebe, 1917) and in Venezuela (Gorzula, 1985).

In *A. mississippiensis* the difference between penis and clitoris is not clearly visible before the 18th month (Joanen and McNease, 1978). In the *C. crocodilus* population studied by us the penis was already much enlarged in male hatchlings. The same holds true for *Crocodylus johnstoni* (Webb et al., 1983b, 1984) and *Crocodylus porosus* (Webb and Messel, 1978; Webb et al., 1984).

In both *A. mississippiensis* (Ferguson and Joanen, 1982, 1983) and *Crocodylus johnstoni* (Webb et al., 1983b; Webb and Smith, 1984) sex was found to be determined by the nest temperature. The existence of unisexual pods in the Coesewijne population of *C. crocodilus* could indicate the same mechanism of sex determination. Measurements of nest temperatures could confirm this. Unfortunately the nests of these unisexual pods were not known to us.

References

Alvarez del Toro, M. (1969): Breeding the spectacled caiman at Tuxtla Gutierrez Zoo. Int. Zoo Yearb. 9: 35-36.

Alvarez del Toro, M. (1974): Los Crocodylia de Mexico. Inst. Mexicano de Recursos Naturales Renovables, A.C., Mexico, D.F., 70 pp.

Beebe, W. (1917): The Alligators of Guiana. In: Tropical wild life in British Guiana, p. 283-290. Beebe, W., Hartley, G.I., Howes, P.G., eds., New York, New York Zoological Society.

Bustard, H.R. (1980): Maternal care in the gharial, *Gavialis gangeticus* (Gmelin). Brit. J. Herpet. 6: 63-64.

Bustard, H.R. (1984): Breeding the gharial (*Gavialis gangeticus*): Captive breeding a key conservation strategy for endangered crocodilians. In: The structure, development and evolution of reptiles, p. 385-406. Ferguson, M.W.J., ed., London-New York-San Francisco, Academic Press.

Campbell, H.W. (1972): Ecological or phylogenetic interpretation of crocodilian nesting habits. Nature (Lond.) 238: 404-405.

Campbell, H.W. (1973): Observations on the acoustic behavior of crocodilians. Zoologica 58: 1-11.

Chabreck, R.H. (1963): Methods of capturing, marking and sexing alligators. Proc. 17th Annual Conf. S.E. Assoc. Game and Fish Comm. 17: 47-50.

Chabreck, R.H. (1965): The movement of alligators in Louisiana. Proc. 19th Annual Conf. S.E. Assoc. Game and Fish Comm. 19: 102-110.

Chabreck, R.H., Joanen, T. (1979): Growth of the American alligator in Louisiana. Herpetologica 35: 51-57.

Chowdhury, S., Bustard, H.R., Tandan, B.K. (1983): Incubation and hatching of eggs of *Gavialis gangeticus* in hatcheries. Brit. J. Herpet. 6: 337-342.

Cott, H.B. (1961): Scientific results of an inquiry into the ecology and economic status of the Nile crocodile (*Crocodilus niloticus*) in Uganda and Northern Rhodesia. Trans. Zool. Soc. London 29: 211-356.

Cott, H.B. (1971): Parental care in the Crocodylia, with special reference to *Crocodylus niloticus*. In: Crocodiles, Proc. 1st Work Meet. Crocodile Spec., New York, March 1971. New Ser. Suppl. Pap. 32: 166-180. IUCN, ed.

Crawshaw, P., Schaller, G. (1980): Nesting of Paraguayan caiman (*Caiman yacare*) in Brazil. Papéis Avulsos Zool., S. Paulo 33: 283-292.

Ferguson, M.W.J. (1985): The reproductive biology and embryology of the crocodilians. In: Biology of the Reptilia, Vol. 14, Development A, p. 329-491. Gans, C., Billett, F., Maderson, P.F.A., eds., New York, John Wiley & Sons.

Ferguson, M.W.J., Joanen, T. (1982): Temperature of egg incubation determines sex in *Alligator mississippiensis*. Nature (Lond.) 296: 850-853.

Ferguson, M.W.J., Joanen, T. (1983): Temperature dependent sex determination in *Alligator mississippiensis*. J. Zool. (Lond.) 200: 143-177.

Freiberg, M.A., Carvalho, A.L. (1965): El Yacare Sudamericano *Caiman latirostris* (Daudin). Physis 25: 351-360.

Goodwin, T.M., Marion, W.R. (1978): Aspects of the nesting ecology of American alligators (*Alligator mississippiensis*) in north central Florida, USA. Herpetologica 34: 43-47.

Gorzula, S.J. (1978): An ecological study of *Caiman crocodilus crocodilus* inhabiting savanna lagoons in the Venezuelan Guayana. Oecologia (Berlin) **35**: 21-34.

Gorzula, S.J. (1985): Are caimans always in distress? Biotropica **17**: 343-344.

Greer, A.E. (1970): Evolutionary and systematic significance of Crocodilian nesting habits. Nature (Lond.) **227**: 523-524.

Greer, A.E. (1971): Crocodile nesting habits and evolution. Fauna (Oslo) **2**: 20-29.

Hagmann, G. (1902): Die Eier von *Caiman niger*. Zool. Jahrb. (Syst.) **16**: 405-410.

Herzog, H.A., Burghardt, G.M. (1977): Vocalization in juvenile crocodilians. Z. Tierpsychol. **44**: 294-304.

Jelden, D.C. (1981): Preliminary studies on the breeding biology of *Crocodylus porosus* and *Crocodylus n. novaeguineae* on the Middle Sepik (Papua New Guinea). Amph.-Rept. **1**: 353-358.

Jelden, D.C. (1984): Die Krokodile Neuguineas. Inaugural-Dissertation, Heidelberg.

Joanen, T. (1969): Nesting ecology of alligators in Louisiana. Proc. 23rd Annual Conf. S.E. Assoc. Fish and Game Comm. **23**: 141-151.

Joanen, T., McNease, L. (1978): The cloaca sexing method for immature alligators. Proceedings a. Conf. SEast Ass. Game Fish Wildl. Agencies **32**: 179-181.

Kushlan, J.A. (1973): Observations on maternal behavior in the American alligator, *Alligator mississippiensis*. Herpetologica **29**: 256-257.

Longman, H.A. (1925): *Crocodylus johnstoni* Krefft. Mem. Queensl. Mus. **8**: 95-102.

Magnusson, W.E. (1980): Hatching and creche formation by *Crocodylus porosus*. Copeia **1980**: 359-362.

Magnusson, W.E., Lima, A.P., Sampaio, R.M. (1985): Sources of heat for nests of *Paleosuchus trigonatus* and a review of crocodilian nest temperatures. J. Herpetol. **19**: 199-207.

Medem, F. (1981): Los Crocodylia de Sur America. Volumen I. Los Crocodylia de Colombia. Bogotá, Colciencias, 354 pp.

Medem, F. (1983): Los Crocodylia de Sur America. Volumen II. Venezuela-Trinidad-Tobago-Guyana-Suriname-Guayana Francesa-Ecuador-Perú-Bolivia-Brasil-Paraguay-Argentina-Uruguay. Bogotá, Colciencias, 270 pp.

Modha, M.L. (1967): The ecology of the Nile crocodile (*Crocodylus niloticus* Laurenti) on Central Island, Lake Rudolf. E. Afr. Wildl. J. **5**: 74-95.

Neill, W.T. (1971): The last of the ruling reptiles. New York, Columbia Univ. Press, 486 pp.

Ogden, J.C. (1978): Status and nesting biology of the American crocodile *Crocodylus acutus* (Reptilia, Crocodilidae) in Florida, USA. J. Herpetol. **12**: 183-196.

Ouboter, P.E., Nanhoe, L.M.R. (in press): Habitat selection, activity and migration of *Caiman crocodilus crocodilus* in a swamp and swamp-forest habitat in Northern Suriname. J. Herpetol.

Pooley, A.C. (1969): Preliminary studies on the breeding of the Nile crocodile *Crocodylus niloticus*, in Zululand. Lammergeyer **3**: 22-45.

Pooley, A.C. (1974): Parental care in the Nile crocodile: a preliminary report on behavior of a captive female. Lammergeyer **21**: 43-45.

Pooley, A.C. (1977): Nest opening response of the Nile crocodile, *Crocodylus niloticus*. J. Zool. (Lond.) **182**: 17-26.

Pooley, A.C., Gans, C. (1976): The Nile Crocodile. Scient. Amer. **234**: 114-124.

Prakash, M. (1971): Crocodile (*Crocodylus palustris*) breeding at the Jaipur Zoo. J. Bombay Nat. Hist. Soc. **68**: 835-837.

Rivero Blanco, C. (1974): Habitos reproductivos de la baba en los Llanos de Venezuela. Natura **52**: 24-29.

Schmidt, K.P. (1919): Contributions to the herpetology of the Belgian Congo. Part. 1. Turtles, crocodiles, lizards and chameleons. Bull. Amer. Mus. Nat. Hist. **39**: 385-624.

Smith, M.A. (1931): The Fauna of British India including Ceylon and Burma. Vol. 1. Loricata, Testudines. London, Taylor and Francis, 185 pp.

Staton, M.A., Dixon, J.R. (1977): The breeding biology of the spectacled caiman, *Caiman crocodilus crocodilus*, from Venezuelan Llanos. U.S. Fish and Wildl. Serv. Wildl. Res. Rep. (5), 21 pp.

Teunissen, P.A. (1978): Overzichtskaart Surinaamse laagland ecosystemen: schaal 1:200.000 (Reconnaissance map Surinam lowland ecosystems: scale 1:200,000). Den Haag, Wotro/Paramaribo, Stinasu.

Varona, L.S. (1966): Notas sobre los Crocodílidos de Cuba y descripción de una nueva especie del Pleistoceno. Poeyana, Serie A, **16**: 1-34.

Waytialingham, S. (1880): Notes on the breeding of *Crocodylus palustris*. Proc. Zool. Soc. London **1880**: 186.

Webb, G.J.W., Buckworth, R., Manolis, S.C. (1983a): *Crocodylus johnstoni* in the McKinlay River area, N.T. III. Growth, movement and the population age structure. Aust. Wildl. Res. **10**: 383-401.

Webb, G.J.W., Buckworth, R., Manolis, S.C. (1983b): *Crocodylus johnstoni* in the McKinlay River area, N.T. VI. Nesting biology. Aust. Wildl. Res. **10**: 607-637.

Webb, G.J.W., Manolis, S.C., Sack, G.C. (1984): Cloacal sexing of hatchling crocodiles. Aust. Wildl. Res. **11**: 201-202.

Webb, G.J.W., Messel, H. (1978): Movement and dispersal pattern of *Crocodylus porosus* in some rivers of Arnhem Land, northern Australia. Aust. Wildl. Res. **5**: 263-283.

Webb, G.J.W., Messel, H., Magnusson, W.E. (1977): The nesting of *Crocodylus porosus* in Arnhem Land, Northern Australia. Copeia **1977**: 238-249.

Webb, G.J.W., Sack, G.C., Buckworth, R., Manolis, S.C. (1983c): An examination of *Crocodylus porosus* nests in two Northern Australian freshwater swamps, with an analysis of embryo mortality. Aust. Wildl. Res. **10**: 571-605.

Webb, G.J.W., Smith, A.M.A. (1984): Sex ratio and survivorship in the Australian freshwater crocodile *Crocodylus johnstoni*. In: The structure, development and evolution of reptiles, p. 319-355. Ferguson, M.W.J., ed., London-New York-San Francisco, Academic Press.

Wermuth, H. (1953): Systematik der rezenten Krokodile. Mitt. Zool. Mus. Berlin **29**: 375-514.

Whitaker, R., Whitaker, Z. (1976): Collection and hatching of marsh crocodile (*Crocodylus palustris*) eggs. J. Bombay Nat. Hist. Soc. **73**: 403-407.

Witte, G.F. (1926): Les Crocodiles du Congo Belge. Rev. Zool. Afr. **14**: 65-81.

Yangprapakorn, U., Cronin, E.W., McNeeley, J.A. (1971): Captive breeding of crocodiles in Thailand. In: Crocodiles, Proc. 1st Work Meet. Crocodile Spec., New York, March 1971. New Ser. Suppl. Pap. **32**: 98-101. IUCN, ed.

Zijp, W.L. (1974): Handleiding voor statistische toetsen. Groningen, Tjeenk Willink, 283 pp.