

NESTING BIOLOGY OF *CROCODYLUS NOVAEGUINEAE* IN LAKE MURRAY DISTRICT, PAPUA NEW GUINEA

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ABSTRACT: The nesting of *Crocodylus novaeguineae* in Lake Murray District, Papua New Guinea is described, based on observations of 121 nests during 1980-1981. Cryptic nest location and wariness of adults inhibited nest discovery. Most nests (68.7%) were built on land, the remainder on floating mats of herbaceous vegetation. The breeding season was protracted, but 95% of nesting occurred in the November-May wet season. Sexual maturity, as evidenced by copulation in captivity, was attained at 1.4 m in females and 1.5 m in males. Oviposition by a captive individual occurred 68 days after mating. Estimated incubation period was 83-91 days. Mean clutch size (21.8 ± 6.9 SD, $n = 44$) did not differ between nests on land and floating mats, although mean egg mass ($103.5 \text{ g} \pm 5.6$ SD, $n = 426$) differed between nest types. Clutch size was highly correlated with female size ($r^2 = 0.77$) and clutch mass ($r^2 = 0.83$). Overall nest (86.7%) and hatching (85.4%) success differed significantly between nests on land and floating mats. Observer handling had no effect on nest success. The probability of an egg hatching in this population was 74.0%. Combined losses of nests to flooding and predation (varanids, feral pigs, humans) were 13.3%. The proportions of nest reuse and site reuse were 10.7% and 43.8%, respectively, with the majority of nesting females (74.4%) smaller than the size protected by law.

Key words: Papua New Guinea; Nesting biology; Clutch characteristics; Crocodylians; *Crocodylus novaeguineae*; Reproductive success; Philopatry

CROCODILES are a commodity of great economic and cultural value to the people of Papua New Guinea (PNG). Both the endemic New Guinea crocodile (*Crocodylus novaeguineae*) and the wide-ranging saltwater or estuarine crocodile (*C. porosus*) inhabit Lake Murray District, PNG. However, *C. porosus* is scarce in that region, comprising less than 1% of the local harvest (Hall, 1983).

Expatriot hunting of crocodiles in PNG began in the late 1940's (Whitaker, 1980a). However, prior to the arrival of European traders, Bosset villagers were harvesting crocodiles for Dutch missionaries in Irian Jaya (Bosset villagers, personal communication). Over two decades of unrestricted harvest followed before economic sanctions, in the form of licensing and upper size limits (51 cm commercial belly width), were established in 1969. A lower size skin limit of 17.8 cm was imposed in 1981. Downes (1971a,b, 1973) described

pre-legislative exploitation and others (Behler, 1977; Bolton, 1980; Lever, 1975; Neill, 1971; Whitaker 1890a,b) discussed its results.

Aside from observations by Neill (1946, 1971), wild crocodiles in PNG were largely unstudied until recently. This paper describes nesting of *C. novaeguineae* in Lake Murray District, based on research during 1980-1981.

STUDY AREA

Lake Murray District (20,562 km²) lies within Western Province of PNG. The Middle Fly and Lake Murray census divisions are subunits that formed the study area (Fig. 1). Human population density is 0.63 per km² (National Census, 1981). The area has a monsoon climate with pronounced wet (November-May) and dry (June-October) seasons which causes fluctuations of up to 3 m in water levels. Aspects of climate were reviewed by McAlpine (1971) and the CSIRO (1971) report provided details of the area's physiography.

Crocodile habitats were classified as

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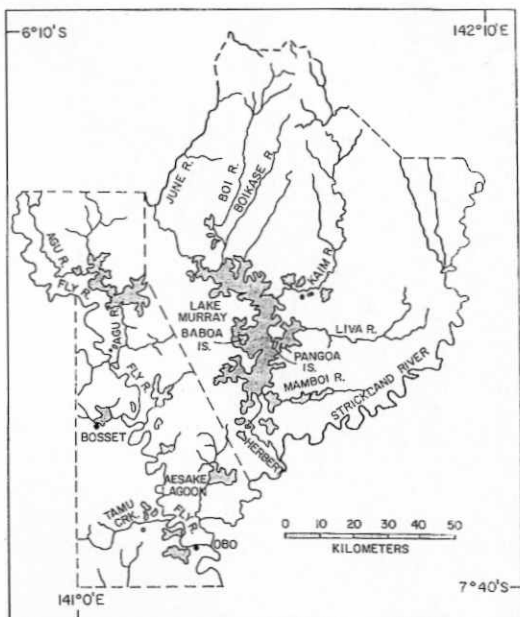


FIG. 1.—Map of study area showing the Lake Murray (right) and Middle Fly (left) subunits within Lake Murray District, Western Province, Papua New Guinea.

Echinochloa or *Saccharum-Phragmites* grass swamp, and mixed swamp woodland-forest (Paijmans, 1971).

Echinochloa grass swamp (*Leersia* grass swamp of Paijmans 1971, 1976) occurs throughout all creeks, lakes, lagoons, and rivers except the Fly, Strickland, and lower Herbert rivers. It is largely restricted to waters of <3.5 m depth, ranging 1.0–2.5 m in height above the water surface. Principal components of this grass swamp are *E. stagnina*, or *Polygonum orientale* and water couch grass (*Pseudoraphis spinescens*) associations along with beds of reed (*Phragmites karka*), sedge (*Thoracostachyum sumatranum*) and the fleshy herb *Hanguana malayana*. *Echinochloa* grass swamp is seasonally inundated and may be dry for several months a year.

Saccharum-Phragmites grass swamp (3.0–5.0 m tall) is characteristic of the Fly, Strickland, and lower Herbert rivers. It is scarce or absent in other localities. The association consists of cane (*S. robustum*) and reed (*P. karka*) along with grasses *Coix lacryma-jobi* and *E. stagnina*.

Mixed swamp woodland-forest is a generalized term for types of mainland growth described by Paijmans (1971). Canopy cover and understory vary widely in density and composition. This is the typical riparian habitat in the study area except for the upper Herbert (*Echinochloa* grass swamp) and the Fly between Obo to 15 km south of the Agu, which is lined by *Saccharum-Phragmites* grass swamp.

METHODS

Interviews were conducted to determine the hunting history, practices, and territories of all villages. Species distribution was determined from the literature, trade records, hunter communication, and personal observations. Harvest data were compiled from buyer and government files. A nest site was defined as a breeding area in which one or more nests occurred. A locality with multiple nests was regarded as a single site if successive nests were no more than 10 m apart. Nests and nest sites were found through hired informants. Nests were classified as incomplete (a partially constructed nest or a fully constructed nest without eggs), active (eggs in incubation), or inactive (posthatching). Eggshells were collected at inactive nests, and three eggs were removed from each active nest. These were returned to the laboratory for species identification and embryo aging (Hall, 1985): Eggs were marked and numbered on the dorsal surface to allow correct replacement and orientation within the clutch cavity. Active nests were visited at least twice to verify hatching date and to record nest and hatching success. Nest success (excluding indeterminate status nests) was calculated as the percentage of nests from which at least one egg hatched. Hatching success was defined as the proportion of eggs in successful nests from which young emerged. Probability of hatching was defined as the product of nest and hatching success. Sites found in 1980 were revisited in 1981 to determine rate of nest and site reuse. Nest reuse was calculated as the number of nests reused, divided by the

number examined for reuse. Site reuse was calculated in the same manner.

Belly width measurements refer to commercial belly width defined by PNG legislation (Parker, 1981): i.e., width across ventral and lateral scales between distal margins of the third transverse row of dorsal scutes. This distance represents about 70% of chest girth. Transformations of belly width measurements to total lengths (except where known) follow the regression equations (nos. 10–12, 39, 40) of Montague (1984).

The chi-square test was used to analyze count data, and most remaining data were analyzed with a two-tailed proportions test (z -statistic; Mendenhall, 1968). Wherever a t -test (two-tailed) was used, a modified test (t') was employed if the null hypothesis of equal variances was rejected (Ott, 1977). Results were considered significant at $P \leq 0.05$. Mean values are reported as ± 1 SD.

RESULTS

Nest Characteristics

Almost all nests encountered were those of *C. novaeguineae*. Including six sites in captivity, 95 nest sites (93 *C. novaeguineae*, 1 *C. porosus*, 1 unidentified) containing 123 nests (121 *C. novaeguineae*) were found. Nests were categorized according to whether on land or on floating mats of herbaceous vegetation. The former were those found in mixed swamp woodland-forest habitat and the latter were in *Echinochloa* grass swamp or *Saccharum-Phragmites* grass swamp. All nests were in areas subject to seasonal flooding. Therefore, classification as to type was based on the position of the nest at the high water level mark as the water supporting a floating mat nest would recede during the dry season. Most nests (70.2%) were located on land in mixed swamp woodland-forest habitat. The invaginated shorelines of Lake Murray formed numerous coves protected from wind and wave action where adjacent *Echinochloa* grass swamp appeared to offer shelter and food for hatchling pods. All but one floating mat nest was found in

Echinochloa grass swamp. Those nests were built on mixed or uniform beds of *Hanguana*, *Phragmites*, or *Thoracostachyum*. The remaining floating mat nest was found in *Saccharum-Phragmites* grass swamp. That habitat type also appeared to provide food and cover for juvenile crocodiles, but an assessment of its importance to nesting crocodiles was precluded by its inaccessibility. The vegetation of the associated backwater swamp may differ, but it was not known if nesting occurred there. Nest discoveries within the study subunits were probably biased in favor of the Lake Murray area due to greater hunter activity there. Also, most Middle Fly habitat is *Saccharum-Phragmites* grass swamp, which was inaccessible to humans and perhaps to adult crocodiles as well.

Both crocodile species in PNG build mound nests. The mean dimensions (cm) for active *C. novaeguineae* nests were as follows: length = 167.5 ± 35.2 ; width = 123.4 ± 15.6 ; height = 45.0 ± 7.5 , $n = 13$. Although these sizes are smaller than those reported for *C. porosus* (Cox, 1985; Webb et al., 1977), the range of values shows a nearly complete overlap between these species. The minimum distance between *C. novaeguineae* nest sites was 20–25 m. However, Cox (personal communication) found active nests as close as 10 m on the Sepik flood plains of northern PNG.

Nests were made from scrapings of surface litter and soil with fresh vegetation sometimes being used. Females appeared to be non-selective in the use of plant species except when nesting occurred in a *Thoracostachyum-Phragmites* bed where they avoided *Thoracostachyum*. No apparent relationship existed between nest size and clutch, egg, or female size.

Nests on land were slightly larger than those in floating mats, presumably due to ease of access to material and movement by females. The space from which scrapings had been made surrounding the nest averaged 64.5 ± 65.2 m² ($n = 12$). Webb et al. (1977) reported a mean value of 46.7 ± 1.2 m² for *C. porosus* nest sites in northern Australia.

Wallows were present at only three sites,

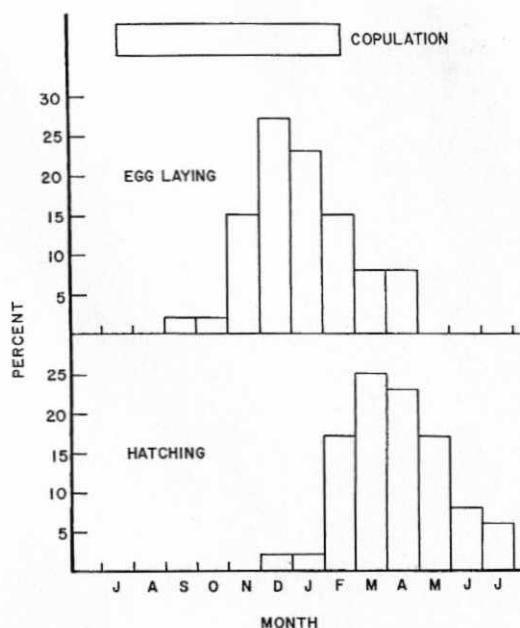


FIG. 2.—Observed annual reproductive cycle of *Crocodylus novaeguineae* at Lake Murray.

all of which were in floating mats. Mean nest distance relative to the horizontal high water mark (excluding nests in captivity or nests on floating mats) was 10.1 ± 13.0 m ($n = 76$). Such nests ranged up to 2 m vertically above the high water level.

Of the 115 *C. novaeguineae* field nests located, 36 were in floating mats and 79 were on land. The most frequently occurring plant genera at floating mat sites were, respectively: *Thoracostachyum*, *Phragmites*, *Hanguana*, *Cyperus*, and *Saccharum*. However, ranked by use in terms of comparative abundance, the order was: *Cyperus*, *Hanguana*, *Thoracostachyum*, *Phragmites*, and *Saccharum*.

Over 80% of all nests were either fully or partly overhung by surrounding vegetation. Nests on floating mats were significantly more exposed than those on land ($z = 4.48$, $P < 0.001$).

Few nests (13 of 121) were potentially visible from the air, and all were located on floating mats. No nests, including those known not to be obscured by vegetation, were seen during a fixed-wing aerial survey of habitat in February 1980.

All nests discovered by informants, excepting those from known or suspected nesting areas, were found by chance (81.2% of the total). At nearly half of these (41 of 95), the adult crocodile (or hatchlings) first saw or heard the informant, took flight, and revealed its position. Nests in floating mats were less likely to be found than those on land, despite offering greater visual access. Significantly fewer ($z = -3.47$, $P < 0.01$) of the former (16 of 36) were encountered during normal hunter activities compared to the latter (61 of 79). Almost all floating mat nests occurred in lakes or lagoons. Nests on land were found nearly equally along lakes/lagoons and creeks or rivers. A proportional bias (reflecting informant activity) toward the discovery of land-based nests existed for the lakes/lagoons subclass.

Inactive nests were usually recognizable at least 1 yr after use, and many for longer periods. However, nests made from *Phragmites* underwent rapid (<3 mo) deterioration. The oldest inactive nest was dated at 9 yr on the basis of informant knowledge.

The greatest age assigned to a specific site was 21 yr. Nesting occurred in 15 of those years. The other sites were used intermittently for 8 and 9 yr, respectively. Whether sites were used by more than one female was unknown.

Breeding Season

Reproductive activity occurred in all calendar months (Fig. 2). Most breeding occurred between September and December. Copulation between a pair of captive *C. novaeguineae* at Baboa on 10 November 1980 was followed by egg deposition 68 days later. Subsequent copulations were not observed, but they may have occurred prior to that date. Reproductive behavior among captive stock at Moitaka commenced 10–12 wk prior to oviposition. A broad overlap between egg laying and hatching periods existed. The earliest and latest laying dates of 48 clutches were 23 September and 28 April, respectively, with corresponding hatching dates of 18 December and 23 July. Over 95% of all laying occurred during the wet season and

was largely coincidental with the rise of the water table. A similar concentration of hatching activity was seen between February and May.

Incubation period was estimated at 83–91 days based on observations of nests monitored in captivity and in the wild. Based on other breeding records for southern PNG (Whitaker, 1980a), *C. porosus* probably maintained a similar reproductive cycle in the study area although its eggs require about 1 wk (± 5 days) longer to hatch (Bolton, 1980; Magnusson, 1979; Magnusson and Taylor, 1980). Spot temperatures of nests at a depth of 15 cm ranged from 28–32 C.

Neonates formed creches at hatching and several hatchling pods were caught by hunters, generally within three days of hatching. By the time crocodiles attained total lengths of 0.6 m, hunter catches were normally of single animals. Dispersal probably occurred within 2–8 mo after hatching.

Size at Breeding

The largest *C. novaeguineae* measured in this study were a 2.65 m (total length) female and a 3.35 m male, both breeding in captivity. Hunters routinely stated that this species commenced breeding at 30–38 cm belly width (1.5–1.7 m length). Sizes of attendant crocodiles seen by hunters were estimated at 43 nest sites and 74.4% were legal-sized (≤ 51 cm belly width, < 2.1 m) animals. A 41 cm belly width female (1.8 m) examined 14 October 1980 and a 43 cm belly width captive female (1.7 m) culled in January 1981 contained non-shelled oviductal eggs. Copulation in captivity was observed between a 33 cm belly width female (1.4 m) and a 1.5 m male.

Clutch Characteristics

Mean clutch size was 21.8 ± 6.9 ($n = 44$) with a range of 8–36. There was no significant difference ($t' = 0.49$, $P > 0.05$) between the size of clutches in floating mats (21.1, $n = 10$) and those on land (21.9, $n = 34$). Nor was there a significant difference ($t' = 1.01$, $P > 0.05$) in clutch sizes between active nests ($\bar{x} = 22.5$, $n =$

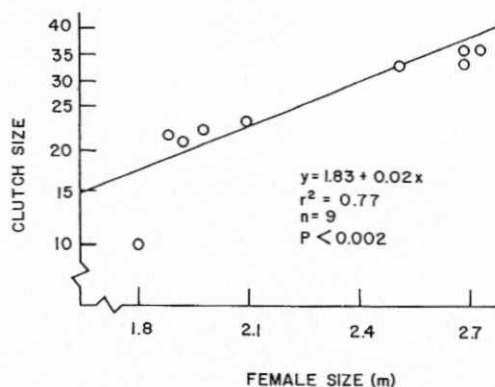


FIG. 3.—Relationship between clutch size ($\sqrt{}$) and female *Crocodylus novaeguineae* size (total length) at Lake Murray.

27) and nests where freshly hatched shells were collected ($\bar{x} = 20.5$, $n = 17$).

Mean linear dimensions (mm) and mass (g) of eggs ($n = 426$) were: axial length = 79.5 ± 2.8 (66.7–94.1); axial width = 46.8 ± 1.1 (35.5–53.7); mass = 103.5 ± 5.6 (59–140). Egg size differences between nest types were slight, but mean egg mass was significantly greater in nests on land ($t' = 7.62$, $P < 0.001$).

Clutch characters differed significantly

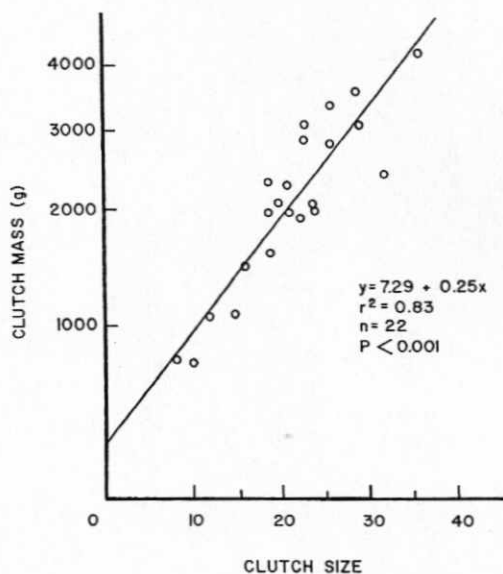


FIG. 4.—Relationship between clutch mass ($\sqrt{}$) and clutch size in *Crocodylus novaeguineae* at Lake Murray.

TABLE 1.—Number and percent of study nests by status category (F = failed, H = hatched, I = incomplete, X = indeterminate) and nest type (FLT = floating mat, LND = land based).

Nest type	Status				Total
	F (%)	H (%)	I (%)	X (%)	
FLT	0	21 (58.3)	1 (2.8)	14 (38.9)**	36
LND	11 (13.9)*	51 (64.6) NS	4 (5.1) NS	13 (16.5)	79
Totals	11 (9.6)	72 (62.6)	5 (4.3)	27 (23.5)	115

* Significant at $P < 0.02$.** Significant at $P < 0.01$ (Proportions test, Mendenhall, 1968).

from north-coastal *C. novaeguineae* (\bar{x} clutch = 34.7, Graham 1981; \bar{x} egg mass = 73.2 g, Cox, unpublished data) with respect to both clutch size ($t = -8.2$, $P < 0.001$) and egg mass ($t' = -46.7$, $P < 0.001$). Harvest returns independently indicated similarity in adult sizes between these populations, which are taxonomically distinctive (Hall, unpublished data).

Correlation analysis (Ott, 1977) indicated a strong positive relationship ($r^2 = 0.77$, $P < 0.002$) between clutch size and female size (Fig. 3). Although clutch mass rather than clutch size may be a better indication of female size (Deitz and Hines, 1980; Graham, 1981), the corresponding size of the female was determinable in too few instances for such analysis. However, there was a high correlation ($r^2 = 0.83$, $P < 0.001$) between clutch mass and clutch size (Fig. 4). Clutch mass of a 2.65 m female in captivity declined 5.3% between successive years while clutch size remained constant. She and her 3.11 m mate were exceptionally large, old individuals and neither clutch contained fertile eggs. This lends support to evidence that reproductive effort declines or ceases in older crocodylians (Graham, 1968, 1976; Joanen and McNease, 1980). Clutch mass was proportionally larger in smaller individuals and varied from 4–7% of adult female body mass. A significant ($r^2 = 0.14$, $P < 0.05$), but weak correlation between mean egg mass and clutch size was observed.

Reproductive Success

The proportion of nests from which some eggs hatched was 86.7% (Table 1) and greater at floating mat sites (100%) than at those on land (82.3%) ($\chi^2 = 4.28$, 1 df, $P < 0.05$). Limited access afforded

better protection to floating nests from predation by feral pigs (*Sus scrofa*), varanid lizards, and humans. There was no difference in nesting success between nests reused and those not reused ($\chi^2 = 0.05$, 1 df, $P > 0.05$) nor between nests at sites reused and nests at sites not reused ($\chi^2 = 0.54$, 1 df, $P > 0.05$). Nesting success also did not differ between inactive nests for which the status was known and nests opened by investigators ($\chi^2 = 0.57$, 1 df, $P > 0.05$).

The hatching rate of 445 eggs from 21 successful nests was 85.4% and significantly higher ($\chi^2 = 4.35$, 1 df, $P < 0.05$) at nests on land (87.1%) than on floating mats (78.1%). Poorer hatching success in floating mat nests may be related to water uptake within the clutch cavity. Despite lower hatching success, the probability of hatching (nesting success \times hatching success) in floating mat nests (78.1%) was significantly greater ($z = 2.60$, $P < 0.01$) than in nests on land (71.7%). The overall probability of an egg hatching in this population was 74.0%. Production in floating mat nests was 16.5 offspring per clutch compared to 15.2 young per clutch in nests on land.

Causes of Failure

The cause of nest failure ($n = 11$) was equally related to human activities and to predation by varanid lizards and wild pigs (91%), with the remaining 9% due to flooding. The overall loss totaled 13% and the effects of human (6%) and non-human (6%) predation as well as the effect of flooding (1%) were slight compared with other crocodylian populations. The pattern of mortality was more similar to the population of *C. niloticus* at Lake Rudolph

TABLE 2.—Comparative reproductive success of crocodylians nesting in the wild.

Species	(A) Nesting success	(B) Hatching success	(A × B) Probability of hatching	Principal cause of failure	Source
<i>Alligator mississippiensis</i>	0.756 (n = 266)	0.770*	0.582	predation—raccoon (<i>Procyon lotor</i>)	Joanen, 1969
	0.100 (n = 110)	0.700	0.070	predation—black bear (<i>Ursus americanus</i>)	Metzen, 1977
	0.615 (n = 13)	0.773 (n = 262)*	0.451	predation—raccoon	Goodwin and Marion, 1978
	0.731 (n = 26) 0.396 (n = 96)*	0.601 (n = 291) 0.506	0.439 0.200	predation—raccoon predation—raccoon	Ogden, 1978 Deitz and Hines, 1980
<i>Caiman yacare</i>	0.262	0.767*	0.201	predation—coati (<i>Nasua nasua</i>) crab-eating fox (<i>Cerdocyon thous</i>)	Crawshaw and Schaller, 1980
<i>Crocodylus acutus</i>	0.650 (n = 40)	0.483 (n = 333)	0.314	embryonic mortality; predation— raccoon	Ogden, 1978
<i>C. niloticus</i>	0.829 (n = 152)	0.828 (n = 6016)	0.686	predation—varanid lizards (<i>Varanus spp.</i>)	Graham, 1968
<i>C. novaeguineae</i>	0.867 (n = 83)	0.854 (n = 445)	0.740	predation—human and varanid liz- ards	This study

* Values differ from those published due to varying methods used by authors for reporting results.

(Graham, 1968) than to other crocodylians (Table 2).

Only 18 of 474 eggs (3.8%) were obviously dead (open and rotted) at the time of clutch inspection, and 45 eggs (9.5%) were recorded as viable but damaged with some containing desiccated embryos. The principle causes of egg failure were infertility and early cleavage death (approximately 10%).

Nest and Site Reuse

Only four available nests had been reused, either successively or in alternate years. Nest reutilization was 10.7% and did not differ between floating and land-based nests ($z = 0.22$, $P > 0.05$, $n = 56$).

Sites with a single nest were most common ($n = 71$). Multiple nests were found at 21 sites and significantly more often at floating mats ($\chi^2 = 7.89$, 1 df, $P < 0.005$). The presence of multiple nests at a site did not represent colonial nesting, because only one nest was ever active while the

remaining nests were from former years. Three sites were not examined for reuse. Site reusage was 43.8%. Sites on floating mats were reused more often (53%) than those on land (36%), but the difference was not significant ($z = 1.14$, $P > 0.05$). It is not known whether the same females reused nest sites.

DISCUSSION

Present distribution of *C. novaeguineae* within the study area was apparently identical with historical distribution. This species occurred throughout the Fly-Strickland river basins, including all major creeks, lagoons, lakes, and river systems.

The fact that most *C. novaeguineae* nests are recognizable for long periods is consistent with observations for *Alligator mississippiensis* (Joanen, 1969; McIlhenny, 1935), *C. acutus* (Ogden, 1978), and *C. porosus* (Deraniyagala, 1939; Webb et al., 1977).

The lack of a significant relationship

between nest size and clutch, egg, or female size has also been reported for *A. mississippiensis* (Metzen, 1977), *Caiman crocodilus* (Staton and Dixon, 1977), and *C. porosus* (Webb et al., 1977).

Hatching in this population is unlikely to occur later than mid-July, because most areas serving as nesting sites and nurseries are dry by September. Length of time between hatching and subsequent receding of water may govern the period of hatching creche maintenance.

The interval between copulation and oviposition in this species (10–12 wk) is comparable to that observed in other crocodylians: 9–10 wk for *A. mississippiensis* (Joanen and McNease, 1980), about 3 mo in *C. crocodilus* (Staton and Dixon, 1977), 9 wk in *C. johnstoni* (Compton, 1981), and 7–9 wk for *C. niloticus* (Modha, 1967).

Although not statistically significant, the difference in clutch size between active *C. novaeguineae* nests and nests where freshly hatched shells were collected (two eggs) suggests that females might eat infertile, rotten, or unhatched eggs during nest excavation, as do *C. niloticus* (Modha, 1967) and *A. mississippiensis* (Kushlan and Simon, 1981).

Mean clutch sizes of 27 (Greer, 1975) and 26 (Whitaker, 1980a) have also been reported for *C. novaeguineae*. Greer's data were confounded, because he regarded *C. mindorensis* as conspecific, and Whitaker's data were derived from captive stock where selection for larger animals was exercised. These references likely include both populations from the north and south coasts of PNG.

Like *C. novaeguineae*, clutch size of *C. niloticus* was significantly correlated ($r^2 = 0.73$ and 0.62) with female size (total length) (Graham, 1968; Greer, 1975). That relationship was not significant in either *A. mississippiensis* (Deitz and Hines, 1980; Joanen, 1969) or *C. crocodilus* (Staton and Dixon, 1977), where imprecise measurement and/or low sample size were cited. Very young breeding crocodiles may show disproportionately low reproductive effort, as do very old individuals. A 1.5 m *C. porosus* at Baboia laid a clutch of only two eggs in her first nesting season.

Metzen (1977) reported that observer monitoring had no effect on predation of *A. mississippiensis* nests. However, Deitz and Hines (1980) found raccoon (*Procyon lotor*) predation on alligator nests opened by investigators to be more than double that of those undisturbed. They believed concurrent use of nests by turtles as nesting sites may have increased predator detection. Another reason for that disparity may be related to length of time recording data (unspecified). Investigations exceeding 45 min may cause females to abandon their nest (Graham, 1976). Results of this study contradict Deitz and Hines' (1980:256) prediction that "manipulation of other crocodylian nests visited by olfactorily-oriented predators (such as varanid lizards) should also increase predation." These results support the contention that the effect of nest disturbance on *C. novaeguineae* is negligible when proper care is exercised, despite contrary fears.

The phenomenon of breeding site fidelity (Greenwood, 1980; Hilden, 1965; Newton, 1979; Wilson, 1975) led us and project associates to assume that adults would reuse a site if it remained undisturbed. Few sites were visibly affected by humans or other causes. A high turnover in breeding population was suggested, because few nest sites were reused prior to 1981. Females may have been killed or failed to breed due to unfavorable environmental factors or other reasons (lack of mate, senescence, sexually quiescent). Abandonment of one site in favor of another may have been occurring, but was unlikely because investigator handling had no effect on nesting success.

Quantitative data on nest and site reuse by crocodylians are scarce. Nest and site reuse for northern PNG populations of *C. novaeguineae* were 7.9% and 79.0% respectively, while values for *C. porosus* were 2.0% and 76.1% (Cox, 1985). Nest reuse by Louisiana *A. mississippiensis* was only 1.3% (Joanen, 1969) and site reuse by Botswana *C. niloticus* was 44% (Graham et al., 1976). Both the latter population and the one under study (43.8% site reuse) experienced prolonged unregulated exploitation until recently. However, anal-

ysis of Ogden's (1978) data on un hunted Florida *C. acutus* showed site reusage of 84.4%, even though some sites had been abandoned due to persistent human harassment. This reveals the extent harvest may dampen crocodilian reproduction if harvest is directed toward sexually mature animals.

The near lack of non-human mammalian predation (one nest was preyed on by feral pigs) may explain the high reproductive success in this population and the close parallel of findings with those of Graham's (1968) study of *C. niloticus* at Lake Rudolph. Losses due to flooding were inconsequential in either population.

This study indicates that sexual maturity in female *C. novaeguineae* may be reached at 1.4 m. Neill (1946, 1971) reported females nesting at 1.5 m. Reproduction by individuals below that length probably seldom occurs, but by 1.8 m (41 cm belly width) most females may be regularly breeding. The mean annual harvest in the study area was estimated at 7000 during 1980-1981 (Hall, 1983). This represents a minimum of 444 clutches at the observed probability of hatching. However, animals of 1.8-2.1 m size (41-51 cm belly width) comprised about 10% of the harvest (Hall, unpublished data). Assuming that 40-50% of the adult segment are female, an annual turnover of 280-350 breeding females (63-79%) needed to sustain the harvest is indicated. Thus, the small proportion of nesting females in this population may reflect high reproductive success and large harvest of sexually mature individuals.

PNG legislation was designed to protect breeding crocodiles of both species over 51 cm belly width and 2.1 m total length. Nearly 75% of nesting females in this study were below that size, and a proposal for uniform size limit reduction to 40 cm was made to promote biologic and economic recovery (Hall, 1983). Montague (1983) and Cox (1985) made similar suggestions based on independent evidence.

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