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Influence of Water Level, Hunting Pressure and Habitat Type on Crocodile Abundance in the Fly River Drainage, Papua New Guinea

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ABSTRACT

Between October 1978 and July 1980, day and night crocodile surveys were conducted at low, normal and high water levels over 2703 km of river and lakeshore in the Western and Southern Highlands provinces of Papua New Guinea. The 1353 crocodiles seen ranged between 0·18 and 2·23 animals per km.

Night counts recorded 12·9 times as many crocodiles as day counts over the same area. This may indicate more nocturnal activity than occurs in other crocodilians. Unhunted areas had a greater proportion of large crocodiles than did hunted regions. As the water level rose, the 'visible juveniles' category decreased as a result of migration into newly flooded adjacent swamplands. The upstream range of New Guinea crocodiles on the Strickland River extended only to the Burnett River junction.

There was an increase in flight distance with increasing body size and this rate of increase was over twice as large for hunted populations as for unhunted ones.

INTRODUCTION

Due to habitat destruction and excessive exploitation, many countries with crocodile populations have banned or restricted hunting and/or trade

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in these animals. In Papua New Guinea (PNG), however, the harvest of crocodile skins is not only a major, but also an expanding, industry.

In the eastern half of the large island of New Guinea, vast areas of prime crocodile habitat are considered to be too remote to be subject to serious harvest pressure (Medem, 1976). This could be assumed to be especially true of the 96 400 km^2 Western Province where there are only 65 000 people and 90 km of permanent roads (Ford, 1973). It is possible to fly over hundreds of kilometres of rivers, swamps and lagoons without seeing a dwelling.

The crocodile population in PNG is judged to be between 100 000 and 200 000 (Pooley, 1976) and the annual harvest of skins is estimated to be between 25 000 and 50 000 (IUCN, 1978).

In many villages, crocodile hunting is the only source of cash income. Of the crocodiles harvested, 75–95% are usually the New Guinea or freshwater crocodile *Crocodylus novaeguineae* with the remainder being the saltwater crocodile *C. porosus* (Lever, 1975; Whitaker, 1980).

The New Guinea crocodile was discovered only 50 years ago (Schmidt, 1928) and is one of the least known of the world's 20 or so crocodilians. It is believed to be restricted to the main island of New Guinea (Lever, 1975; Whitaker, 1980). Neill (1946) has stressed the need for research into the species' population dynamics and habitat preferences. In addition, Pooley (1976) has emphasised that it is essential to test the assumption that the current harvest is not excessive in relation to the present population.

A crocodile hunting and skin industry is likely to be part of Papua New Guinea's commerce for years to come. A Food and Agriculture Organization of the United Nations (FAO) project PNG/74/029 'Assistance to the Crocodile Skin Industry' was established to guide exploitation over the period 1977–1981. Although it has been stated (Gore, 1978) that the New Guinea crocodile is the only crocodilian not in danger of extinction, this opinion has not been verified nor have basic population data been determined.

If a proper management policy can be established for crocodiles in New Guinea, it is felt that this will be a contribution to crocodilian conservation programmes everywhere. The present study was conducted from 22 October 1978 to 18 July 1980 in the Southern Highlands and the Western Provinces of Papua New Guinea. It was designed to determine: (1) the population distributions and density indices of both species of crocodiles; (2) their age and size structure; (3) the extent of habitat utilisation at various water levels; and (4) the effects of hunting pressure on flight distance with guidelines for crocodile management.

STUDY AREA

The areas surveyed (Table 1) were located between latitude 5°19′S and 7°58′S and between longitudes 140°55′E and 142°34′E on Lake Murray, the middle Fly River and its major tributaries including the Strickland River (Fig. 1). Lake Kopiagu, the highest point studied, is situated 1349 m above sea level. The Strickland River Gorge, at the highest point surveyed on the main river, is 370 m above sea level and ranges in width from 1 m in the Kagwezi Chasm to over 800 m wide in its lower reaches. The average depth is 9 m and flow rate 11–12 km h^{-1} (Paijmans *et al.*, 1971).

The gorge, upper and middle regions of the Strickland River (Fig. 1) had not been fully explored prior to this survey. In the Strickland Gorge, the river drops from 388 m to 100 m over a 100 km course. This steep fall within the river's narrow width produced almost continuous rapids, some perhaps the largest anywhere. In addition, water temperatures there ranged 3–4 °C lower than on the lower Strickland. Within the gorge and 436 km from the mouth, a 6 m waterfall may have been a physical barrier to upstream crocodile dispersal.

The upper Strickland extends downstream from the gorge. It drops from an elevation of 110 m to 50 m and has no adjacent swamplands. Its shoreline is soft gravel or sandstone. Its tributaries, the Burnett, Murray, Carrington and Cecilia Rivers, are clear, fast, boulder-strewn, mountain streams. The Damami is a typical lowland river.

On the next section downstream, the middle Strickland, sand and clay substrate replaced the stone and gravel of the upper streambed. Shore areas were generally shallow and muddy, with protected coves containing many fallen trees. In this section the current was slow and the course twisted.

Lake Murray is 750 km^2 and irregularly shaped (Fig. 1). Lying roughly at the centre of the study site, it averages 7 m in depth, fluctuating by up to 3 m between most wet and dry seasons and up to 5 m during 7-year drought years (1958, 1965, 1972, 1979) (Roberts, 1978). In the wet season the area of Lake Murray may be enlarged five times (Wheeler, 1979).

Surprisingly, among world streams only the Amazon and the Congo

TABLE 1

Location and Description of Waterways Surveyed, Southern Highlands and Western Provinces, Papua New Guinea, 1978–1980

Waterway	*Location*	*Bank vegetation*[a]	*Water levels*[b] Low	Normal	High
Agu River	141°7′E, 7°5′S[c] to 74 km upstream	Savanna, swamp forest	×	×	×
Aiema River	142°E, 7°6′S[c] to 30 km upstream	Rainforest	×		
Boi River	141°25′E, 6°50′S[c] to 22 km upstream	Rainforest	×	×	×
Damami River	142°4′E, 6°13′S[c] to 6 km upstream	Rainforest	×		
Fly River, middle	141°7′E, 7°5′S to 141°23′E, 7°35′S	Savanna	×	×	×
Fly River, lower	141°23′E, 7°35′S to 141°52′E, 7°58′S	Savanna, rainforest	×		
Herbert River	141°34′E, 7°20′S[c] for entire length	Savanna	×	×	×
June River	141°21′E, 6°20′S[c] to 51 km upstream	Savanna, rainforest	×	×	×
Kaim River, upper	62 to 104 km upstream	Rainforest	×		
Kaim River, lower	141°32′E, 6°54′S[c] to 62 km upstream	Savanna, rainforest	×	×	×
Lake Kopiagu	142°32′E, 5°23′S (centre) (4 km around lake)	Croplands	×		
Lake Murray	141°30′E, 7°S (centre) (87 km N.W. shore)	Swamp forest	×		
Leva River	141°36′E, 7°S to 20 km upstream	Swamp forest	×		
Mamboi River	141°2′E, 7°10′S[c] to 44 km upstream	Swamp forest	×		
Nomad River[d]	142°8′E, 6°19′S[c] to 142°14′E, 6°18′S	Rainforest	×		
Rentoul River	142°4′E, 6°21′S[c] to 142°8′E, 6°19′S	Rainforest	×		
Strickland River, gorge	142°19′E, 5°19′S to 142°10′E, 5°47′S	Rainforest	×		
Strickland, upper	142°10′E, 5°47′S to 142°5′E, 6°38′S	Rainforest	×		
Strickland, middle	142°5′E, 6°38′S to 141°34′E, 7°20′S	Rainforest	×		
Strickland, lower	141°34′E, 7°20′S to 141°23′E, 7°35′S	Gallery rainforest	×	×	×
Tomu River	142°7′E, 6°37′S[c] to 6 km upstream	Rainforest	×		

[a] After Paijmans *et al.* (1971).
[b] At the time(s) of (mostly nocturnal) surveys.
[c] Coordinates of the river mouths.
[d] Day counts only.

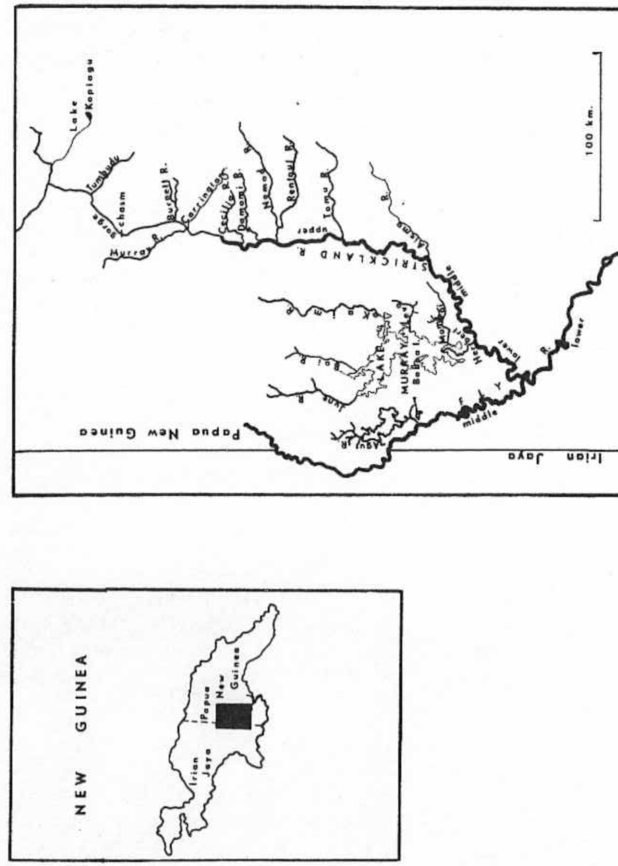

Fig. 1. Waterways of the study area in the Southern Highlands and Western Provinces of Papua New Guinea.

are greater in volume than the Fly (Roberts, 1978). The Fly's width ranges from 250 to 920 m in the study area and has a 4–5 km h^{-1} speed. Its bed is only 19 m above sea level at a point 800 km from the mouth. Both the Strickland and the Fly flood 2 m or so above their banks during the wet season. Their water temperatures range from 21·7 °C in the Strickland Gorge to 31·0 °C in Lake Murray.

The local climate (Paijmans *et al.*, 1971) is mild tropical with a mean annual temperature of 26·7 °C, a diurnal temperature range of 8·3 °C, and a mean monthly variation of only 2·2 °C. Maximum temperatures of 31–35 °C occurred daily in the early afternoon. Rainfall at Lake Murray averages 325 cm $year^{-1}$ but could be as high as 500 cm $year^{-1}$ on the upper Strickland River. Rainfall is greatest during the somewhat warmer and less humid January to June period. Relative humidity is high, with monthly means ranging from 80 % in the wet season to 90 % during the dry.

During 1979, the sun shone 342 days (recorded at Baboa by the crocodile station manager) for an average of 4·5 h day^{-1} (3·9 and 5·2 h day^{-1} for the January–June and July–December periods respectively).

The soils of rivers and swamps are alluvial clays while those of extensive floodplains are high in organic matter, with sloppy alluvial clay. All of the study area below the Tomu River on the Strickland River is without visible rocks or stones. The substrate on the upper Strickland, near the beginning of the gorge, is mainly granite or limestone.

The vegetation in the upstream Fly River areas, north of the bulge toward Irian Jaya and upstream from the Herbert/Strickland junction on the Strickland River, is open rainforest-woodland. The swamp regions near the river are characterised by dense sago palm *Sago sago* stands. South of those points, the vegetation was primarily marsh-grass *Gracilius indicus* and wild sugar cane *Saccharum robustum* with thin strips of swamp forest and waterlogged open rainforest. The back swamps (flooded areas away from the river) were mostly *Melaleuca* savannas (Brandes, 1929; Paijmans *et al.*, 1971).

Exploratory expeditions in the past reported that nocturnal sightings and/or signs of crocodiles were plentiful on the middle Fly River drainage but few crocodiles were seen during the day (Bauerlen, 1886; Everill, 1886; Hurley, 1924; Hides, 1936; Archbold & Rand, 1940). Commercial hunting for crocodile skins began in 1948 and by the mid 1950s was a firmly established industry in the area. Most hunting was by the indigenous peoples who traded skins with expatriate skin-buyers for salt

and cartridges. Until 1966, the area supplied 5000–7000 skins per year, primarily adults of both species (Bustard, 1968*a*; Whitaker, 1980). After that year, crocodiles became scarce both on the middle Fly River and in Lake Murray (Neill, 1971; Lever, 1975; G. Craig, pers. comm.).

METHODS

All surveys except for Lake Kopiagu and the gorge, upper and middle sections of the Strickland River, were made from one of two square-ended flat-bottomed boats, either a 5·6 m aluminium craft with a 35 hp outboard motor or a 6·6 m wooden barge with two 25 hp outboards. Lake Kopiagu was investigated from a hand-paddled 5 m dugout canoe. The Strickland Gorge was explored using two 5 m inflatable white-water boats with steerage oars. The upper and middle Strickland counts were made from a 4 m inflatable runabout with a 25 hp motor. In addition to studies by boat, a portion of the upper Strickland River was surveyed from Iroquois helicopters.

Studies were carried out at high, normal and low water levels which roughly corresponded to the months of February–April, June–August, and September–December, respectively. The night surveys began a half-hour after complete darkness. Since wave size was found (Woodward & Marion, 1979) to be negatively correlated with night sightings for the American alligator *Alligator mississippiensis*, surveys were not conducted on windy nights. At the beginning of each survey the name of the observer(s), operator, boat and motor, starting location and time, water level, and weather conditions (moon brightness and/or cloud cover, rainfall, air and surface water temperature) were recorded. Upon completing a night count the stopping location, time, and distance covered were recorded.

The tapetum of the crocodilian eye reflects bright red when exposed to a light at night (Chabrek, 1966; Whitaker & Whitaker, 1978; Woodward & Marion, 1979), thus permitting them to be counted. The light used for all but one night count was a 12-volt, 100 watt, hand-held, sealed-beam light powered either by a 12-volt wet-cell battery or a Honda EM 300 portable generator. Lake Kopiagu was surveyed with a 6-volt headlamp. The 12-volt light was effective to 300 m, while the 6-volt's range was limited to 75 m.

The spotlight illuminated the watercourse for navigational as well as counting purposes. On rivers 100 m or less in width, the survey craft was operated in midstream and the light was oscillated in front of the boat from bank to bank in an arc of approximately 180°. On the rivers over 100 m wide and on lakes, the boat was operated 30–50 m off one shore and the light was oscillated in a 120° arc from mid-river to the near bank perpendicular to the boat. A fairly constant cruising speed of 18–22 km h^{-1} was maintained.

The observer sat in the bow of the boat behind a safety rope, while the boat-handler sat in the stern near the motor(s). The light was held ahead of the boat's bow in the hope that this would prevent the craft from becoming visible to the crocodile. The majority of all surveys were made with the same boat-handler/observer combination, as was suggested by Chabrek (1966) and Woodward & Marion (1979). It was necessary for the observer to wear eye protection due to the numbers of flying insects.

When a crocodile was spotted, the observer vibrated the beam at the crocodile's location as a signal to the operator. Without stopping or reversing the boat, the animal was then approached as closely as possible, following an arc that went first next to the shore and then extended toward mid-stream. This pattern was followed in order to prevent having to reverse back out into the mainstream after each sighting. When a crocodile was spotted, the observer dictated on a small tape recorder the time of the sighting, the side of the river, the flight distance, if possible, the species of crocodile, the animal's size and the habitat situation. The flight distance has been described (Heathwole, 1968; Bustard, 1968*b*; Webb & Messel, 1979) as the distance a potential predator (here, the observer and boat was substituted) can approach a prey before the latter flees.

Salt-water crocodiles were distinguished from New Guinea crocodiles by their sleeker appearance, lighter colour, sharper scute-crests and lack of ossified scutes on the dorsal portion of the neck between the nuchal rosette and the skull plate (Neill, 1971; Lever, 1975; Whitaker, 1979, 1980).

Field estimates of a crocodile's size are based on the distance between the eyes and the snout tip (Chabrek, 1966; Graham, 1968; Messel *et al.*, 1977). Since it was the standard and familiar reference used in PNG, the size was recorded in classes of inches belly-width (bw) (Lever, 1975). The belly-width size categories used were: ≤4 in (10·2 cm) (hatchling), 5–6 in (12·7–15·2 cm), 7–9 in (17·8–22·9 cm), 10–12 in (25·4–29·5 cm), 13–15 in (33–38·1 cm), 16–19 in (40·6–48·3 cm), 20–24 in (50·8–61 cm) and ≥24 in (61 cm). The ranges of the belly-width categories were progressively increased for each larger size class because the possibility of mistaking the size of a crocodile is greater with bigger animals (Messel *et al.*, 1977). Those above 20 in bw were considered to be adults (Tago, 1977) and their maximum known belly width was 34 in in the wild. An 'eyes only' (EO) category was given to crocodiles that submerged before being classified or which were in shallow water (designated 'S') or among obstructions ('O') which prevented close approach.

The habitat location upon initial observation was classed according to a system modified from Messel *et al.* (1978): (1) MS (mid-stream), where crocodiles were well out from shore in water so deep that their limbs could not contact the substrate, (2) SWOE (shallow water on edge), where the animals were in open water near shore and presumably could touch bottom, (3) OB (on bank), where they were on bare soil between the water's edge and the line of vegetation, (4) IV (in vegetation on shore), (5) IVIW (in emergent vegetation in the water), (6) ILIW (in logs in the water), where crocodiles lay among dead wood. Crocodiles seen feeding or exhibiting unusual behaviour were so noted.

Day counts, which were conducted the day before the night counts, were similar to these except that animals were not approached. If a crocodile was spotted, the time, species and belly width were recorded. Where crocodile 'slides' were seen on the bank, the belly-width was estimated from marks in the mud or soil.

RESULTS

Distribution and abundance

Very few crocodiles could be identified to species. Data for New Guinea and saltwater crocodiles were necessarily grouped together.

The night count conducted on Lake Kopiagu revealed no crocodiles (Table 2), a result confirmed by local Duna people.

The Strickland Gorge was surveyed for 30 km downstream from the Tumbudu River Junction from inflatable white-water boats and revealed no crocodiles. After the white-water expedition ended, helicopter flights over the rest of the gorge still disclosed no crocodiles above the Burnett River (Fig. 1).

Two adult New Guinea crocodiles were seen at the Burnett Junction. Tom Hoey (pers. comm.) also found crocodiles on an extensive foot patrol along the Burnett River in 1970. Keith Tetley (pers. comm.) had

TABLE 2

Number of Crocodiles Seen During Low-Water Night Counts on the Unhunted Gorge, Upper and Middle Portions of the Strickland River, Western and Southern Highlands Provinces, Papua New Guinea, 1979

Area	*Numbers*	*Distance (km)*	*Crocodiles per km*	*Sizes in inches (cm) belly-width*								
				≤4 (10·2)	*5–6 (12·7–15·2)*	*7–9 (17·8–22·9)*	*10–12 (25·4–29·5)*	*13–15 (33–38·1)*	*16–19 (40·6–48·3)*	*20–24 (50·8–61)*	*>24 (61)*	*EO*[a]
Lake Kopiagu	0	4										
Strickland River, gorge	0	95										
Strickland River, upper	166	136	1·22	4	33	37	24	8	8	9	7	36
Strickland River, middle	479	215	2·23	29	136	91	52	14	18	19	9	111
Damami River	8	6	1·33		3	1	1			1		2
Rentoul River	5	12	0·42		2	1	1	1				
Tomu River	1	6	0·16		1							
Aiema River	2	30	0·07		1			1				
Totals	661	504	1·6[b]	33	176	130	78	24	26	29	16	149
Percentages	100			5·0	26·6	19·7	11·8	3·6	3·9	4·4	2·4	22·5

[a] 'Eyes only' no estimates of size possible (but judged to include a preponderance of large animals, see text).
[b] Average density index only for stretches containing crocodile populations.

made the same observation in 1968. Though no evident barriers to crocodile range expansion occurred there, the upstream limit of New Guinea crocodiles on the Strickland River was evidently in this region at a 110 m elevation.

Downstream on the upper Strickland, the Damami River was the first tributary in which crocodiles were recorded (density index 1·33 km^{-1}, Table 2). The crocodile density index on the upper Strickland was 1·22 km^{-1}. Only a day count could be conducted on the Nomad River (Fig. 1, Table 1) but three adult crocodile slides were noted, indicating that a breeding population occurred there.

Crocodile numbers of 2·23 km^{-1} on the middle Strickland (Table 2) were the highest found during the study. Except for the Damami, tributaries of the upper and middle Strickland (Table 2) had lower density indices (0·42, 0·16 and 0·07) than the main river (1·22 and 2·23).

All crocodiles positively identified during night counts on the upper and middle Strickland were New Guinea crocodiles. But two belly slides of 100 and 125 cm width were seen at km 195 and no wild New Guinea crocodiles of that size have been recorded. It may be, therefore, that saltwater crocodiles range as far upstream.

No crocodile hunting was known to occur in the gorge, or on the upper and middle Strickland River and its tributaries (Table 2). Hunting was practised, however, during low water on the lower Strickland; this area, with a density index of 1·66 crocodiles km^{-1}, was similar to the remaining portion of the study area in that it had vast areas of adjacent swamplands. Several large saltwater crocodiles were seen there during day counts, though none were identified at night.

Lake Murray, with a density index of only 0·09 crocodiles km^{-1} of shoreline, had the lowest (and probably most-depleted) crocodile stocks (Tables 3 and 4). Many of that lake's tributaries, including the Boi, Lower Kaim and Leva Rivers (Fig. 1) with crocodile density indices of 0·32, 0·29 and 0·30 km^{-1}, respectively, were judged to have been overhunted. Other streams entering that lake, such as the upper Kaim, June and Mamboi Rivers, nevertheless had considerably higher crocodile density indices (0·76, 1·51 and 1·0 crocodiles km^{-1}, respectively). These low population densities corresponded to areas of known high hunting pressure.

Crocodile numbers were much lower (0·35 crocodiles km^{-1}) on the middle Fly River and its tributary the Agu River (0·43 crocodiles km^{-1}) than on the otherwise similar habitat of the lower Fly River (1·8 crocodiles km^{-1}) where hunting pressure was much lower (Table 3). Except for Lake

TABLE 3

Numbers of Crocodiles Seen During Low-Water Night Counts on Hunted Areas. Western Province, Papua New Guinea, 1978–1980

Area	*Numbers*	*Distance (km)*	*Crocodiles per km*	*Sizes in inches (cm) belly-width*								*EO*[a]	*Hunting pressure*[b]
				≤4 (10·2)	*5–6 (12·7–15·2)*	*7–9 (17·8–22·9)*	*10–12 (25·4–29·5)*	*13–15 (33–38·1)*	*16–19 (40·6–48·3)*	*20–24 (50·8–61)*	*>24 (61)*		
Agu River	32	74	0·43	7	11	7	1	1	1			4	2
Boi River	9	22	0·41	4	1	2		1				1	2
Fly River, lower	116	129	1·8[c]	30	52	13	2	3		2	1	13	1
Fly River, middle	28	160	0·35[c]		9	7	4	1				7	3
Herbert River	22	36	0·61	5	8	3	1			1		4	3
June River	77	51	1·51	30	14	11	2	3	2	4	1	10	1
Kaim River, lower	18	62	0·29	4	6	3		1		1		3	2
Kaim River upper	32	42	0·76	9	6	8	5	1				2	1
Lake Murray	8	87	0·18[c]		3	3			2				3
Leva River	6	20	0·30	1	2	3							3
Mamboi River	44	44	1·00	17	10	1	2	3	1			10	2
Strickland River, lower	59	71	1·66[c]	15	33	9				1	1		1
Total	451	798	0·83[c]	122	155	70	15	14	6	10	3	54	
Percentages	100			27·0	34·4	15·5	3·8	3·1	1·6	2·2	0·7	12·0	

[a] See Table 2.
[b] Hunting pressure was judged to lie between 0 (trace–nil) and 3 (severe year round hunting) based on general knowledge of the area.
[c] Density indices doubled from counts of one streambank.

TABLE 4

Summary of All Low-Water Night Crocodile Counts. Western and Southern Highlands Provinces, Papua New Guinea, 1979–1980

	Numbers	*Distance (km)*	*Crocodiles per km*[b]	*Size in inches (cm) belly-width*								*EO*[a]
				≤4 (10·2)	*5–6 (12·7–15·2)*	*7–9 (17·8–22·9)*	*10–12 (25·4–29·5)*	*13–15 (33–38·1)*	*16–19 (40·6–48·3)*	*20–24 (50·8–61)*	*>24 (61)*	
Total	1112	1302	1·09	155	331	200	95	38	32	39	19	203
Percentages	100			13·9	29·8	18·0	8·5	3·4	2·9	3·5	1·7	18·3

[a] See Table 2.
[b] Density index only for stretches containing crocodile populations and includes counts doubled from one streambank.

Murray, the middle Fly River was the most overhunted waterway on the study area (Table 3).

Size and age composition versus hunting pressure

Size (age) composition of the crocodile population was markedly different on unhunted and hunted areas (Tables 2, 3 and 4). Only 5% of the population in the unhunted areas were ≤4 in bw (about 40 cm body length, Fig. 2) while in hunted areas these small crocodiles averaged 27%. Sub-adults (10 in–19 in bw) comprised 19·3% of the population on the upper and middle Strickland but only 8·2% on the hunted areas. The proportions of animals in the ≥20 in bw and EO classes were 29·3% versus 14·9% for unhunted and hunted regions, respectively.

The upper and middle Strickland populations were primarily of adults and sub-adults and exhibited a low rate of reproduction. Indicating a stable condition, these two areas were judged to be at historic population levels. This was in marked contrast to the hunted regions (Table 3) where almost 77% of the crocodile population were <10 in bw, indicating a

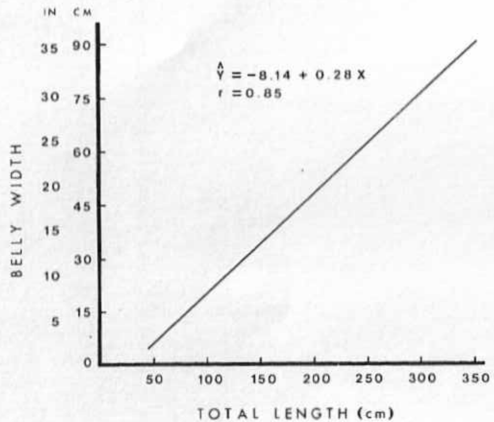

Fig. 2. Relationship of belly-width (Lever, 1975) to total length based on measurements of 500 New Guinea crocodiles captured in Western Province, Papua New Guinea, 1979–1980.

population far below habitat carrying capacity. Reduced numbers, seemingly due to hunting by the local people, were evident in all size classes <10 in bw. Adults of known breeding size (≥20 in bw) comprised only 2·9% of the population, although much of the 12% EO class would probably add to the total of mature animals. These proportions, nevertheless, were much lower than the 6·8% known adults and 22·5% EO for the unhunted upper and middle Strickland areas (Table 2).

Water-level effects

Seasonal changes in water level had a marked effect on the numbers of crocodiles seen and possibly on crocodile densities. High-water numbers per kilometre of shoreline were 56% below and low-water counts were 46% above those recorded during periods of normal water levels (Tables 3, 4, 5 and Fig. 3). While counts of crocodile belly slides (Fig. 3) were a poorer indicator of abundance than night counts and were useless during high water, they do indicate that crocodiles moved out of adjacent swamplands and were more concentrated in rivers during low water. Changes in water level also affected the distribution of crocodile by size class. In high water, 38·6% of the visible population (including EO) were <10 in bw (Table 6) but during low water were only 23·1% (Table 3). Larger crocodiles seemed to stay in the rivers regardless of water level while smaller ones tended to disperse into adjacent flooded swamps.

Night counts versus daytime tallies

Since 12·9 times as many crocodiles were seen at night than during the day (Table 7, Fig. 4), day counts were weak representations of crocodile abundance. Day counts (Table 8) favoured the sighting of large crocodile slides. Seventy-three per cent of the slides seen were from animals ≥10 in bw while in the corresponding low-water night counts over the same area, only 23·1% of the population (including EO's) were ≥10 in bw. Big crocodiles were simply easier to see during the day than were small ones. But slides showed a more realistic distribution of the larger size classes than did either of the live crocodile survey types.

The number of crocodiles seen on one bank of a river during 23 night counts involving 534 crocodile sightings were not significantly different (two tailed 't' test, $\alpha = 0{\cdot}05$, Steel & Torrie, 1980) from the number seen on the other bank.

TABLE 5

Numbers of Crocodiles Seen During Normal Water-Level Night Counts on Hunted Areas. Western Province, Papua New Guinea, 1978–1980

Area	*Numbers*	*Distance (km)*	*Crocodiles per km*	*Sizes in inches (cm) belly-width*								*EO*[a]	*Hunting pressure*[b]
				≤4 (10·2)	*5–6 (12·7–15·2)*	*7–9 (17·8–22·9)*	*10–12 (25·4–29·5)*	*13–15 (33–38·1)*	*16–19 (40·6–48·3)*	*20–24 (50·8–61)*	*>24 (61)*		
Agu River	18	74	0·24		1	3	1	1	3	1		8	2
Boi River	16	22	0·73	3	5	2	1	1	1			3	2
Fly River middle	16	160	0·20[c]	2	10	1				1		2	3
Herbert River	11	36	0·31	1	3	4	1			1		1	3
June River	42	51	0·85	15	6	5	5	1		1		9	1
Kaim River, lower	16	62	0·26	7	5				2	2		2	2
Strickland River, lower	49	71	0·69	9	19	4			2	4		11	1
Total	168	476	0·39[c]	37	49	19	8	3	8	8		36	
Percentages	100			22	29·1	11·3	4·8	1·8	4·8	4·8		21·4	

[a] See Table 2.
[b] See Table 3.
[c] Density indices doubled from counts of one streambank.

TABLE 6

Numbers of Crocodiles Seen During High-Water Night Counts on Hunted Areas. Western Province, Papua New Guinea, 1978–1980

Area	*Numbers*	*Distance (km)*	*Crocodiles per km*	*Sizes in inches (cm) belly-width*								*EO*[a]	*Hunting pressure*[b]
				≤4 (10·2)	*5–6 (12·7–15·2)*	*7–9 (17·8–22·9)*	*10–12 (25·4–29·5)*	*13–15 (33–38·1)*	*16–19 (40·6–48·3)*	*20–24 (50·8–61)*	*>24 (61)*		
Agu River	2	74	0·027									2	2
Boi River	7	22	0·32			2	1	1	1			3	2
Fly River, middle	3	160	0·038[c]					1		1		1	3
Herbert River	6	36	0·17	1	1				1	2		1	3
June River	11	51	0·22	5	1			1	1			3	1
Kaim River, lower	3	62	0·048							2		1	2
Strickland River, lower	40	71	0·56	14	11	3	1	2				9	1
Total	72	476	0·16[c]	20	13	5	2	5	3	5		20	
Percentages	100			27·8	18·1	6·9	5·6	6·9	1·4	6·9		27·8	

[a] See Table 2.
[b] See Table 3.
[c] Density indices doubled from counts of one streambank.

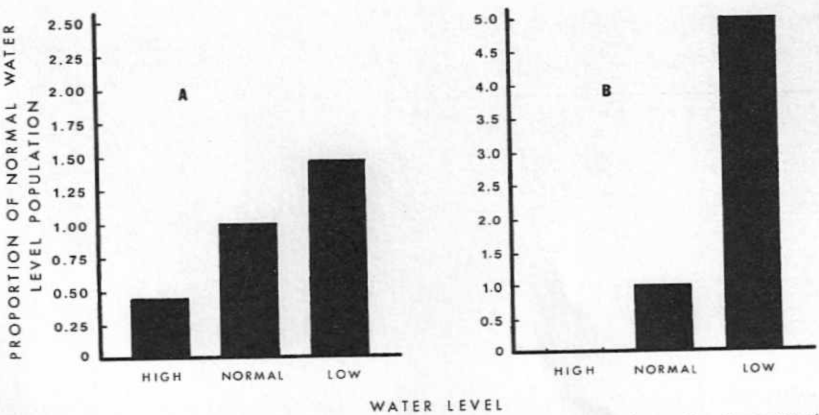

Fig. 3. The relative abundance of crocodiles during each of three water-level periods on seven rivers as based upon (A) night counts (N = 484 crocodiles) and (B) day counts of belly slides (N = 255 slides), Lake Murray district, Papua New Guinea, 1978–1980.

TABLE 7
Summary of All the Crocodiles Seen During All Night Counts, Western Province, Papua New Guinea, 1978–1980

	Total	*Distance (km)*	*Crocodiles per km*	*Size in inches (cm) belly-width*								*EO*[a]
				≤4 (10·2)	*5–6 (12·7–15·2)*	*7–9 (17·8–22·9)*	*10–12 (25·4–29·5)*	*13–15 (33–38·1)*	*16–19 (40·6–48·3)*	*20–24 (50·8–61)*	*>24 (61)*	
Numbers	1353	2703	0·50	212	394	224	105	46	43	52	19	259
Percent	100			15·7	29·1	16·6	7·8	3·4	3·2	3·8	1·4	19·0

[a] See Table 2.

TABLE 8
Percentages by Size-Class of Crocodiles and Belly Slides as Determined from Low-Water Day Counts on Seven Rivers, Papua New Guinea, 1978–1980

	Sizes in inches (cm) belly-width							
	≤4 (10·2)	*5–6 (12·7–15·2)*	*7–9 (17·7–22·9)*	*10–12 (25·4–29·5)*	*13–15 (33–38·1)*	*16–19 (40·6–48·3)*	*20–24 (50·8–61)*	*>24 (61)*
37 crocodiles	5·4	2·7	18·9	13·5	—	18·9	10·8	29·7
301 crocodile slides	7·0	5·6	11·6	15·3	12·3	26·2	19·6	8·6

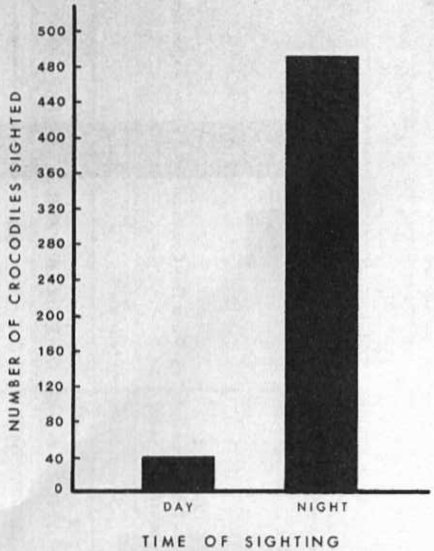

Fig. 4. Relationship between the number of crocodiles sighted by day and night on seven rivers, Western Province, Papua New Guinea, 1978–1980.

Habitat use

General preferences

The habitat locations in which crocodiles were most commonly sighted were, in decreasing order of use (Table 9), SWOE, IVIW, OB, MS and least frequently, IV category. The three that were used most, where 76·2 % of the crocodile population were seen, were the SWOE, IVIW, and ILIW. While no surveys were conducted to indicate precise habitat availability, they were judged to be in the decreasing order: MS, IV, SWOE, IVIW, OB, and ILIW. Considering that it was probably the least available, ILIW seemed to be the most preferred habitat location. Almost every time that a clump of deadwood was seen during a night count, it had crocodiles in it. In contrast, only 0·9 % of the population were seen in the IV location which was the second most common in the environment.

TABLE 9

Habitat Locations of Different Size Crocodiles for All (47) Night-Light Surveys, Western Province, Papua New Guinea, 1978–1980

Size (belly width) in inches	Numbers seen	Percentages of crocodiles in each size class per habitat location[a]						
		MS	*SWOE*	*OB*	*IVIW*	*IV*	*ILIW*	*% Total*
≤4 (10·2 cm)	202	1·5	34·7	16·8	28·2	1·5	17·3	100
5–6 (12·7–15·2 cm)	272	1·1	34·2	22·1	20·9	0·0	21·7	100
7–9 (17·8–22·9 cm)	143	3·5	30·1	17·5	25·1	0·0	23·8	100
10–12 (25·4–29·5 cm)	59	8·5	35·5	16·9	9·2	1·1	28·8	100
13–15 (33·0–38·1 cm)	30	33·3	33·3	10·0	10·0	3·4	10·0	100
16–19 (40·6–48·3 cm)	27	18·5	25·9	18·5	22·3	0·0	14·8	100
20–24 (50·8–61·0 cm)	33	27·3	24·2	6·1	27·3	0·0	15·1	100
>24 (61·0 cm)	13	15·4	61·5	7·7	7·7	0·0	7·7	100
EO[b]	176	13·1	33·0	7·4	22·2	1·1	23·2	100
Total	955	6·8	33·9	16·0	22·3	0·9	20·0	100

[a] MS (mid stream); SWOE (shallow water on edge); OB (on bare bank); IVIW (in vegetation in water); IV (in vegetation on land); ILIW (in logs in water).
[b] See Table 2.

During any one night, an average of 16·9 % (16·0 % OB and 0·9 % IV) of the population were seen on land. On the upper and middle Strickland areas, 17·4 % of the crocodiles were on land. Only 13·3 % were seen on land, though, during low-water surveys in hunted areas.

Preferences related to belly size

When the size classes of crocodiles in each habitat situation are compared with the average in those habitats (Table 9), it becomes apparent that:

(1) Larger crocodiles (> 12 in bw) were more likely than smaller ones to be found in mid-stream.
(2) Juvenile crocodiles (< 12 in bw) were twice as likely than the rest of the population (not including EO) to be in the ILIW situation.
(3) Juveniles were more evident on bare banks than adults and sub-adults.
(4) The SWOE, IVIW and IV locations were utilised about equally by all size segments of the population.
(5) The EO class most closely resembled the 'over 24 in' class, as also found by Messel *et al.* (1977). But the large percentage of EO in the IVIW situation probably indicates that some juveniles were also seen 'eyes only'.
(6) The 'zero sightings' of four size-classes in the IV situation may not be significant but there is evidence (see beyond) that they were absent, not merely hidden, by foliage.

Preferences related to water-level

When the percentages of crocodiles in each habitat situation are compared with changes in water level (Fig. 5), it can be seen that:

(1) Use of the IVIW and IV location increased as water levels rose.
(2) Use of the SWOE location was negatively correlated with water level.
(3) The same proportion of the crocodile population was seen in mid-stream regardless of water levels.
(4) Crocodiles used bare banks (OB) and fallen trees (ILIW) locations more at normal water level than at any other time. The low and high water usages were about the same for OB but use of ILIW was greater during low water.

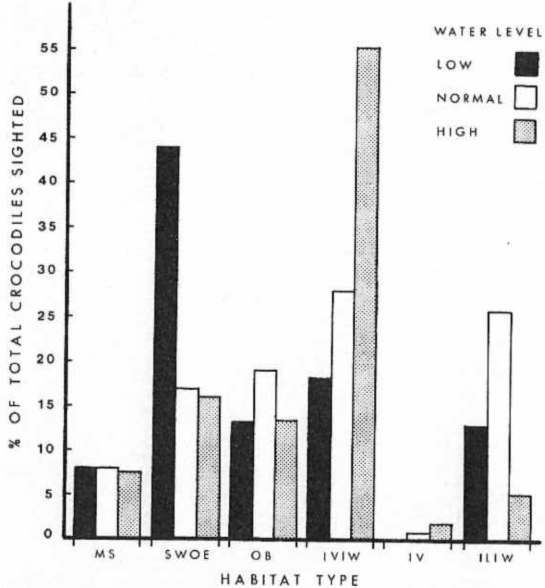

Fig. 5. Percentages of crocodiles sighted in each habitat location in relation to water level. Data are from three surveys on the same portions of seven rivers. Lake Murray district, Papua New Guinea, 1978–1980. (See Table 9 for key to habitat type.) (N = 401 crocodiles.)

Wariness

There is an increase in flight distance with increasing crocodile size (implying age and experience) and with hunting pressure (Fig. 6). The average flight distance increases from 2·5 m and 3·5 m for the ≤4 in bw class, to 25·0 m and 52·4 m in the 20–24 in bw size class, respectively, for unhunted and hunted populations. When a least squares regression (Neter & Wasserman, 1974) is plotted of crocodile size against flight distance, the rate of increase in flight distance for the hunted population is 2·2 times that of unhunted populations (Fig. 6). Evidently, hunting pressure was over twice as important as age in determining flight distance.

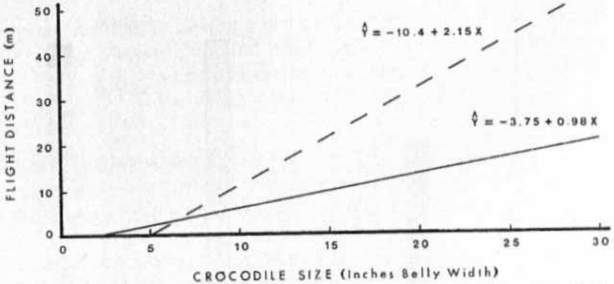

Fig. 6. Relationship between crocodile size and flight distance on unhunted (solid line, N = 241) and hunted areas (dashed line, N = 389), Western Province, Papua New Guinea, 1978–1980.

The average approach distance of the several size classes ≥16 in bw was similar to that of the EO class, which presumably indicated that these EO sightings mainly were larger crocodiles, which further supported Messel *et al.* (1977, 1981).

The percentage of crocodiles in each size class approached to within 1 m or less (Fig. 7), the distance at which a village crocodile hunter would

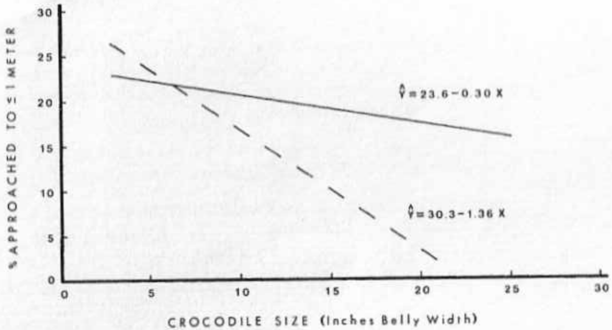

Fig. 7. Relationship between the percentage of crocodiles approached to within 1 m or less ('sure kills') and the animal's size on unhunted (solid line, N = 193 crocodiles) and hunted (dashed line, N = 322 crocodiles) regions, Western Province, Papua New Guinea, 1978–1980.

have nearly 100 % success with spears or harpoons, ranged from 35·0 % and 27·2 % for the ≤4 in bw size class to 0·0 % and 9·5 % in the 20–24 in bw size class for hunted and unhunted populations respectively. It can be seen (Fig. 7) that hunting pressure had a greater effect than size in determining flight distances of 1 m or less. The slope of the hunted population's regression line was over 4·5 times as steep as the one from the unhunted areas. Comparing this proportional difference of 4·5 to the 2·2 in the regressions plotting flight distance against size (Fig. 6) indicates that hunting pressure was $4{\cdot}5/2{\cdot}2 = 2{\cdot}05$ times as important in determining the percentage of approaches ≤1 m in each size class than it was in determining flight distances in general.

CONCLUSIONS

Distribution and abundance

The absence of crocodiles in Lake Kopiagu and the Strickland Gorge seems likely to be due to a scarcity of forage fishes rather than to physical obstacles or high altitudes. Fish are the largest part of a crocodile's diet (Cott, 1954; Corbett, 1960) and local Duna tribesmen reported (in conversation) that Lake Kopiagu declines to a mere mud hole during drought years. Roberts (1978) found that fish also were scarce in the mountainous regions of the upper Fly River, an area similar to the Strickland Gorge.

Since it has been found that fish diversity and numbers increase as one travels down the Fly, a river similar to the Strickland (Roberts, 1978), this may be correlated with the continuous increase in crocodile density observed on the latter. The crocodile density index on the upper Strickland was $1{\cdot}22\,km^{-1}$. The middle Strickland, the next section downstream, had an index of $2{\cdot}23\,km^{-1}$. This change in the density index from 1·22 to 2·23 is an 83 % increase. If this rate of increase can be extrapolated so as to apply to the lower Strickland, an index of about $4\,km^{-1}$ would occur rather than the 1·66 found in the survey. If that extrapolation is justified, a considerable reduction in the crocodile population, probably due to hunting, may be indicated. At present in PNG, streams with two or more crocodiles km^{-1} must be considered to be maintaining healthy populations. The density index of 2·23 animals

km^{-1} however, is not impressive when compared with some other crocodilian populations. Neill (1971) reported an American alligator density index of 9·3 km^{-1}. Nile crocodiles *C. niloticus* numbered 20 km^{-1} on Ethiopia's Awash River (Cott & Pooley, 1972). Graham (1968) reported 56 crocodiles km^{-1} on portions of Lake Turkana in Kenya. Aside from this last location, though, many of the high densities reported in the literature were for shorter distances than surveyed on the middle Strickland. Isolated exceptional index levels could have yielded inflated results due to encounters with one or more atypical groups of crocodiles.

The lack of adjacent swamplands on the upper and middle Strickland may be a reason that crocodile densities were much lower on the tributaries than on adjacent portions of the main river (Table 2). Low water in the upper regions presumably would affect the tributaries first as opposed to the swamplands in the lower areas. Crocodiles probably move out of the tributaries of the upper reaches during periods of low water much as the crocodiles lower down move out of the swamplands.

Crocodiles were plentiful in Lake Murray during the 1940s and 1950s (Bustard, 1968*a*; Neill, 1971) and supported densities (G. Craig and Kune', tribesmen, pers. comm.) that were higher than any of the lake's tributaries. If Lake Murray did have a greater density index than the 1·51 km^{-1} (Table 3) noted for its June river tributary, then the crocodile population in the lake has been reduced by about 88% (1 − 0·18/1·51) from its original level.

Crocodiles seem to be making a comeback on the lower Fly River and, to a much lesser degree, on the middle Fly and Lake Murray. Bustard (1968*a*) and Neill (1971) reported sighting only four crocodiles per night on the lower and middle Fly River and one per night on Lake Murray in 1967, yet the present study revealed density indices of 1·8, 0·35, and 0·18 crocodiles km^{-1} on these respective areas. This improvement probably results from the National Crocodile Project's efforts toward better legislation, public education and management.

While some of the rivers and Lake Murray had low crocodile stocks, there was some evidence that additional crocodiles occurred in the lagoons and backwaters. The low water surveys of over 1302 km of river and lakeshore on this study area resulted in a count of 1331 crocodiles (Table 4). Messel *et al.* (1981) suggested that 63% of crocodiles actually present are seen on night counts. If this percentage is accepted, it could be concluded that actually there were (1331/0·63) 2113 crocodiles present. In this same area in 1980 alone, however, 2002 small live crocodiles plus approximately 1100 skins were taken out. Undoubtedly, the permanent swamplands adjacent to the main navigable areas yielded the additional animals. Furthermore, the saltwater crocodile's primary habitat is riverine and not flooded backwaters (Lever, 1975). The low percentage of this species in the harvest would be a further indication that much hunting probably takes place in backwater areas.

Saltwater crocodiles were undoubtedly scarce in the Lake Murray District. Of 2002 small live crocodiles purchased on the study area in 1980, only 1·1% were saltwater crocodiles (Balson, 1980). If captive saltwater crocodiles were available, especially as mature specimens, then even a small-scale restocking programme might increase this species population above its critically-low level.

Habitat use

That juvenile crocodiles dispersed into flooded areas during high water (Tables 3 and 6) was also determined by Chabrek (1965), who observed that juvenile American alligators tend to disperse with increasing water levels. Juvenile crocodiles may suffer harassment (Messel *et al.*, 1981) and even cannibalism (Nichols *et al.*, 1976) from larger members of their species. Hence, small crocodiles may tend to seek sanctuary in areas away from large crocodiles when suitable habitats are made available by flooding.

The fact that 12·9 times (Fig. 4) as many crocodiles were seen at night as by day may explain why early explorers into the middle Fly drainage reported seeing few live crocodiles during the day despite the many belly-slides present. Chabrek (1966) reported that between 5 and 12% of American alligator populations were seen on land during night counts in Louisiana. His figure closely approximates the 16·9% observed in this study. Lang (1979) also found that American crocodiles *C. acutus* spend most of their on-land time at night. Crocodiles in the study region were a reclusive group that were seldom out of the water except at night.

The low values (0·9%) in the vegetated (IV) location may have been affected by poor visibility due to foliage. Yet since the proportions of on-land (OB and IV) sightings were not below those on-land sightings for other crocodilian species may indicate that crocodiles IV were not being overlooked.

Juvenile crocodiles were more likely to be found OB than were adults and sub-adults, because young crocodiles tend to seek warm places (Lang, 1981) to a greater degree than larger crocodiles. Also, large crocodiles have more difficulty moving on land than do small ones.

The use of the mid-stream (MS) habitat type by mainly larger-sized crocodiles was also observed by Messel *et al.* (1977, 1981). The smaller crocodiles may be reluctant to leave the safety of near-shore cover and to venture out into the open water with its dangers of inter- and intra-specific predation (Nichols *et al.*, 1976; Valentine *et al.*, 1972). Large crocodiles, on the other hand, have no predatory enemies in New Guinea other than man.

Juvenile crocodiles (≤ 12 in bw) utilised ILIW habitat more than larger crocodiles probably because the smaller size-class feeds heavily on the schools of small fish (Corbett, 1960) that frequent brushy areas.

Evidently, the differential utilisation of habitat types with changing water level was more the result of changes in availability and accessibility of habitats rather than changes in habitat preference. The MS category was the only habitat location whose availability was not altered by fluctuations in water level. And, there was no significant difference in the use of MS across water levels (Fig. 5).

As water levels rose, SWOE locations became IVIW. It seemed likely that as the water level beyond the line of emergent aquatic plants became too deep for crocodiles to rest their feet or tails on the substrate, they moved back into the vegetation near shore where they could touch bottom. The decrease in the proportion of crocodiles found SWOE was balanced by a corresponding increase in the proportion using IVIW (Fig. 5).

The slight increase in the use of the IV habitat with rising water levels probably resulted from the fact that walking distance to on-land vegetation from the water's edge was shorter as water rose. The small proportion of the population using ILIW habitat in high water probably resulted from the fact that as the water came up, dead wood either floated away or became submerged. Likewise, when the water level was down, many woody snags and brush piles were left out of the water. The amount of ILIW habitat available was greatest during normal water levels when falling trees on the bank of a river were not likely to be carried away nor to fall short of the water. Normal water was when the greatest proportions of crocodiles were found in the ILIW type (Fig. 5).

Wariness

Flight distance data (Fig. 6) indicate that wariness in New Guinea and saltwater crocodiles (Webb & Messel, 1979) was a learned response which increases slowly with age under natural conditions. But wariness resulting from an unpleasant experience associated with boats, motors, lights and/or people was in addition to that mentioned above. The hatchling (≤ 4 in bw) class was an exception to this trend because they were more wary in the unhunted area (Figs 6, 7 and Webb & Messel, 1979). This phenomenon may be the result of hunters not attempting to catch small crocodiles and thus imparting no unpleasant experience by their activities.

Hunting pressure was 2·05 times as important as size in determining approaches ≤ 1 m (Fig. 7) than it was in determining flight distances in general (Fig. 6). Once a flight distance is achieved which allows crocodiles to escape hunters, evidently there is little value in extending the flight distance further.

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