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African Dwarf Crocodiles in the Likouala Swamp Forests of the Congo Basin: Habitat, Density, and Nesting

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Strip-transect methods were used to assess distribution and density of the dwarf crocodile, *Osteolaemus tetraspis osborni*, in a pristine region of the Likouala swamp forest, east of the Batanga River, northern Congo Republic, during the 1995 and 1996 dry seasons. Surveys by day were undertaken to locate the presumably solitary animals that occupied the few remaining permanent pools. The cumulative percentage of inhabited pools (n = 34) was a function of the perpendicular distance of the center of the pool from the transect line. The effective distance was 19.5 m (strip width = 39 m). Strip surveys covered a linear distance of 28.36 km and yielded a total of 57 "permanent" pools, subjectively deemed suitable for crocodiles. Eight pools were associated with nests guarded by an attendant female. Crocodiles were not found in the interior of swamp forests but were limited to a peripheral zone, approximately 2.5 km wide, adjacent to terra firma forest. Within this zone minimum population density was calculated at one per 3.62 ha (0.28 crocodiles per ha).

THE dwarf crocodile, *Osteolaemus tetraspis* Cope, 1861, is endemic to lowland equatorial rain forests of west and central Africa. Although it is primarily a deep-forest species, most observations have concerned populations that occur in forested rivers (Waitkuwait, 1989; Kofron, 1992); this simply reflects the inherent difficulties of studying crocodiles living in heavily vegetated wetlands. *Osteolaemus* occurs in 17 countries, yet all but one report concern observations on rivers; mangroves and swamp areas are only mentioned in Gabon (Waitkuwait, 1989). Schmidt (1919) suggested that the eastern subspecies *O. t. osborni* inhabits shallow river margins bordered by swamps, although such rivers can become reduced to muddy pools during the dry season.

Waitkuwait (1986, 1989) described *Osteolaemus* as a denizen of pools in periodically flooded swamp forests, where it frequently used burrows beside the waterline. Some individuals also inhabited isolated pools in savannah. Dwarf crocodiles apparently made nocturnal, terrestrial forays after rains, returning to their pools afterward.

Two subspecies of the monotypic genus *Osteolaemus* are thought to exist. The western subspecies (*O. tetraspis tetraspis*) ranges from Senegal to Angola, whereas the other (*O. t. osborni*), a Congo basin form, is centered upon northeastern Democratic Republic of the Congo (formerly Zaire). The ecology of both subspecies is poorly known. Habitat destruction and hunting for meat have severely depleted *O. tetraspis* populations in the western part of this range (Kofron and Steiner, 1994). However, the status of the Congo subspecies is unknown, even though thousands are captured annually in the northern Likouala swamp forests of the Congo Republic for markets in Brazzaville (Behra, 1990; Agnagna et al., 1996). Clearly population estimates are urgently needed to make sensible decisions about this species' harvest.

In 1995, we undertook a reconnaissance of the Likouala swamp forests which was followed by a detailed survey in 1996. We determined population estimates based on the density of small pools inhabited by adult *Osteolaemus* in the dry season. Here we present our conclusions regarding the habitat utilization and population status of this species in a prime habitat.

MATERIALS AND METHODS

Study area.—The study was conducted in the Likouala swamps, a 62,500 km² sedimentary basin that straddles the equator with 60% of the region either permanently or periodically inundated (Burgis and Symoens, 1987; Hughes and Hughes, 1992). The flat, alluvial plains are at an altitude of 300–350 m with ferraltic, hydromorphic alluvial soils having an acid pH and low fertility. West of the Oubangui River were swamp forest, flooded forest, limited terra firma forest, and seasonally inundated savannahs (Blake, 1993; Fig. 1B). The vegetation was swamp thicket and swamp forest interspersed with *Raphia* thicket (Begue, 1967; Hughes and Hughes, 1992). The meteorological data for Impfondo (1°40′N; 18°4′E), near to the study area, give an annual precipitation of 1793 mm with the dry season extending from late December to March/April. Average monthly precipitation in the dry season was 104 mm compared

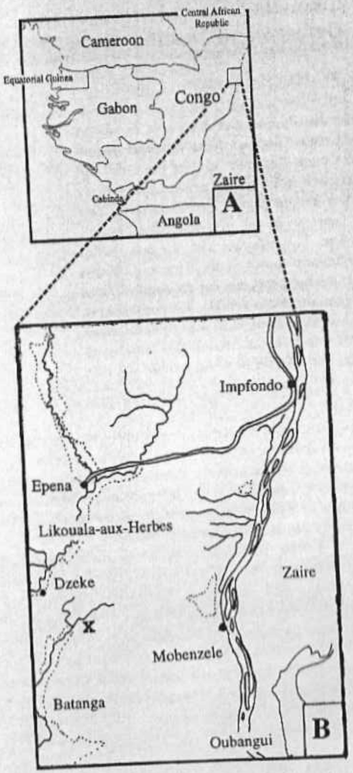

Fig. 1. (A) The Impfondo/Mobenzele study area (inset square), within the Congo Republic. (B) Impfondo in relation to the road to Epena, the Likouala-aux-herbes River, and its tributary the Batanga River. The center of the 1996 study area (X) is indicated and the dotted lines demarcate savannahs.

to 173 mm in the wet season. The mean temperature was 25 ± 1 C (Begue, 1967).

Permanent bodies of water were scarce at the height of the dry season even though the terrain remains perpetually waterlogged (Fig. 2A–B). In the wet season, forests flooded to a depth of at least 0.5 m and although small islands of dry ground are occasionally seen, these are never more than a few meters in diameter, except for the transition zones to terra firma forest near villages (Blake, 1993). The swamps were drained south by the Likouala-aux-Herbes River, running roughly parallel to the Oubangui River and our study area lay between these two rivers and close to the Batanga River (Fig. 1B).

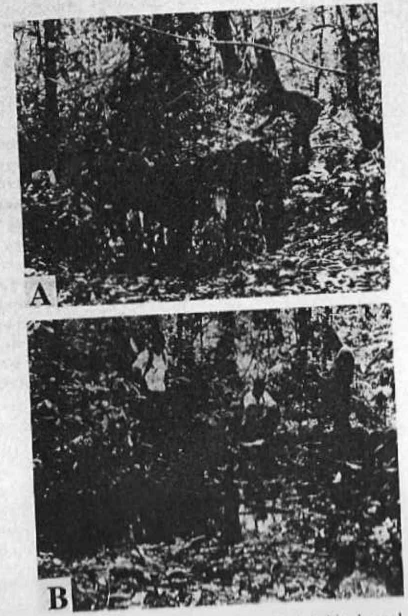

Fig. 2. (A) A typical crocodile-inhabited pool. There was evidence of tracks around this pool, but water was turbid next to the burrow which had been excavated under tree roots overhanging the left hand side of the pool. (B) A complex of two pools. Unusually the burrow system containing the crocodile had been excavated from within the smaller pool (bottom right) under tree roots (right, not visible), although both pools were very turbid.

Habitat survey.—Major vegetational zones within the study area were drawn directly from the 1963 Carte de L'Afrique Centrale 1/200,000 map (feuille Mobenzele NA-33-VI)) and shown in Figure 3. The positions of transects were determined by Garmin 750 GPS readings taken in small forest clearings whenever feasible since the entire region was blanketed by dense, mostly closed-canopy forest; at least one location per transect was attempted (Fig. 3).

Census methods.—Because visibility in swamp forests was limited, crocodiles were counted by day when they occupied the few remaining permanent pools (Fig. 2A–B). Pools contained partially flooded burrows that were excavated beneath the roots of bordering stilt-rooted trees. Visual clues to a crocodile's presence included turbid water resulting from the animal's recent activity and tracks leading from the pool for up to 20 m. These were particularly obvious over boggy terrain and between adjoining pools. Confirmation was obtained by locating the burrow entrance and probing with a long spear to detect the crocodile within.

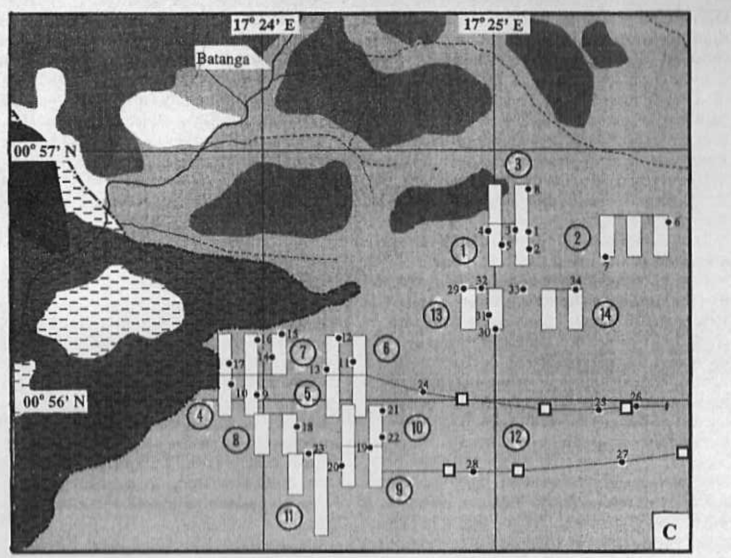

Fig. 3. Detail of the 1996 study area with the addition of part of Lac Mboukou (black, top left) shown connected to the Batanga River via a narrow channel. Transects (circled numbers 1–14) are shown with each crocodile-inhabited pool marked by a numbered solid circle. Transect 12 indicates the parallel transects to the interior of the swamp forest and the square symbols are GPS locations taken en route. The grid lines are seconds of latitude and longitude and each square has a 1.86 km side. Terra firma forest (= dark grey) and savannah (= white), parts of which may be seasonally inundated (= horizontal hatch) are shown together with swamp forest (= light grey).

Even after heavy rains and partial flooding during the second census period, permanent pools were still obvious. Flooding also emphasized crocodile tracks, although the criterion of water turbidity was a less reliable indicator of crocodile presence in a pool. Pools with adjacent nests were recorded.

Transects.—Following a pilot survey in 1995 to become acquainted with the area, we surveyed during two sampling periods (28 March to 2 April and 12–28 April, 1996) by using fixed transect-width methods. Each transect included three local hunter/observers and the senior author. To facilitate orientation in the dense forest, all transects were either N–S or E–W.

In a typical strip transect, each arm was surveyed by three observers walking abreast, approximately 10 m apart, followed by the senior author. A 300-m baseline was laid from west to east and left in situ for the duration of a transect. At its east end another 300-m long transect, perpendicular to the first and either north or south, was followed by a 100-m transect E–W, and finally a parallel transect of 300 m north or south back to the baseline. The latter was followed to the 100-m marker, and the process was repeated back to the origin. Distances were measured from a 300-m surveying line which was secured to vegetation at intervals. A band at least 30 m wide was slowly surveyed, a typical block was defined by a square of 330 m on a side, and the total linear distance surveyed by any one observer was 1700 m. If rain fell continuously, transects were abandoned but were resumed to completion the following day. For convenience, some transects utilized both sides of a single baseline, and in two transects the baseline was extended by 200 m (Fig. 3). In the southernmost block, a 600-m transect to the south was made to avoid overlap with a previously surveyed area north of the baseline (Fig. 3). Censuses were undertaken between 1000 and 1500 h.

The dimensions of permanent pools were measured to the nearest 0.5 m. A rough sketch was made of the occupied pool and burrow, and its relationship to any neighboring pools. The length and direction of any tracks were also recorded. To calculate the detection distance, we measured the perpendicular distance from the nearest edge of an occupied pool to the transect line, but to calculate population, density we used the distance from the center of an occupied pool and the distance along the transect.

Osteolaemus nests.—Nests were particularly conspicuous in swamp forest habitats. Nest guarding occurs (Waitkuwait, 1989), and to avoid undue disturbance, no attempt was made to find the attendant female in the adjoining pool or burrow. The top of the nest was excavated sufficiently to confirm the presence of eggs, but these were not handled or counted and were immediately repacked under dry leaf mold. We measured nest height above water level and the length of the slope up which the female had pushed vegetation from the adjacent pool during nest construction.

Limit of crocodile distribution.—A strip transect was undertaken into the swamp interior extending due east beyond the common baselines of transects 5 and 6 (numbered 12 in Fig. 3). A 30-m wide tract was surveyed as before but the positions of pools/nests were estimated with reference to infrequent GPS fixes (denoted by square symbols in Fig. 3). The outward route was followed for an estimated 3 km beyond the last crocodile (No. 26), and the return transect was made on a parallel tract 300 m to the south.

Estimation of minimum total crocodile number.—The major vegetational zones of the Mobenzele map were overlaid onto tracing paper and the swamp forest zone was subdivided to calculate the area of each habitat in km² (Table 1). We then derived a rough estimate of crocodile abundance for swamp forests by assuming that all the dwarf crocodile populations resided within the 2.5-km wide, peripheral band of swamp

TABLE 1. THE AREAS OF MAJOR VEGETATIONAL ZONES WITHIN THE MOBENZELE MAP, WEST OF THE OUBANGUI RIVER. The two areas underlined represent the swamp forest domains thought to harbor the bulk of the *Osteolaemus* population.

Vegetational type	% of total area	Area (km²)
Savannah	13.1	870
Terra firma forest	30.9	2048
Swamp forest	27.2	1625
Permanently inundated swamp forest	13.5	897
2.5-km band of swamp forest bordering terra firma forest	13.3	883
2.5-km band of permanently inundated swamp forest bordering terra firma forest	1.9	123
Total	100	6625

forest bordering gallery terra firma forests. The estimated area of swamp forest, and the density of crocodiles as determined from line transects, were multiplied to extrapolate a population estimate for the region.

RESULTS

Osteolaemus-inhabited pools.—Of the 39 swamp-forest crocodiles found (5 in 1995; 34 in 1996), 38 inhabited pools, 37 of which were judged to be permanent. There was no evidence in the surveyed area (i.e., burrows or tracks) to indicate that crocodiles habitually hid anywhere else during the day. Crocodiles were rarely seen abroad in this survey. One crocodile was glimpsed briefly while at a pool surface. Another, with a total length of 40 cm and possibly a two-year-old juvenile, was caught while probing a burrow in a pool that was surrounded by tracks evidently made by a much larger crocodile. The combined lengths of every new trail walked by individual observers in 1995/96 totaled at least 150 km, and only one dwarf crocodile was ever found outside of a pool (in 1995, close to the common baseline of transects 1 and 3), walking at about 1500 h. Another animal, a nest-guarding female (also from the 1995 study) occupied a very shallow, temporary, leafy pool, about the size of a crocodile and adjacent to its nest.

Maximum pool depth rarely exceeded 1 m, but the uneven, soft bottom precluded accurate measurement. Excluding crocodiles, pools contained little noticeable animal life, apart from neustonic arthropods such as pond-skaters (Gerridae), whirligig beetles (Dytiscidae) and fisher spiders (Pisauridae) and, occasionally, small fish. Three small catfish (Clariidae; *Clarias* sp.) were caught for identification. Typically, occupied pools ($n = 34$) were small: 28 pools had a maximum dimension of < 5.3 m (mean $= 2.6 \times 3.6$ m; range 1×1–5×5.3 m); five pools were in the 6–8 m range, and the largest inhabited permanent pool found was 2.5×12 m; Fig. 2A–B). Twelve inhabited pools were closely associated with another, often smaller permanent pool (Fig. 2B), and in all cases prominent crocodile tracks ran between such pools.

All but one of the unoccupied pools (this measured 2×8 m) had a maximum diameter of < 4 m (mean $= 2.0 \times 2.9$ m; range 1.5×1.5–3×4). Burrows were detected in eight pools, two of which were associated with old nests. However, permanent pools, left by the root systems of fallen trees ($n = 2$) were not used for burrows, nor were two pools that had surfaces only just below that of the surrounding terrain. Thus 19 pools, similar both in size and depth to those occupied by crocodiles, were uninhabited and the overall density of permanent pools, both occupied and unoccupied, was one per 2.3 ha.

In contrast, shallow temporary pools had a firm bottom with less turbid, light brown water. Pools intermediate between these types existed and they were probed for burrows and crocodiles.

Crocodile distribution.—In 1995, during our traverse of the swamp forests toward Mobenzele, crocodiles were found at the first of two swamp forest surveys, approximately 4 and 15 km east of Mboukou village, but neither suitable pools, nor crocodiles, were seen at the second site and for about 35 km of the ensuing traverse. Nearer to Mobenzele crocodiles appeared again in swamp forest (pools) bordering terra firma forest on the extensive levees of the Oubangui River. When crocodile pools were mapped on the parallel transects (numbered 12; Fig. 3), it became evident that dwarf crocodiles were confined to the periphery of swamp forests. There were no suitable pools east of crocodiles 26 and 27 and no signs of crocodiles beyond this point in a surveyed area of about 19 ha (30×6300 m). The bulk of the population occupied the approximately 2.5-km wide band of swamp forest that bordered terra firma forest (Fig. 3).

Osteolaemus nests.—Both active and old nests were particularly conspicuous, even in dense forest, and all were built against tree trunks and tree roots. Seven completed mounds were found that had been constructed during the dry

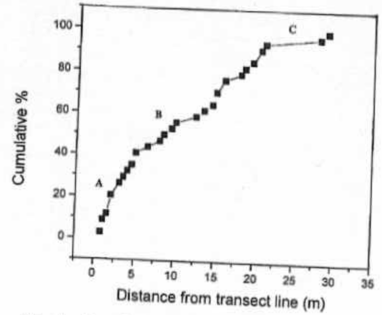

Fig. 4. Cumulative percentage of sightings as a function of the perpendicular distance from the transect line to the center of an inhabited pool. Break-point regressions (A, B, and C) that best fit these points give intersections at 5.0 and 19.5 m. The slope of C does not differ from zero.

season and one was in an early stage of construction. Those that bore obvious signs of the recent addition of rotting vegetation ($n = 5$) contained eggs deposited 50 cm below the apex. Three nests had been depredated via large lateral holes excavated at egg level, and shell debris was evident, although one still had eggs. This damage was attributed to Nile monitors (*Varanus niloticus*), two of which were seen along the transects. Nest mounds were interwoven by plant roots mostly from the ubiquitous ginger plant (*Aframomum angustifolium*). The desiccating effect of the roots caused the eggs to remain relatively dry within the mound. Nests stood 1.05–2 m (mean $= 1.36 \pm 0.37$ m) above the water table. The length of the slope up which the female had shoveled peat, sludge, and leaves from an adjoining pool to the mound apex was 2.2–2.5 m.

Minimum density calculation.—Assuming that actual densities across the area surveyed were relatively constant and even, a decreasing probability of pool detection with increasing distance from the transect line was confirmed (Fig. 4). Applying a stepwise break-point regression model to Figure 4 shows that the total error sums of squares is minimized by a three-line model, whose equations are Line A: $y = 1.41 + 8.02x$ (95% limits by x; $\pm$ 0.42, where $y = \%$ occupancy and $x =$ distance from the transect line; Line B: $y = 22.5 + 3.2x$ (95% limits by x; $\pm$ 0.10); Line C: $y = 74.7 + 0.84x$ (95% limits by x; $\pm$ 0.087). The slope of C was not significantly different from zero ($P > 0.05$), indicating that the probability of sighting pools beyond 19.5 m from the transect line was very low. Lines A and B are significantly different from one another ($P < 0.05$), indicating an effective distance of 19.5 m and including 29 crocodiles, 85.3% of those discovered. Population density was calculated using this effective detection distance (band width 39 m over 28.36 km of transect) giving a total area surveyed of 110.6 ha. To account for overlaps at corners, we subtracted 5.6 ha to calculate 29 crocodiles in an area of 105 ha, for a minimum density estimate of one crocodile per 3.62 ha (or 0.28 croc. per ha). The 95% confidence limits of line B yielded upper and lower intercepts on the y-axis equivalent to 29.04 and 28.63 crocodiles, respectively, suggesting a range of final minimum densities of one crocodile per 3.62 ha to one crocodile per 3.67 ha. It must be emphasized, however, that this represents a range of minimum density estimates based on a relatively preliminary methodology. In future studies, the same methodology would be used, but alternative statistical models, such as those reviewed by Eberhardt (1978) would also be evaluated.

The density estimates applied only to the 2.5-km band of swamp forest bordering gallery forest, not for the swamp forest as a whole. The density of permanent pools was one per 2.3 ha, and minimum distance between occupied pools was about 100 m (as measured directly from Fig. 3).

Estimation of crocodile abundance in Congo basin swamp forests.—The total area of the 2.5-km band of seasonally or permanently inundated swamp forest bordering terra firma forest on the Mobenzele map was 1006 km² (Table 1). Assuming a density of 0.28 crocs/ha, a minimum population estimate was crudely calculated as 28,258. The mapped area covers approximately 10% of the permanently or seasonally inundated forest of the northern Congo Republic, and a fractionally greater area of swamp forest is found in the Democratic Republic of the Congo (formerly Zaire; Hughes and Hughes, 1992).

Discussion

The Likouala swamp forests constitute a relatively unexploited, prime habitat for *O. tetraspis*. *Osteolaemus* activity in the dry season was centered upon a pool, as found by previous studies (Waitkuwait, 1986, 1989; Kofron, 1992). Waitkuwait (1989) observed the activity of 10 individuals of different sizes throughout the year in the same small pools. Some undertook short journeys, especially after rain, but always returned to their pools afterward. In terrestrial habitats such as savannah or terra firma forests, regular access to a lagoon or pool appeared to be essential to a predominantly nocturnal, foraging lifestyle (Waitkuwait, 1989).

The evidence suggests that the availability of permanent pools with an adjoining burrow determines the dry season distribution of crocodiles. However, the presence of well-used tracks suggests that crocodiles frequently forage or commute between other pools (permanent or otherwise) within the swamp forests.

On the other hand, studies of an ecological analogue of *O. tetraspis* may caution against such a naive interpretation. The smooth-fronted caiman *Paleosuchus trigonatus* inhabits small, clear streams in Amazonian rain forests with little vegetation at ground level. However, adults spend much of their time in terrestrial retreats < 90 m from the streams (Magnusson and Lima, 1991). Radiotelemetry studies found that of 79 encounters with tagged *P. trigonatus*, 70 were associated with animals sequestered within retreats such as a hollow log, debris cavities under tree falls or burrows, even when these were far from water. Magnusson and Lima (1991) also concluded that *P. trigonatus* were familiar with, or at least used, regular routes within their home ranges.

It is unknown whether the behavior of *O. tetraspis* parallels that of *P. trigonatus*. Cryptic behavior by *P. trigonatus* would enable them to escape predators such as jaguars (Magnusson and Lima, 1991). Similarly, *O. tetraspis* that reside in flooded burrows may escape forest leopards (*Panthera pardus*) that hunt in the swamps even at the height of the wet season (Blake, 1993).

Burrows are commonly excavated by *O. tetraspis* into banks of forest streams and savannah pools (Guggisberg, 1972; Waitkuwait, 1989; Kofron, 1992), and excavations are probably facilitated in soft, peaty substrates near the periphery of swamp forests. Neither permanent pools, nor signs of crocodiles, were found toward the center of swamps where terrain was generally firmer and the canopy higher. Our preliminary data suggest that only the larger, heavier crocodiles leave well-defined tracks over soft, peaty substrates. Smaller crocodiles would leave faint tracks, and it is unlikely that small animals can be detected by probing. We were unable to determine how many animals resided in a burrow. Males and females presumably do consort for protracted periods in pools during the breeding season, and females remain with their hatchlings for some months (Tryon, 1980). If family groups jointly occupy a pool/burrow for protection, then the present approach, based on pool

surveys, would provide an underestimate of the total population. To what extent dwarf crocodiles disperse in the wet season is unknown. A combination of pool availability, and the limits to which riverine fish penetrate into swamp forests during wet season inundation, may combine to restrict dwarf crocodiles to the fringes of swamp forests in both wet and dry seasons.

In the Ivory Coast, nest construction by *O. tetraspis* begins at the end of the dry season (April) when fallen leaves are available for nest mounding (Waitkuwait, 1986, 1989). In our study area, recent leaf fall, which was significant in this semideciduous forest, was only a minor component of the nest; instead nests were made from a slurry of peat, twigs, and debris swept up from the bed of an adjoining pool. Nest elevation in the Likouala forests (mean = 1.36 m), was higher than that recorded in the Ivory Coast (Waitkuwait, 1986; mean 0.47 ± 0.17 m) and may reflect differences in flood characteristics during the wet season for the two localities.

Kofron and Steiner (1994) stated that "the African dwarf crocodile is one of the most critically endangered crocodilians in the world." This might be true for the western subspecies (Kofron, 1992), but the latest IUCN/SSC Status Survey (Ross, 1998), although highlighting the lack of survey data, concluded that the species had a low risk of extinction despite extensive local use. Clearly populations of *O. t. osborni* in swamp forests appear robust at present, but even here hunting pressures are increasing (Blake, 1993). However, because dwarf crocodiles mostly occur in close proximity to terra firma forest they remain highly vulnerable to exploitation. Our quantitative study of *Osteolaemus* in a prime habitat includes an efficient line-transect methodology that would facilitate surveys at other locations, and thereby attain a better understanding of the ecology and exploitation of *Osteolaemus*.

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