Habitat Use by *Crocodylus johnstoni* in the Lynd River, Queensland

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Crocodilians often display habitat partitioning within their aquatic environments and microhabitat preferences may be particularly evident when multiple species are syntopic (Magnusson, 1985; Herron, 1994). Differential habitat use by crocodilians has been attributed to territoriality during the breeding season (Rootes and Chabreck, 1993a), to divergent foraging modes (Magnusson et al., 1987), to reducing intraspecific competition (Hutton, 1989), or to predator avoidance (Cott, 1961). Size-related habitat segregation is known in *Alligator mississippiensis* (Joanen and Mc-Nease, 1970; Joanen and McNease, 1972; McNease and Joanen, 1974; Goodwin and Marion, 1979), *Caiman crocodilus* (Fitzgerald, 1988; Herron, 1994), *Melanosuchus niger* (Herron, 1994), *Caiman latirostris* and *C. yacare* (Medem, 1983; Scott et al., 1990), *Crocodylus acutus* (Thorbjarnarson, 1988), *C. niloticus* (Cott, 1961; Hutton, 1989; Kofron, 1991), *C. novaeguineae* (Montague, 1983), and *C. porosus* (Webb and Messel, 1978; Messel and Vorlicek, 1987). Considering the many foregoing examples, it is surprising that the topic of habitat use remained relatively neglected for *C. johnstoni* as the species is otherwise comparatively well known (Webb and Manolis, 1989).

In the sole study of *C. johnstoni* to address habitat use (Webb et al., 1983), crocodiles strongly favored deep pools during the dry season and pool occupancy was independent of water clarity or pool type. Occu-

pancy of a pool was thought to be associated with the availability of adequate food or nesting habitats but limited data were provided on those points (Webb et al., 1983). We concluded that additional investigations were warranted to determine correlates of gender, size, and maturity with habitat use by C. johnstoni.

We studied habitat differentiation among freshwater crocodiles with data from a long-term mark-recapture study. Relative habitat preferences of C. johnstoni were inferred by comparing capture locations with specific microhabitat availabilities during the dry season. The findings allowed us to pose three central questions: (1) how often do ontogenetic shifts in habitat occur, (2) at what size classes do such shifts occur, and (3) is the magnitude of the shifts large enough to significantly alter the spatial distribution of crocodiles?

We surveyed 62 km along the upper Lynd River and its major tributary, Fossilbrook Creek, in north central Queensland (near 17°50'S, 144°20'E) as part of an ongoing population monitoring project between 1976–1995 (Tucker et al., 1994). The drainage flows through an upstream region of basaltic soils before reaching the granitic substrates of the Einasleigh Uplands (1:100,000 topographic series, Lyndbrook 7762). Altitude ranges from 360–520 m across the study site. These elevations place the Lynd study population in more extreme thermal conditions than populations experience at lower altitudes. The study site experienced an annual wet-dry climatic cycle. In the dry season, the drainage consisted of pools 15–30 m wide and from 0.5–3.0 m deep connected by rapids or short cascades but clear distinctions between pools can be obscured by rising water levels during the wet season. Mean rainfall during the dry season (April–November) totals 152 mm and during the wet season (December–March) totals 649 mm (Commonwealth Bureau of Meteorology, 65 yr means for Mt. Surprise). Mean minimum-maximum climatic conditions for the region vary from 9.6–26.4 C in mid winter to 19.7–35.1 C in midsummer but with recorded mean monthly minima and maxima ranging from 3.4 to 40.2 C. Mean water temperatures in an isolated backwater of the Lynd ranged from 21 to 31.5 C between winter to summer (Seebacher, 1994) but these temperatures are considered substantially warmer than found in the current of the main stream.

We made field trips during the dry season to include late winter (August–September) and early summer (December–January) samples. We captured crocodiles by a combination of methods, including seining, noosing, fixed nets, hand collection, and prodding them out of burrows (Walsh, 1987) to ensure that all size classes were represented. We designated four microhabitat classifications: rapids were <0.5 m deep with swift moving currents over short elevational gradients, margins were <0.5 m deep with little current along the stream bank, pools were midstream areas >0.5 m deep with little current, and burrows extended several meters or more into undercut stream banks. We used the location of the original sighting as the habitat type if a crocodile moved during the capture. After processing, all animals were released at their capture location.

We measured crocodiles with a straightened tape measure to the nearest 0.1 cm for snout-vent length

TABLE 1. Proportional availability (%) of microhabitats used in calculations of habitat preference for C. johnstoni.

Rapids	Margin	Pool	Burrow
2.5	2.5	94	1
2.5	7.5	89	1
5	5	89	1
7.5	2.5	89	1
5	10	84	1
7.5	7.5	84	1
10	5	84	1
10	10	79	1

(SVL). We marked animals individually by notching the tail and affixing a numbered tag to the hind foot webbing. We determined sex by spreading the cloaca to visually examine the genitalia and assessed sexual maturity for all animals >70 cm SVL. Females were recorded as sexually mature if soft or hard shelled eggs could be felt by palpation or if vitellogenic follicles or corpora lutea were observed via laparoscopy (Limpus, 1984). Maturity of males was determined by visual examination of the testis and associated ducts using laparoscopy and by microscopic examination of sperm smears (scored S0–S3 for visual estimates of none, few, common, or abundant sperm, respectively). We obtained sperm by gently wiping a small spatula along the penile groove to collect mucous-like fluid. The fluid was smeared across a numbered microscope slide with the edge of a second microscope slide. Slides were placed into a covered slide box having a few drops of buffered formalin to provide vapor for fixation. Slides were stained with hematoxylin and eosin at the lab. When gonads were examined visually, adult males were identified as having a convoluted epididymis. Adult males in active spermatogenesis were identified by sperm smear scores of S2 or S3.

We tested for overall differences in habitat use by sex, maturity, and season using maximum likelihood log-linear modeling (McCullagh and Nelder, 1989). We grouped crocodiles into 10 cm SVL categories to test for size differences in habitat use across sexes and seasons using the same procedure. We calculated diversity indices for habitat use among size classes by Shannon indices for diversity and evenness, Levins' index of resource breadth, and Horn's index of resource overlap with programs DIVERS and NICHE and calculated habitat preference by Ivlev's electivity index with program PREFER (Krebs, 1989).

To calculate habitat overlap and preference, we varied microhabitat ratios among margin, rapid, pool, and burrow categories to account for the full range of conditions along the study site (Table 1). We based the ratios on subjective estimates derived during extensive ground truthing and conservatively held the availability of burrows constant at 1% since burrows were infrequent. Changing microhabitat ratios made no difference in calculations for habitat overlap as an identical resource overlap matrix was produced. However, changing microhabitat ratios in calculations for habitat preference did result in different outcomes for habitat preference. To account for the computational variance, we averaged Ivlev electivities generated by
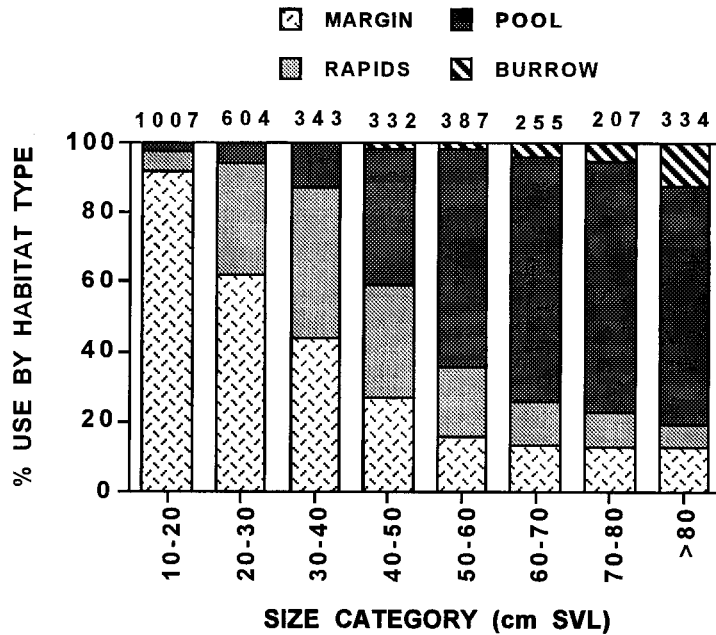
FIG. 1.   Proportional habitat use by different size categories of *C. johnstoni* in the Lynd River. Sample size for the size category appears above the bars.

each combination of microhabitat ratios (refer to Table 1) to plot a mean electivity (±1 SD) for each size category. Ivlev's electivity index was scaled symmetrically from −1 to 1 with 0 representing non-selection, i.e., use in proportion to availability. We interpreted values between −1.0 to −0.6 as strong avoidance, −0.6 to −0.2 as moderate avoidance, −0.2 to 0.2 as neutral, 0.2 to 0.6 as moderate preference, and from 0.6 to 1.0 as strongly preferred.

We inferred that capture locations provided an accurate and unbiased sample of habitat preference but biases could arise if capture probabilities varied among habitats or size classes. We considered this potential for bias in light of the following features of sampling. First, we used multiple capture techniques to address size or habitat specific capture discrepancies. Second, we presumed that habitat preferences of captured crocodiles were similar to preferences of crocodiles that were not seen or captured. Third, the ability to detect crocodiles in water of given clarity may depend on water depth but not on crocodile size. Fourth, many crocodiles were seen only by their distant eyeshines so accurate size estimates were unavailable even if it was obvious which habitat they occupied. Lastly, sample sizes were generous and roughly equivalent across size classes. For these reasons, we concluded that sample biases due to size or habitat were not of major consequence but did not quantitatively test this assumption.

We found that overall habitat use was strongly oriented along stream margins (49.1%) with moderate use of rapids (19.0%) and pools (29.7%) and infrequent use of burrows (2.2%). However, the pattern of habitat use was clearly influenced by body size (Fig. 1). Crocodiles <20 cm SVL remained near streamside margins, crocodiles 20–50 cm SVL shifted from occupancy near rapids to spending time equally among all

habitats, and crocodiles >50 cm SVL primarily existed in midpool areas. Crocodiles <60 cm SVL were seldom found in burrows.

Microhabitat use by sex and maturity (Table 2) differed between immatures and adults ($\chi^2 = 480.54$, 3 df, $P < 0.001$) and because of sex ($\chi^2 = 14.00$, 3 df, $P = 0.003$) but the nature of the difference between sexes was inconsistent for adults and immatures (Table 2). Immature animals tended to use all habitats except burrows equally while adults showed strong declines in proportional use of margin and rapids and increases in use of pool and burrow habitats. Adult males were found equally between pools and burrows whereas adult females were 4.5 times more likely to be encountered in pools than in burrows.

An apparent seasonal shift occurred in habitat use (Table 2), but the initial finding was confounded by two methodological biases: summer samples were predominated by naive hatchlings and winter samples included crocodiles that were caught selectively by netting and prodding burrows. To standardize the seasonal comparison, hatchlings were omitted from the summer sample and only captures by the same method (hand capture) in both seasons were used (Table 2). Following this standardization, no seasonal differences were noted among the three habitat types ($\chi^2 = 3.91$, 2 df, $P = 0.14$).

Habitat use differed by sex within each size class (Fig. 2) for pools ($\chi^2 = 14.86$, 7 df, $P = 0.04$) but not within rapids ($\chi^2 = 1.94$, 7 df, $P = 0.96$) or margins ($\chi^2 = 14.01$, 7df, $P = 0.051$). Using the standardized seasonal contrast, no differences were detected between seasons in habitat use by size classes (Fig. 3) for margins ($\chi^2 = 13.13$, 7 df, $P = 0.07$) or pools ($\chi^2 = 7.21$, 7 df, $P = 0.41$) but seasonal differences were noted for use of rapid microhabitats ($\chi^2 = 37.26$, 7 df, $P < 0.001$).

TABLE 2. Summary of habitat use by sex, maturity, and season for *C. johnstoni* in the Lynd River. The standardization (refer to text) omitted any animals caught by net from the winter sample and any hatchlings from the summer sample.

	Margin	Rapids	Pool	Burrow	N
Male, immature	38%	26%	36%	1%	1220
Female, immature	35%	29%	34%	2%	1062
Male, adult	10%	5%	43%	41%	184
Female, adult	8%	7%	70%	15%	196
Winter	33%	23%	41%	3%	2446
Summer	86%	11%	4%	—	1040
after standardization					
Winter	51%	38%	11%	—	1428
Summer	45%	44%	11%	—	244

Crocodiles 10–20 cm SVL had the lowest diversity of habitat use, breadth of habitats used, and evenness of use among habitats (Table 3). Crocodiles between 40–60 cm SVL showed the greatest diversity of habitat use, breadth of habitats used, and evenness of use among habitats (Table 3). Habitat overlaps were lowest between the largest and smallest size categories which indicated that these groupings were spatially segregated from one another (Table 4). A high degree (>85%) of habitat overlap occurred among all crocodiles >40 cm SVL.

Habitat segregation among size classes was evident for rapids and margins versus pool and burrows, being most pronounced for crocodiles <40 cm SVL (Fig. 4). The close association in mean electivities and overlapping standard deviations showed similar ranking for margins and rapids except in the 10–20 cm SVL class which had yet to disperse from the nest region. Margins were strongly selected by all crocodiles <50 cm SVL and moderately preferred by crocodiles larger than this. Rapids were strongly preferred by most crocodiles between 20–50 cm SVL and moderately preferred by crocodiles larger than this. In contrast, pool habitats were strongly avoided by all crocodiles <40 cm SVL, moderately avoided by crocodiles between 40–50 cm SVL, and were selectively neutral for crocodiles >50 cm SVL. The small standard deviations in mean electivity for pools confirmed that avoidance was highly consistent among all individuals <50 cm SVL. The abrupt shift in burrow preference was in contrast to the moderate changes shown for the other habitat categories. A strong avoidance of burrows by crocodiles <40 cm SVL was shown before a slight preference by 40–60 cm SVL animals and a strong preference for burrows among all larger crocodiles.

Several related aspects of crocodilian ecology may account for the ontogenetic habitat shifts we observed. A primary change in habitat use was related to maturity status, evident by the habitat differences between immature and adult *C. johnstoni* (Table 2). While a shift in habitat use was obvious between the extremes of the size spectrum, small differences in habitat use between adjacent size classes may be obscured when substantial variation in size at maturity occurs.

Consistent habitat differences were seen at sizes >70 cm SVL as males preferred pools to a greater degree than females and as female use shifted to margins and rapids. Because of the timing of the field trips, we suspect that the gender difference in habitat use was due to female attendance near nests situated on the banks. Differential use of habitats is common in adult male and female crocodilians (Joanen and McNease, 1970; Joanen and McNease, 1972; Hutton, 1989) but remains absent among the sexes as juveniles (McNease and Joanen, 1974; Hutton, 1989). It is pertinent to note that this behavioral similarity exists despite substantial differences between lentic and lotic aquatic habitats.

We found the lack of seasonal habitat changes a striking departure from the expected behavior pattern for most ectotherms. Given simple biophysical properties related to temperature, mass, and thermal time constants for crocodiles (Grigg and Gans, 1993), we expected that seasonal habitat shifts might be evident in smaller crocodiles that tracked a preferred body temperature but not necessarily for larger *C. johnstoni*. A mechanism that may account for lack of a detectable seasonal shift is the physiological possibility raised by Seebacher (1994) of thermal acclimatization in populations that experience substantial thermal flux. Despite its tropical latitude, the thermal conditions at the Lynd study site are certainly atypical relative to *C. johnstoni* at lower altitudes.

Because our study was conducted during the middle and late dry season, we could not assess habitat selection during the mating season or the wet season which occur before and after our samples, respectively. Those specific periods would be informative as increased movement and habitat shifts are noted among other crocodilians at that seasonal change. For example, wide dispersions coinciding with elevated water levels are known for *Caiman crocodilus* (Gorzula, 1978; Ouboter and Nanhoe, 1988; Drews, 1990), *A. mississippiensis* (Chabreck, 1965; Joanen and McNease, 1972), *C. niloticus* (Cott, 1961; Pooley, 1969; Hutton, 1989; Kofron, 1991), *C. porosus* (Webb and Messel, 1978), *C. novaeguineae* (Montague, 1983), and *C. johnstoni* (Webb et al., 1982; Cooper-Preston, 1992). When water levels reside, crocodiles become restricted to the available aquatic habitats and social interactions become more frequent, particularly during mating and breeding seasons. At high densities both in the wild (Modha, 1967; Kofron, 1991) and in captivity (Lang, 1987), crocodilians maintain a size dependent hierarchy manifested though spacing behavior (Johnson, 1973; Staton and Dixon, 1975; Drews, 1990). The high occurrence of tail and body injuries in *C. johnstoni* results from such behavioral hierarchies (Webb and

FIG. 3. Seasonal use of margin, rapids, and pool habitats by different size classes of *C. johnstoni* in the Lynd River. Black bars are winter, hatched bars are summer. Burrows were not sampled in both seasons and so were omitted.
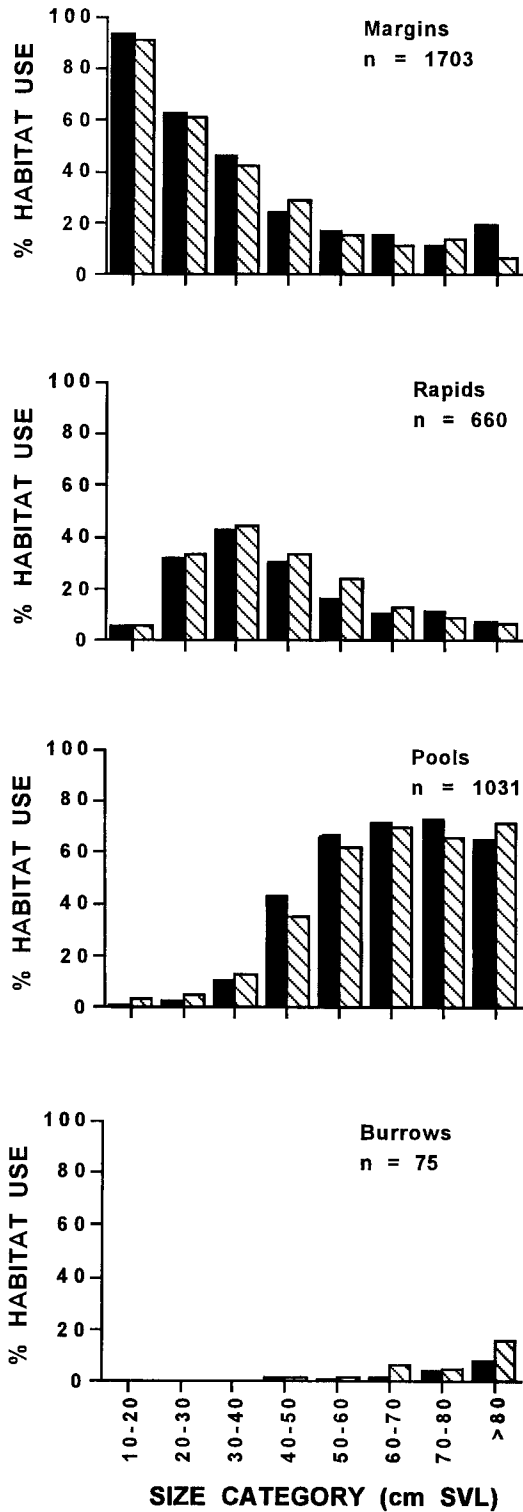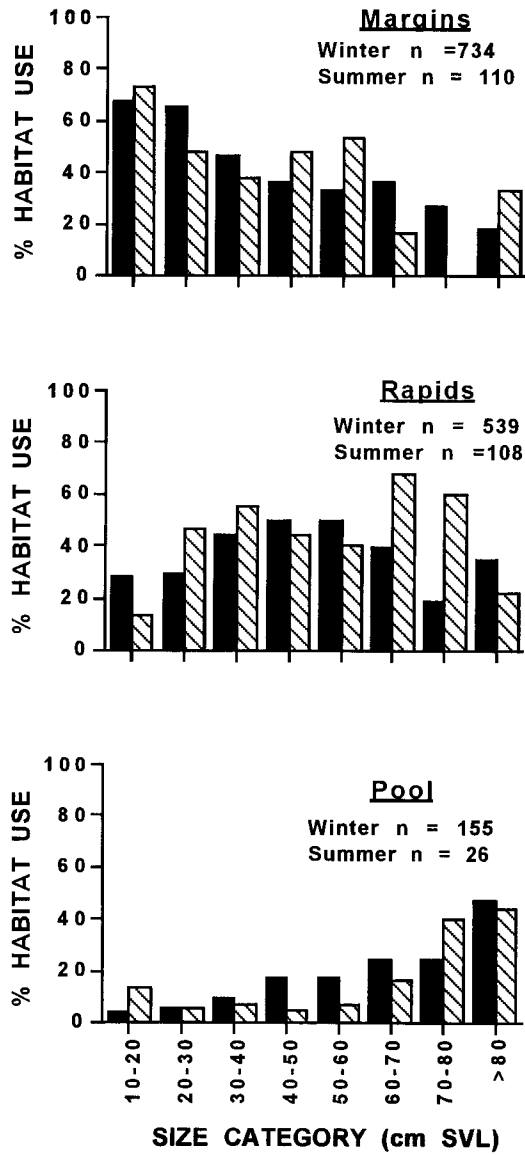
FIG. 2. Aquatic habitat use (margin, rapids, pool, and burrows) by sex and size categories of *C. johnstoni* in the Lynd River. Black bars are males, hatched bars are females.

Manolis, 1983). Social displacement can therefore provide a mechanism that generates habitat partitioning.

Our study found the most polarized preferences or avoidances among small crocodiles with strong avoidance of pools and strong preference for marginal and rapid habits (Fig. 4). Small crocodiles feed mainly in the shallows (Webb et al., 1982; Cooper-Preston, 1992, Tucker et al., unpubl.) but the strong negative preference for pool microhabitats (Fig. 4) suggests that pool avoidance may be due in part to risk avoidance. Because cannibalistic tendencies are documented in some crocodilians (Rootes and Chabreck, 1993b), in-

TABLE 3. Indices of habitat diversity (h'), evenness (j'), and breadth (Levins') for three microhabitats used by *Crocodylus johnstoni* in the Lynd River during the dry season. H' = Shannon-Wiener index of diversity, J' = evenness, ECH = # of equally common habitats, ECH/4 microhabitats = percent of habitat use.

Size category (cm SVL)	H'	J'	Breadth	ECH	ECH/4
10–20	0.48	0.30	0.10	1.39	0.35
20–30	1.19	0.75	0.52	2.29	0.57
30–40	1.42	0.90	0.76	2.67	0.67
40–50	1.67	0.84	0.68	3.18	0.80
50–60	1.40	0.70	0.39	2.63	0.66
60–70	1.31	0.66	0.30	2.48	0.62
70–80	1.28	0.64	0.28	2.42	0.61
>80	1.39	0.70	0.33	2.62	0.66

cluding *C. johnstoni* (Smith, 1987), avoidance of intraspecific predation may promote negative habitat associations. Other predators at the Lynd River that are capable of eating small crocodiles include raptors, wading birds, pelicans, snakes, turtles, and large fish. Negative habitat associations due to avoidance of dominant conspecifics and other vertebrate predators would be difficult to distinguish from positive habitat associations that improve foraging efficiency for given prey types. Whether smaller crocodiles prefer the shallows to maximize feeding or to minimize interference or predation from larger vertebrates remains an open question.

Toft (1985) stated that interspecific resource partitioning by reptiles and amphibians was associated more often with habitat partitioning than dietary partitioning but provided no references for crocodilians. However, the relatedness of the two resources seems prominent in crocodilians even at the intraspecific level. For example different habitats are occupied by four sympatric species in Brazil (Magnusson, 1985) and the diet of each is fundamentally different (Magnusson et al., 1987). Interspecific differences in habitat use occurs between *Melanosuchus niger* and *Caiman crocodilus* in addition to their intraspecific patterns of microhabitat use (Herron, 1994); the latter differences were attributed to either foraging mode or predator avoidance. *Caiman crocodilus* undertake seasonal dispersals from dry season refugia to flooded grasslands and later return to isolated habitats with residing water levels; their diets change dramatically as a result (Staton and Dixon, 1975). A concurrent dietary study for *C. johnstoni* showed distinct changes that paralleled shifts in intraspecific habitat preferences (Tucker et al., unpubl.). Thus, there are clear links between the habitat selection and energetic returns for crocodilians whether the topic is considered from an interspecific, an intraspecific, a spatial, or a temporal context.

Our study showed evidence of three major shifts in size-specific habitat use by *C. johnstoni*. Habitat associations may arise from divergent foraging patterns, intraspecific behavioral interactions, thermal preferenda, or predator avoidance. Future experiments that
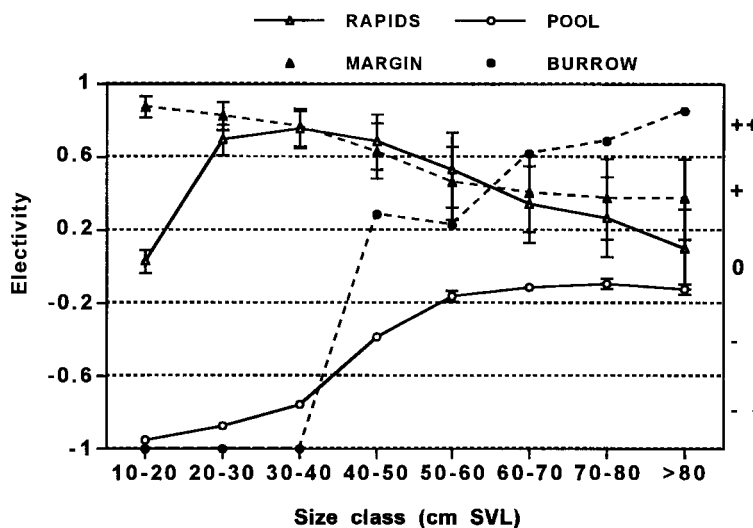

FIG. 4. Mean electivity (± 1 SD) for stream margin, rapid, pool, and burrow microhabitats by different sizes of *C. johnstoni* in the Lynd River. Means are Ivlev's electivity as calculated using the habitat ratios listed in Table 1. The symbols along the right side indicate zones of strong preference (++), slight preference (+), neutral (0), slight avoidance (−), and strong avoidance (−−).

TABLE 4. Horn's index of resource overlap for habitat use by differently sized *C. johnstoni* in the Lynd River during the dry season.

Size class (cm SVL)	10–20	20–30	30–40	40–50	50–60	60–70	70–80	>80
10–20	1.000							
20–30	0.900	1.000						
30–40	0.794	0.974	1.000					
40–50	0.640	0.840	0.918	1.000				
50–60	0.497	0.676	0.776	0.958	1.000			
60–70	0.449	0.591	0.688	0.913	0.987	1.000		
70–80	0.427	0.561	0.659	0.895	0.978	0.999	1.000	
>80	0.414	0.522	0.613	0.856	0.942	0.981	0.987	1.000

manipulate these factors will be necessary to identify the underlying causes of habitat partitioning.

LITERATURE CITED

CHABRECK, R. H. 1965. The movement of alligators in Louisiana. Proc. Southeast Assoc. Game Fish Comm. 19:102–110.

COOPER-PRESTON, H. 1992. Geographic variation in the population dynamics of *Crocodylus johnstoni* (Krefft) in three rivers in the Northern Territory, Australia. Unpubl. Ph.D. Diss., Univ. New England, Armidale.

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

DREWS, C. 1990. Dominance or territoriality? The colonization of temporary lagoons by *Caiman crocodilus* L. (Crocodylia). Herpetol. J. 1:514–521.

FITZGERALD, L. A. 1988. Dietary patterns of *Caiman crocodilus* in the Venezuellan llanos. Unpubl. M. S. Thesis, Univ. New Mexico, Albuquerque.

GOODWIN, T. M., AND W. R. MARION. 1979. Seasonal activity ranges and habitat preferences of adult alligators in a north-central Florida lake. J. Herpetol. 13:157–164.

GORZULA, S. J. 1978. An ecological study of *Caiman crocodilus* inhabiting savanna lagoons in the Venezuelan Guyana. Oecologica 35:21–34.

GRIGG, G. C., AND C. GANS. 1993. Morphology and physiology of the Crocodylia. *In* C. J. Glasby, G. J. B. Ross, and P. L. Beesley (eds.), Fauna of Australia. Vol. 2A Amphibia and Reptilia, pp. 326–336. Australian Government Publishing Service, Canberra.

HERRON, J. C. 1994. Body size, spatial distribution, and microhabitat use in caimans, *Melanosuchus niger*, and *Caiman crocodilus*, in a Peruvian Lake. J. Herpetol. 28:508–513.

HUTTON, J. 1989. Movements, home range, dispersal and the separation of size classes in Nile crocodiles. Amer. Zool. 29:1033–1050.

JOANEN, T., AND L. MCNEASE. 1970. A telemetric study of nesting female alligators on Rockefeller Refuge, Louisiana. Proc. Ann. Conf. S. E. Assoc. Fish and Wildl. Agencies 24:175–193.

——, AND ——. 1972. A telemetric study of adult male alligators on Rockefeller Refuge, Louisiana. Proc. Ann. Conf. S. E. Assoc. Fish and Wildl. Agencies 26:252–275.

JOHNSON, C. R. 1973. Behavior of the Australian crocodiles, *Crocodylus johnstoni* and *C. porosus*. Zool. J. Linn. Soc. 52:315–336.

KOFRON, C. P. 1991. Courtship and mating of the Nile crocodile (*Crocodylus niloticus*). Amphibia-Reptilia 12:39–48.

KREBS, C. J. 1989. Ecological Methodology. Harper and Row, New York.

LANG, J. W. 1987. Crocodilian behavior: implications for management. *In* G. J. W. Webb, S. C. Manolis, and P. J. Whitehead (eds.), Wildlife Management: Crocodiles and Alligators, pp. 273–294. Surrey Beatty: Chipping Norton, NSW.

LIMPUS, C. J. 1984. Identification of ovarian follicles and oviducal eggs by cloacal examination of live Australian freshwater crocodiles, *Crocodylus johnstoni*. Aust. Wild. Res. 11:203–204.

MAGNUSSON, W. E. 1985. Habitat selection, parasites, and injuries in Amazonian crocodiles. Amazonia 9:193–204.

——, E. V. DA SILVA, AND A. P. LIMA. 1987. Diets of Amazonian crocodilians. J. Herpetol. 21:85–95.

MCCULLAGH, P., AND J. NELDER. 1989. Generalized Linear Models. 2nd ed. Chapman and Hall, New York.

MCNEASE, L., AND T. JOANEN. 1974. A telemetric study of immature alligators on Rockefeller Refuge, Louisiana. Proc. Ann. Conf. S. E. Assoc. Fish and Wildl. Agencies 28:482–500.

MEDEM, F. 1983. Los Crocodylia de Sur América. Vol. II Inst. Cien. Nat., Mus. Hist. Nat. Univ. Nac. Colombia, Bogota.

MESSEL, H., AND G. VORLICEK. 1987. A population model for *Crocodylus porosus* in the tidal waterways of Northern Australia: management implications. *In* G. J. W. Webb, S. C. Manolis, and P. J. Whitehead (eds.), Wildlife Management: Crocodiles and Alligators, pp. 189–198. Surrey Beatty: Chipping Norton, NSW.

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

MONTAGUE, J. 1983. Influence of water level, hunting pressure and habitat type on crocodile abundance in the Fly River Drainage, Papua New Guinea. Biol. Cons. 26:309–339.

OUBOTER, P. E., AND L. M. R. NANHOE. 1988. Habitat selection and migration of Caiman crocodilus in a swamp and swamp-forest in northern Surname. J. Herpetol. 22:283–294.

POOLEY, A. C. 1969. Preliminary studies on the breeding of the Nile crocodile Crocodylus niloticus in Zululand. Lammergeyer 3:22–44.

ROOTES, W. L., AND R. H. CHABRECK. 1993a. Reproductive status and movement of adult female alligators. J. Herpetol. 27:121–126.

———, AND ———. 1993b. Cannibalism in the American alligator. Herpetologica 49:99–107.

SCOTT, N. J. JR., A. L. AQUINO, AND L. A. FITZGERALD. 1990. Distribution, habitats, and conservation of the caiman (Alligatoridae) of Paraguay. Vida Silv. Neotrop. 2:43–51.

SEEBACHER, F. 1994. Thermal relations of Crocodylus johnstoni (Krefft 1873) in the wild. Unpubl. Ph.D. Diss., Univ. Queensland, Brisbane.

SMITH, A. M. A. 1987. The sex and survivorship of embryos and hatchlings of the Australian freshwater crocodiles, Crocodylus johnstoni. Unpubl. Ph.D. Diss., Australian National Univ., Canberra.

STATON, M. A. AND, J. R. DIXON. 1975. Studies on the dry season biology of Caiman crocodilus from the Venezuelan Llanos. Memoria Soc. Cienc. Nat. La Salle 101:237–265.

THORBJARNARSON, J. B. 1988. The status and ecology of the American crocodile in Haiti. Bull. Florida St. Mus. Biol. Sci. 33:1–86.

TOFT, C. A. 1985. Resource partitioning in amphibians and reptiles. Copeia 1985:1–21.

TUCKER, A. D., H. I. MCCALLUM, C. J. LIMPUS, AND K. R. MCDONALD. 1994. Crocodylus johnstoni in the Lynd River, Queensland: continuation of a long-term field study. Proc. IUCN Crocodile Specialists Group, 2nd Regional Meeting: 469–473. IUCN, Gland, Switzerland.

WALSH, B. 1987. Crocodile capture methods used in the Northern Territory of Australia. In G. J. W. Webb, S. C. Manolis, and P. J. Whitehead (eds.), Wildlife Management: Crocodiles and Alligators, pp. 249–252. Surrey Beatty: Chipping Norton, NSW.

WEBB, G. J. W., AND S. C. MANOLIS. 1983. Crocodylus johnstoni in the McKinlay River Area, N. T. V. Abnormalities and injuries. Aust. Wildl. Res. 10:407–420.

———, AND S. C. MANOLIS. 1989. Crocodiles of Australia. Reed Books: Frenchs Forest, NSW.

———, AND H. MESSEL. 1978. Movement and dispersal patterns of Crocodylus porosus in some rivers of Arnhem Land, Northern Australia. Aust. Wildl. Res. 5:263–83.

———, S. C. MANOLIS, AND R. BUCKWORTH. 1982. Crocodylus johnstoni in the McKinlay River Area, N. T. I. Variation in the diet and a new method of assessing the relative importance of prey. Aust. J. Zool. 30:877–899.

———, S. C. MANOLIS, AND R. BUCKWORTH. 1983. Crocodylus johnstoni in the McKinlay River area, N. T. II. Dry-season habitat selection and an estimate of the total population size. Aust. Wildl. Res. 10:373–382.