

Ontogenetic Dietary Partitioning by *Crocodylus johnstoni* during the Dry Season

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We examined size-related dietary patterns in a Queensland population of the Australian freshwater crocodile (*Crocodylus johnstoni*). In three consecutive dry seasons, we stomach flushed crocodiles ($n = 324$) to record the numerical frequency and percent occurrence of prey items. Prey included spiders, aquatic insects, terrestrial insects, shrimp, fish, anurans, turtles, snakes, mammals, and birds. The diet of *C. johnstoni* showed ontogenetic shifts as the cranium broadened and once body size exceeded 60 cm SVL. With increasing crocodile size, the ingestion of spiders, insects, and anurans declined strongly whereas the consumption of fish, turtles, and snakes increased strongly. Shrimp were eaten at low and variable levels by all size classes of crocodile. The low overall prevalence of mammals and birds suggested that they were consumed opportunistically by the larger crocodiles. With increasing crocodile size, there were overall increases in prey richness and significant declines in realized dietary niche, dietary breadth, and mean number of prey items per crocodile. There were no significant changes in dietary diversity, evenness, or number of equally common prey species.

MANY studies of crocodylians have described resource partitioning in terms of food (Cott, 1961; Magnusson et al., 1987), space (Chabreck, 1971; McNease and Joansen, 1977), time (Valentine et al., 1972; Taylor, 1979; Webb et al., 1991), or their interaction. Despite these examples, crocodylians are not represented in reviews of resource partitioning among amphibians and reptiles (Toft, 1985) for two reasons. First, the focus has been on interspecific rather than intraspecific resource partitioning (Toft, 1985), and relatively few species of crocodylians are syntopic (however, see Magnusson et al., 1987). Second, existing studies of resource use by crocodylians have provided no quantitative niche indices such as diversity, breadth, or overlap. An improved understanding of resource partitioning by crocodylians, in particular dietary partitioning, will therefore require quantitative approaches to their foraging ecology.

Foraging hypotheses must consider ontogenetic aspects in both morphology and ecology as crocodylians exhibit dramatic growth-related changes in cranial and body dimensions and because size-dependent morphology can exert a strong influence on many ecological aspects of foraging (Peters, 1983). The detection of ontogenetic changes in body or cranial size provides a logical point of departure for related investigations of foraging mode, habitat use, or prey selection (Werner and Gilliam, 1984).

The present study tested whether ontoge-

netic changes in cranial morphology and body size of Australian freshwater crocodiles were associated with dietary changes. Two earlier studies in the Northern Territory of Australia described the diet of *Crocodylus johnstoni* (Webb et al., 1982; Cooper-Preston, 1992) but omitted a quantitative niche approach. This prompted us to examine the stomach contents of *C. johnstoni* at different ontogenetic stages and quantify the dietary niche during the dry season, a period of reduced food availability in northern Australia (Webb et al., 1982) when dietary variation was hypothesized to be most pronounced (Schoener, 1974). We discuss the results with regard to digestive, seasonal, morphological, and behavioral aspects of feeding by *C. johnstoni* and other crocodylians.

MATERIALS AND METHODS

Study site and capture methods.—We collected *C. johnstoni* from the upper Lynd River and its major tributary, Fossilbrook Creek (Australian 1:100,000 Topographic Surveys, sheet 7762-Lyndbrook), in north central Queensland (near 17°50'S, 144°20'E) during a study conducted by the Queensland Department of Environment and Heritage (QDEH). The study area includes 62 km of drainage across altitudes between 360 m and 520 m. At this altitude, freshwater crocodiles experience a more extreme seasonal fluctuation than is common over most of their geographic distribution. The mean monthly mini-

mum/maximum temperatures are 9.6 C/26.4 C in winter and 20.9 C/35.1 C in summer (Australian Bureau of Meteorology, 65-yr average for station 30086 at Mount Surprise).

The region undergoes an annual wet-dry cycle typical of tropical Australia (Webb, 1991), and our collections coincided with low water levels during the late winter dry period (Aug.–Sept.). In the dry season, the river consists of pools 20–40 m wide and 0.5–3.0 m deep connected by rapids or short cascades but pools become united by rising water levels during the wet season. The study site occurs on heavily grazed cattle properties, and stream banks are usually rocky or with sparse emergent vegetation. Dense subaquatic vegetation and algal mats occur in shallow reaches of the waterway. *Callistemon*, *Casuarina*, *Melaleuca*, and *Pandanus* trees are found along the banks and crocodiles make burrows beneath their root structures.

We captured crocodiles by a combination of methods, including seining, noosing, set nets, Pilsstrom® togs, hand collection, and prodding them from burrows (Webb and Messel, 1978). We secured each crocodile's jaws with a rubber band for safety during transport and while being processed. All crocodiles were returned to their capture location after processing.

Morphometrics.—We measured snout-vent length (SVL) = straight line distance from snout tip to the anterior edge of the cloaca) with a straightened steel tape measure to the nearest 1 mm while crocodiles were supine. We obtained cranial measurements with Vernier calipers to the nearest 0.1 mm except for dorsal cranial measurements > 30 cm. For the large animals, we measured dorsal cranial length to the nearest 1 mm by hooking the end of a measuring tape on the supraoccipital and extending the tape to the snout tip. We remained consistent with cranial measurements and acronyms of earlier studies (Iordansky 1973, Hall and Portier 1994) but introduced acronyms for measurements taken only by the present study (marked by an asterisk): (1) NO* = length from posterior border of external nares to anterior orbital border; (2) SL = length from snout tip to anterior orbital border, measured diagonally; (3) DCL = length from anterior tip of snout to posterior tip of supraoccipital; (4) PO* = postorbital length from anterior orbital border to posterior tip of supraoccipital, calculated as the difference between measurements 3 and 2; (5) IOW = minimum interorbital width; (6) WCR = width of the cranial roof between posterolateral corners of the squamosals; (7) CW = width lateral surfaces of the mandibular condyles of

the quadrates; (8) NW* = width at posterior border of external nares, and (9) SW = width across anterior orbital border. Measurements for NW and SW were taken only during the 1994 and 1995 seasons. Full measurement sets were unavailable for some crocodiles that were processed and released at the capture site instead of in camp.

We fit the untransformed morphometric data with least-squares linear regressions to establish predictive relationships. We regressed SVL and DCL separately as independent variables because both measurements are commonly used by crocodile biologists. Because these morphometrics are highly related, they can provide a reasonable reconstruction of SVL from DCL (Hall and Portier, 1994). We compared ratios of DCL: CW against SVL to plot major changes in cranial dimensions during growth.

Dietary analysis.—Samples were collected during the 1977–1979 dry seasons. We obtained stomach contents within a few hours of capture by stomach flushing with the “scoop and pump” method (Taylor et al., 1977) until further flushes consisted only of water. Samples were stored in 10% formalin prior to analysis. We viewed stomach contents with a dissecting microscope and identified prey from appropriate field guides and a reference collection of prey taken from the study site. We identified prey to order and grouped items functionally as either terrestrial or aquatic and as vertebrate or invertebrate. We summarized prey by numerical occurrence and percent occurrence for each 10 cm SVL size class of crocodiles < 80 cm SVL and pooled all crocodiles > 80 cm SVL. Prey found in < 1% of the samples were considered of insignificant dietary importance and omitted from the calculations. We applied a standard arcsine square-root transformation to percentage data before searching for trends in dietary composition across size classes. To address the potential problem of secondary ingestion, we calculated a correlation matrix among prey which were likely to cause bias in the results (e.g., crocodiles eat insects but also frogs that contain insects). We examined crocodile size classes that only included frogs or fish at $\geq 5\%$ occurrence in the diet to avoid spurious correlations if prey were rare or absent.

To quantify prey size, we adopted the target size (TS) index developed to quantify prey size eaten by *C. johnstoni* (Webb et al., 1982). Target sizes began with TSI at 0.0156 cm² and each successive target size was four times larger in area up to TS8 at 256 cm². Other dietary studies

have modified the approach to provide a continuous series of target sizes rather than discrete categories (Magnusson et al., 1987; Cooper-Preston, 1992), but we adopted the original method to facilitate comparisons among studies.

Dietary niche indices.—We examined a plot of cumulative number of prey species against cumulative samples by the method of Hurlbuta (1973) to ensure that sufficient samples were available for analysis in each size category; all categories met this criteria. We calculated the Shannon index to estimate dietary diversity (Krebs, 1989). Because crocodiles are opportunistic feeders, a Type I measure to weight rare resources was appropriate as we expected that large but valuable prey were taken less frequently than small and common prey. Indices were calculated using a base of \log_{10} from percent occurrence (frequency of prey categories within stomachs) rather than numerical occurrence to minimize variability from individual feeding responses. Diversity indices increase as the number of dietary resources increase so that low values represent dietary specialists and high values represent generalists. The Shannon evenness index gave a standardized measure of dietary predominance on a 0–1 scale (Krebs, 1989). Low evenness values indicated predominance, and high evenness values represented little dominance of prey types in the diet. Dietary breadth was calculated from Levin's (1968) measure to determine uniformity of resource use.

We calculated Horn's index (Horn, 1966) to estimate dietary overlap among size classes because it was the least biased index for the number of resource categories we recorded (Krebs, 1989). As a conservative index, this method detected the major changes in feeding ecology but was less sensitive to subtle dietary shifts. The index was scaled from 0–1, and the fewer the commonly used resources the lower the overlap measure. The number of equally common prey (ECP) in the diet were compared with the number of prey resources (PR) used by the size category. The ratio (ECP/PR) gave an approximation of the realized dietary niche (realized or actual niche as a proportion of the potential niche; Schoener, 1989) for each size category.

Dietary preference.—We calculated a relative dietary preference for each size category to rank prey choice. No adequate faunal studies of prey availability existed for the region because of the difficulty of sampling terrestrial, aquatic, and aerial prey types so we assessed food availability

from analysis of stomach samples pooled over all size classes (Pianka, 1986). This relative dietary preference provided only a general overview of prey preference or avoidance and was not an absolute probability of prey use.

We approximated relative dietary preference by making several assumptions about crocodile feeding ecology. Because the Lynd River flows throughout the dry season, we assumed that aquatic prey were renewed constantly, in other words, that localized food depletion did not occur as a result of the crocodiles' feeding activity. We assumed that prey availability was the same for all crocodiles but that different sized crocodiles were not equally efficient in prey capture or necessarily occupied the same microhabitats. This assumption allowed us to consider potential differences in prey selection by ontogenetic classes. Presence of a prey type merely indicated that the prey could be eaten by that particular size class but absence could be the result of a number of factors, such as prey being too large, too small, avoidance, or low encounter rate. Finally, we assigned the maximum proportion recorded for each of the major prey types as the minimum availability within the environment so that calculated dietary preferences were a conservative maximum. Given these assumptions, we calculated Ivlev's electivity as the "relative" index of dietary preference using program PREFER (Krebs, 1989). In this index, electivity was scaled symmetrically from -1 to 1, with 0 representing nonselection, i.e., prey taken in the same proportion as their occurrence. 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 0.6 to 1.0 as strongly selected.

RESULTS

Morphometrics.—Males and females followed the same ontogenetic patterns in SVL and DCL although males attained a larger absolute size. Slopes and intercepts for nine cranial morphometrics on SVL or DCL were compared by an analysis of covariance. There were no significant differences between sexes in either slope or intercept so we pooled the data to obtain overall predictive relationships (Table 1). Growth coefficients indicated a faster rate of lengthwise cranial growth than in widthwise growth overall except for the change when cranial width (CW) became greater than the post-orbital growth (PO). A scatter plot of the ratio of dorsal cranial length to width (DCL: CW) against SVL showed some individual variation

TABLE 1. LINEAR REGRESSION COEFFICIENTS FOR RELATING CRANIAL MEASUREMENTS OF *Crocodylus johnstoni* TO SNOUT-VENT LENGTH (SVL) AND DORSAL CRANIAL LENGTH (DCL). Measurements in centimeters. Other acronyms as in Methods.

Independent variable	Slope	Intercept	r ²	(n)
(1) NO*	SVL 0.21	-1.23	1.00	(1741)
	DCL 0.66	-1.34	1.00	(1738)
(2) SL	SVL 0.25	-1.19	1.00	(1740)
	DCL 0.77	-1.30	1.00	(1740)
(3) DCL	SVL 0.32	0.06	1.00	(2348)
	DCL 0.68	0.08	1.00	(1730)
(4) PO*	SVL 0.23	1.30	0.98	(1740)
	DCL 0.62	1.30	0.96	(1737)
(5) IOW	SVL 0.07	-0.14	0.96	(1732)
	DCL 0.07	0.63	0.99	(1740)
(6) WCR	SVL 0.22	0.60	0.99	(1734)
	DCL 0.13	0.13	0.99	(1796)
(7) CW	SVL 0.41	0.10	0.99	(1791)
	DCL 0.03	0.23	0.98	(218)
(8) NW*	SVL 0.10	0.20	0.98	(218)
	DCL 0.08	0.19	0.99	(218)
(9) SW	SVL 0.25	0.11	0.99	(218)
	DCL 0.25	0.11	0.99	(218)

in cranial growth but an overall nonlinear trend ($y = 1.9116 + 0.019x - 0.00014x^2$, $P = 0.0001$, $r^2 = 0.57$) with a maxima occurring between 63–65 cm SVL. The change in ratio reflected a reverse in relative growth rates of the two cranial measures and a decline from the maximum ratio of ~ 2.5 (Fig. 1) as the cranium broadened at this ontogenetic stage.

Dietary analysis.—We sampled 324 crocodiles by

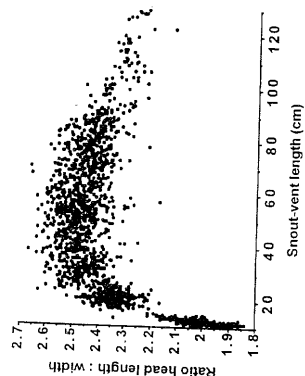


Fig. 1. Ratio of head length:width to snout-vent length for *Crocodylus johnstoni* in the Lynd River, Queensland.

stomach flushing, including posthatchlings to adults of both sexes (size range = 13.6–125.9 cm SVL). Stomach contents yielded 1283 prey items (Table 2) that were categorized into functional prey groupings similar in habitat and target size. Prey included spiders, aquatic insects, terrestrial insects, crustaceans, fishes, anurans, snakes, turtles, mammals, and birds. The proportional occurrence and numerical representation of prey followed distinct trends with respect to ontogeny (Table 3). The percentages of terrestrial and aquatic insects showed monotonic declines with increasing crocodile size ($r = -0.96$ and -0.97 , $P < 0.0001$ and 0.0002 , respectively). Percentages of spiders declined overall with increasing crocodile size ($r = -0.83$, $P < 0.01$) because of a step function decline in crocodiles > 60 cm SVL. The pattern of anurans in the diet followed a polynomial equation ($y = 1.362 + 0.66x - 0.101x^2$ with y as the transformed percentage of anurans in the diet and x representing the crocodile size class). Percentages of fish, turtles, and snakes increased significantly with crocodile size ($r = 0.73$ – 0.88 , $P = 0.02$ – 0.004), with fish more than doubling in importance for crocodiles > 60 cm SVL. Mammal and bird categories had no statistically significant trends even though mammals increased in the diet of crocodiles > 70 cm SVL ($r = 0.31$, $P = 0.46$) and birds were eaten only by the largest size class ($r = 0.58$, $P = 0.13$). The collective representation of vertebrates other than fish was reasonably modeled as a step function since significantly more vertebrates were found in the diets of crocodiles > 60 cm SVL ($\chi^2 = 11840$, $P < 0.0001$). Shrimp were consumed at low but variable levels (5–14%) by all size classes ($r = 0.09$), after excluding the crocodiles < 20 cm SVL which ate none. The mean number of prey per crocodile declined overall with body size ($r = -0.78$, $P = 0.02$), markedly so in animals > 60 cm SVL (Table 3). Prey of increasingly larger target sizes were added in the diets of larger crocodiles (Table 3).

We found no evidence of potential biases resulting from secondary ingestion among crocodiles that included fishes or anurans at more than 5% in the diet. Crocodiles > 20 cm SVL had inverse relationships between the percent occurrence of fish prey and terrestrial insects ($r = 0.73$, $P = 0.06$), aquatic insects ($r = 0.76$, $P = 0.04$), or spiders ($r = 0.96$, $P = 0.0007$) in the diet. Crocodiles ≤ 70 cm SVL had no significant associations between the percent occurrence of frog prey and terrestrial insects ($r = 0.55$, $P = 0.25$), aquatic insects ($r = 0.57$, $P = 0.24$), or spider prey ($r = 0.26$, $P = 0.62$).

TABLE 2. PREY ITEMS* IDENTIFIED FROM STOMACH SAMPLES OF 324 *Crocodylus johnstoni* FROM THE LIND RIVER IN THE DRY SEASON.

Grouping	Target sizes	Taxon or order
Spiders	5	Lycosidae, Araneidae, and unidentified
Aquatic insects	4	Coleoptera (diving beetles, water striders, and water scorpions) Hemiptera
Terrestrial insects	4	Odonata (larvae) Lepidoptera (caterpillars) Coleoptera (beetles) Orthoptera (mole crickets, field crickets, grasshoppers) Hymenoptera (ants) Dermaptera (earwigs) Odonata (dragonflies) Lepidoptera (moths) Macrobrychum spp. (small) Macrobrychum rosenbergii Hephaestus fuliginosus (sooty grunter) Nematoda erubi (bony bream) Oxyeleotris lineolata (sleepy cod) Arius leptaspis (fork-tailed catfish) Neosilturus argenteus (eel-tailed catfish) Tandanus tandonus (tandan catfish) Melanotaenia spp. (rainbowfish) Toxotes chalarus (archer fish) Craterocephalus spp. (hardhead) Glossamia aprion (mouthalmighty) Strongylura breffii (longtom) Margarida margaritula (purple-spotted gudgeon) Glossogobius spp. (unidentified goby) Amalthea poroides (striped grunter) Leptobotryon unicolor (spangled perch) Liloria caerulea (green tree frog) L. variegata (blue-plum tree frog) L. rotii (Roth's tree frog) Bijlo marinus (cane toad) Elysa latiderrum (saw-shelled turtle, small) Achoerobates arafurac (file snake) Troglodanopsis marini (keelback) Anhinga melanogaster Pteropus scapulatus (little red flying fox) Microchiroptera, unidentified Muridae, unidentified
Auratus	6	
	5	
	6	
Turtles	5-7	
Snakes	6	
	6-8	
Birds	8	
Mammals	7-8	

* Items recorded as < 1% and omitted from further analyses: 1. bee, 1. mantid, 2. small bioles, 1. roach, 1. centipede, 2. unidentified insect egg masses.

Other stomach contents.—Crocodiles > 50 cm SVL had empty stomachs more often than did smaller crocodiles ($F_{1,6} = 14.06, P = 0.01$). The percent of crocodiles containing gastroliths was positively correlated ($r = 0.74, P = 0.037$) with increasing body size (Table 3). A nonlinear trend for presence of plant matter peaked among crocodiles between 40 cm and 60 cm SVL (Table 3). There was no obvious association between the presence of plant matter and any particular prey category.

Trends for the presence of two internal parasites differed slightly (Table 3). Nematode

prevalence was significantly related to crocodile size ($r = 0.76, P = 0.027$) because of an elevated level of parasitism found in crocodiles > 60 cm SVL. Nematode burdens corresponded closely with the proportion of fish in the diet ($r = 0.86, P = 0.005$). Trematodes were recorded only among crocodiles > 70 cm SVL and superficially corresponded to the inclusion of turtles in the diet, but the association was tentative because of small sample sizes.

Dietary diversity, evenness, and breadth.—Dietary diversity (H') did not change significantly across

TABLE 3. PREY CATEGORIES RECOVERED FROM SIZE CLASSES OF *Crocodylus johnstoni* DURING THE DRY SEASON. n = number of crocodiles in size category, N = number of prey items, % = percent occurrence in individual stomachs containing prey. Diversity indices are listed in the following order: Shannon diversity, N = Shannon evenness, Levin's resource breadth, the number of equally common prey (ECP), the number of prey resources consumed (PR), and the realized niche (ECP/PR).

Category	n/N	%	15/31%	18/40%	17/41%	2/8%	5/11%	8/12%	135/31%	Overall mean N/n
Spiders	10-19/9	25/48%	45/45%	15/31%	18/40%	17/41%	2/8%	5/11%	8/12%	135/31%
Aquatic	10-19/9	75/66%	154/66%	110/59%	24/35%	17/23%	4/17%	7/12%	401/39%	401/39%
Terrestrial	10-19/9	29/55%	71/52%	119/42%	150/33%	22/29%	3/6%	2/5%	528/35%	528/35%
Shrimp	10-19/9	0/—	3/5%	9/10%	4/14%	2/8%	2/6%	5/10%	27/7%	27/7%
Auratus	10-19/9	3/10%	21/31%	18/34%	9/21%	5/13%	2/8%	1/—	6/17%	6/17%
Fishes	10-19/9	1/3%	7/7%	13/16%	19/19%	10/15%	20/75%	22/56%	115/27%	115/27%
Turtles	10-19/9	0/—	0/—	0/—	0/—	0/—	0/—	0/—	0/—	0/—
Snakes	10-19/9	0/—	0/—	0/—	0/—	0/—	0/—	0/—	0/—	0/—
Birds	10-19/9	0/—	0/—	0/—	0/—	0/—	0/—	0/—	0/—	0/—
Mammals	10-19/9	0/—	1/2%	1/2%	0/—	0/—	0/—	0/—	1/0.3%	1/0.3%
total prey/mean # prey/animal	132	302	299	193	203	53	49	53	1283	4.0
No prey	3/10%	3/5%	1/2%	4/9%	10/26%	3/13%	3/17%	6/17%	10/24%	40/12%
Catroliths	17/59%	55/89%	40/82%	39/91%	34/87%	23/96%	34/94%	38/91%	280/86%	49/15%
Plant matter	3/10%	8/13%	7/14%	9/21%	8/21%	5/21%	6/17%	3/7%	48/15%	3/1%
Trematodes	0/—	0/—	0/—	0/—	0/—	0/—	0/—	0/—	0/—	0/—
Nematodes	7/24%	9/15%	13/27%	5/12%	9/23%	13/54%	16/44%	23/55%	95/29%	95/29%
Diversity	1.90	2.25	2.44	2.48	2.53	2.15	2.38	2.40	2.40	2.40
Evenness	0.82	0.80	0.87	0.85	0.84	0.77	0.75	0.76	0.76	0.76
Breadth	0.60	0.55	0.65	0.65	0.66	0.57	0.57	0.57	0.57	0.57
ECP	3.74	4.76	5.42	5.56	5.76	4.44	5.22	5.26	5.26	5.26
PR	5	7	7	6	8	7	9	9	9	9
ECP/PR	0.75	0.68	0.77	0.93	0.72	0.63	0.58	0.58	0.58	0.58

size classes ($r = 0.32$, $P = 0.45$) (Table 3) although diversity was lowest for yearlings and highest for 30–60 cm crocodiles. Moderate dietary dominance occurred in the 10–30 cm SVL categories because of a high but equal reliance upon a limited selection of prey (spiders and insects). Low dietary dominance was found for the 30–60 cm SVL categories as the prey base widened although the predominance of invertebrate prey remained. Highest dietary dominance occurred in crocodiles > 60 cm SVL because of heavy reliance upon fishes despite a wide range of prey categories ingested.

There was no significant difference in dietary breadth among crocodiles < 40 cm SVL but a linear decline for crocodiles ≥ 40 cm SVL ($r = 0.90$, $P = 0.04$). Crocodiles in the 40–50 cm SVL class were the most generalist, and crocodiles > 60 cm SVL scored as more specialized because of high selectivity of fishes within the broad spectrum of prey (Table 3). The number of equally common prey resources (ECP) in the diet was not significantly different among size categories ($r = 0.31$, $P = 0.46$) although prey richness (PR) increased significantly ($r = 0.84$, $P = 0.009$; Table 3). A negative trend for realized niche dimensions (ECP/PR) with increased body size was not significant ($r = -0.58$, $P = 0.13$). However, taking into account the overall variation across size classes, there remained an underutilization of niche dimensions by crocodiles > 60 cm SVL. Crocodiles in the 40–50 cm SVL category occupied the potential dimensions of their predatory niche to the greatest degree.

Dietary overlap and preference.—The greatest degree of change (14–25% differences) in dietary overlap occurred at the 60 cm SVL boundary for all size categories of crocodiles (Table 4). Dietary overlap was high (> 90%) among all crocodiles < 60 cm SVL but declined by < 5% between intervals for crocodiles larger than this.

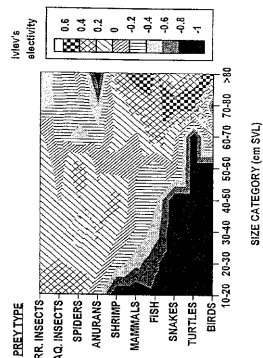


Fig. 2. Dietary preference (Ivlev's selectivity) for 10 major prey types by ontogenetic size classes of *Crocodylus johnstoni* found in the Lynd River during the dry season. Size categories are 10 cm SVL. Strong avoidance is indicated by values from -1 to -0.6, moderate avoidance by values from -0.6 to -0.2, no preference by values from -0.2 to 0.2, and moderate preference by values from 0.2 to 0.6. No values for strong preference (0.6 to 1.0) were recorded.

Distinct transitions in prey selection and avoidance (Ivlev's selectivity) were evident among size classes (Fig. 2). Each size category of crocodiles obtained a unique ranking of relative resource preferences that did not coincide with the next closest size category. Crocodiles < 30 cm SVL showed strong preferences for spiders, aquatic or terrestrial insects. Those between 30 cm and 50 cm SVL selected either anurans or shrimp augmented by terrestrial insects, or spiders. Crocodiles between 50 cm and 60 cm SVL selected spiders, terrestrial insects and anurans. Fishes were highly preferred by all crocodiles > 60 cm SVL. Large vertebrate prey received high ranking preferences in the two largest sizes of crocodiles even though these prey represented a small proportion of the dietary occurrence.

TABLE 4. HORN'S INDEX OF RESOURCE OVERLAP FOR DIETS OF ONTOGENETIC SIZE CLASSES OF *Crocodylus 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	0.960	1.000						
30-40	0.913	0.984	1.000					
40-50	0.902	0.957	0.971	1.000				
50-60	0.898	0.945	0.950	0.966	1.000			
60-70	0.640	0.707	0.782	0.821	0.810	1.000		
70-80	0.529	0.612	0.690	0.717	0.764	0.912	1.000	
>80	0.501	0.576	0.658	0.690	0.727	0.862	0.961	1.000

We found that *C. johnstoni* shifted from a diet of small invertebrates to one dominated by fish and other vertebrates. These results agree with previous studies for the species (Webb et al., 1982; Cooper-Preston, 1992). However, dietary analyses based upon stomach samples have several limitations resulting from digestive variation among prey types and the possibility of secondary ingestion (Jackson et al., 1974; Magnusson et al., 1987). Crocodile metabolic and digestive rates also vary in a mass-specific and thermally dependent manner (Coulson and Hernandez, 1983; Coulson and Coulson, 1986; Lang, 1987) such that gut passage time will affect the interpretation of stomach contents (Garnett, 1985; Webb et al., 1991). Small prey digest faster than large prey, but indigestible parts remain longer (Garnett, 1985; Delany and Abercrombie, 1986). Delany and Abercrombie (1986) reasoned that scaleless fish and amphibians would be underrepresented in stomach content analyses because they are rapidly digested whereas scaled fish, insects, reptiles, birds, and mammals would be overrepresented (scales, chitin, elytra, scutes, feathers, and fur are poorly digested).

The foregoing conclusions were relevant to our study because, if a substantial fraction of invertebrates derived from the guts of anurans or fish prey, then dietary shifts were less extreme than our data indicated. Bias from secondary ingestion would arise mainly in the 20–50 cm SVL crocodiles which consumed the most anurans. We discounted secondary ingestion of invertebrates by fish or anurans as a substantial source of bias because these prey categories showed no statistical correlations or were inversely related. The fact that insects remained in the diet when anurans were absent suggests that the magnitude of any bias from secondary ingestion is at least small. Previous dietary studies for *C. niloticus* (Cott, 1961), *Alligator mississippiensis* (Jackson et al., 1974), and *C. johnstoni* (Webb et al., 1982) concluded that varying retention times were a more practical limitation than secondary ingestion. For example, comparisons of gut samples versus fresh prey remains for juvenile *C. porosus* showed 21–26% overestimates for percent occurrence of prey resulting from the retention of indigestible prey remnants (Webb et al., 1991).

We did not distinguish between fresh and old prey, so we cannot say whether our results were similarly affected. Our analysis within prey categories tended to minimize that bias (Magnusson et al., 1987; Thorbjarnarson, 1993), i.e.,

any digestibility bias was consistent within a prey type regardless of variation among prey types. However, digestion rate (as opposed to digestibility) would be affected across ontogenetic size classes because smaller crocodiles had higher metabolic rates (Coulson and Hernandez, 1988). When insects (a prey type relatively resistant to digestion) predominated the diet despite an increased digestive turnover of small crocodiles, it was likely that prey consumption was underestimated for small crocodiles, more so than for the larger crocodiles with slower metabolisms. Even accounting for bias, dietary shifts from invertebrate to vertebrate-based diets remained qualitatively and quantitatively distinct.

Seasonal constraints on resource availability.—The dietary pattern during the dry season provided empirical data relevant to the controversy on limiting similarity and variance in niche overlap for changing resource environments (Pulliam, 1986). One view suggests that dietary overlap and habitat overlap should be low during resource scarcity if animals disperse (Pyke, 1984; Stephens and Krebs, 1986). The contrasting suggestion is that high overlap occurs in both diet and habitat during periods of resource scarcity if animals do not disperse widely (Schoener, 1974). Our study during the dry season supported the latter view (Table 4) in that high dietary overlap occurred among similarly sized crocodiles, and low dietary overlap was found among differently sized crocodiles. However, it is equivocal whether the result was the result of low food availability or metabolic depression.

For example, small terrestrial prey living along the river banks were less active or simply unavailable during the cool season (KRM, unpublished). Dry season samples would also differ because of lowered reptilian metabolism during a prolonged cool period (Coulson and Coulson, 1986). Less fresh food was taken during the cool dry season in three separate populations of *C. johnstoni* (Cooper-Preston, 1992). Prey composition fluctuated for *C. johnstoni* between wet and dry season samples though with little change in prey size (Webb et al., 1982). Seasonal changes in food quantity or composition have been documented in *A. mississippiensis* (Fogarty and Albury, 1968; McNease and Joann, 1977; Valentine et al., 1972), *Caiman crocodilus* (Gorzula, 1978; Thorbjarnarson, 1993), and *C. niloticus* (Whitfield and Blaber, 1979; Hutton, 1987). In contrast, there was no seasonal variation in the quantity of food ingested by *C. porosus* although dietary composition did change (Taylor, 1979; Webb et al., 1991). Thus, seasonal variation can readily influence dietary composition among

crocodilians. Additional dietary samples from the warm wet season would be needed to clarify any temporal variation in dietary overlap for the Lynd River.

Structural constraints of cranial morphology.—The present study found that dietary variation was associated with changes in cranial morphology. Large prey were excluded from the diets of small crocodiles because of simple mechanical constraints in handling. As the cranium widened (reflected by changing ratios of dorsal cranial length:width), more large vertebrate prey were added to the diet. The dietary shift evidently corresponded to the necessary increase in gape capacity for seizing and swallowing larger prey (Hall and Portier, 1994). Dietary shifts accompany similar changes in cranial dimensions (*C. niloticus* (Hutton, 1987), *A. mississippiensis* (Dodson, 1975), *C. porosus* (Webb and Messel, 1978), and *C. novaeguinae* (Hall and Portier, 1994). In these species, large vertebrates were added to the diet as the DCL:CV ratio changed near the ratio 2.4–2.6 (cf. 2.5 for *C. johnstoni*). The similar shift of cranial ratios indicates a common structural threshold for accepting large prey despite biomechanical differences in feeding among long-snouted and broad-snouted crocodilians. Longirostrine crocodiles (like *C. johnstoni*) have a snout structure best suited to resist lateral stress and are usually fish eaters whereas the robust secondary palate of platyrostrine crocodilians withstands high compressive and torsional loading when large prey are made into smaller bites (Busbey, 1995).

Ontogenetic changes in prey size and composition.—Cranial development clearly provided an increased dietary scope. Yet despite an expanded capacity of adults to consume prey of all sizes, the ingestion of smaller prey declined. The size-related foraging patterns of *C. johnstoni* conform with two predictions of optimal diet theory (Stephens and Krebs, 1986) in that larger crocodiles preferentially selected more profitable prey and consumed lower quality prey less frequently. It remains unclear whether the empirical findings supported another general prediction, that selection of less profitable prey was unaffected by encounter rate (Stephens and Krebs, 1986).

Even when prey composition does not change appreciably with increasing body size, mean prey size usually does (Webb et al., 1982; Magnusson et al., 1987; Thorbjarnarson, 1993). Therefore, it is remarkable that freshwater crocodiles showed an ontogenetic telescope pattern rather

than an ontogenetic shift in the lower size limit of prey (Arnold, 1993). Because secondary ingestion was only a minor concern, the retention of small invertebrates in the diet of large crocodiles raises two possibilities. First, prey encounter rates in the dry season may be sufficiently scarce that even small prey are not by-passed. This contention fits with the low prey availability found by other studies of *C. johnstoni* in the dry season (Webb et al., 1983; Cooper-Preston, 1992). Second, the retention bias mentioned for indigestible material provides an equally parsimonious explanation. In either case, an efficient response to lower metabolism with increasing body size in crocodilians (Coulson and Hernandez, 1983) is to eat food of maximal energetic content regardless of size class differences in dietary preference or prey availability.

Size-related ecological interactions.—We found high dietary overlap between adjacent size classes but low overlap between the smallest and largest crocodiles. Overlap alone is insufficient evidence of competition (Schoener, 1989), but behavioral interactions among differently sized crocodiles would obviously cause ecological separation if intraspecific predation, aggression, or competition influenced where crocodiles feed (Cott, 1961; Hutton, 1987). In a companion study of habitat use on the Lynd River (Tucker et al., 1997), we found that different sizes of *C. johnstoni* had clear preferences among rapids, stream margins, and pool microhabitats. Therefore, some of the ontogenetic dietary shifts noted for *C. johnstoni* probably related to foraging in different habitats.

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Mobbing Behavior in Juvenile French Grunts (*Haemulon flavolineatum*)

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Juvenile French grunts (*Haemulon flavolineatum*) form extremely site-specific and long-lasting diurnal resting shoals (Helfman and Schultz, 1984). Although the resting shoals often congregate near reef structures such as coral heads or grassbeds, when threatened by a potential predator, they rarely enter shelter holes. Instead, they begin schooling and perform anti-predator behavior typical of fish schools (Pitcher and Wyche, 1988; Pitcher and Parrish, 1993). This behavior differs from many other species of coral reef fishes which shelter in crevices in the reef during periods of rest and to avoid predation (Hobson, 1975; Hixon and Beets, 1989, 1993).

In addition to normal schooling behaviors, a specific form of aggressive anti-predator behavior was observed in diurnal resting shoals of juvenile French grunts. Here I describe this behavior, equate it with mobbing behavior observed in other animals, and discuss possible functions of this type of behavior. This is the first observation of mobbing behavior in French grunts and one of the few observed in juvenile fish.

Methods.—All observations were made utilizing snorkel gear at 1030-1100 h on 1 and 6 Feb. 1995. The behavior took place in *Thalassia testudinum* seagrass beds 2-3 m deep behind the barrier reef adjacent to Tobacco Caye, Belize. The two separate *H. flavolineatum* resting shoals exhibiting this behavior were located 300 m and 325 m behind the reef crest in the lagoon. The first shoal contained an estimated 75 French grunts [mean fork length (FL) = 63 mm \pm 4 SD; n = 60] with three bucktooth parrotfish (*Sparisoma radiatum*), whereas the second contained an estimated 1000 fish composed of 88% French grunts (mean FL = 70 mm \pm 8 SD; n = 638) and 12% caesar grunts, *H. carbonarium*. Only French grunts participated in the observed anti-predator behavior which was in both cases directed toward individual barracuda, *Sphyraena barracuda*, estimated at 140 mm FL at the first site and 400 mm FL at the second.

Results.—The anti-predator behavior consisted of four stages: evasion, approach, attack, and return. When a barracuda slowly entered a resting shoal, the French grunts began schooling, the school compacted slightly, and the grunts closest to the predator appeared to be herded by it (Pitcher and Wyche, 1988). The grunts then evaded the predator through the fountain maneuver (Pitcher and Parrish, 1993). During this maneuver, individual grunts in front of the barracuda initially began to flee, moving slowly parallel to it and in the same direction. They then turned and passed along the side of the predator facing the opposite direction. When fully behind the barracuda, they again turned to face in the same direction as it. This maneuver initially maximized the grunts' velocity relative to the predator (Pitcher and Parrish, 1993). During this entire sequence, the grunts and barracuda moved relatively slowly, appearing unhurried.

After assembly behind the barracuda, individual French grunts began to approach it from behind, slowly and sequentially. Approximately five individuals were in different stages of approach at any given time. After approaching within 10 cm, an individual fish attacked by darting forward and nipping at the barracuda's tail. It was unclear whether contact was made. After the attack, the grunt returned to the part of the school behind the predator at a speed slightly faster than the approach, while another individual performed an attack. Different individual grunts continued this behavior for 45-120 sec until all other fish completed the fountain maneuver and were behind the barracuda, which then moved away from the school. It was unclear whether any individual performed the approach-attack-return sequence more than once, although many individuals cycled through this sequence. When the barracuda moved 2-3 m from the school, the French grunts resumed schooling behavior.

When the approach-attack-return sequence began, both barracudas responded by approximately doubling swimming speed, although no reaction to individual attacks was detected. In one instance, the barracuda lunged forward suddenly, a probable predatory attack, and the grunts responded by darting 75 cm away then, after 10 sec, returning to the behavioral sequence described above. This resembled the evasion behavior of flash expansion (Pitcher and Wyche, 1988). The predatory attack was unsuccessful.