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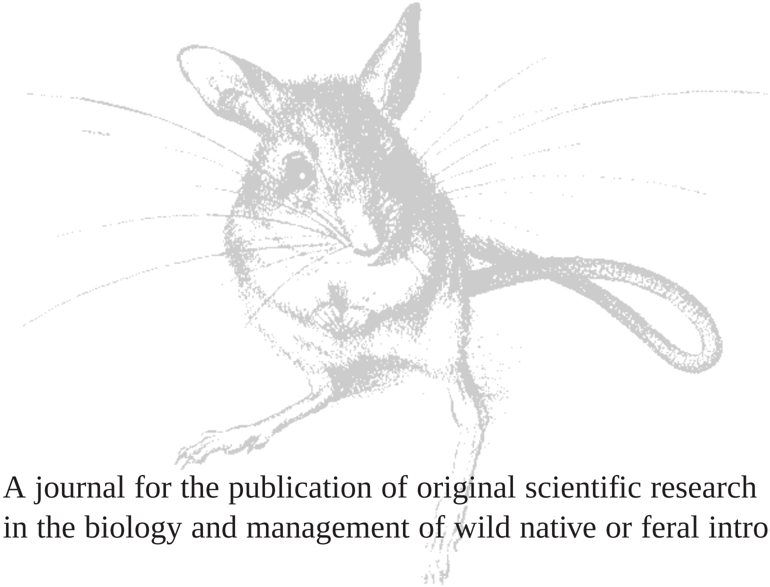

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Movements and Home Ranges of *Crocodylus johnstoni* in the Lynd River, Queensland

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Abstract

Movements of Australian freshwater crocodiles, *Crocodylus johnstoni*, were examined by a mark–recapture study spanning 20 years in the Lynd River, Queensland. After adjustment for detection bias, there was a minor upstream direction to movements. Seasonal changes of location were not evident from field trips taken only twice yearly. Annual movements averaged less than 1 km except for those of pubescent males, which appeared to be nomadic. Creche dispersal was randomly directed but associated with a threshold in mass/length ratio. On average, males were found further from previous capture sites than were females. Adults of both sexes moved shorter distances than did immature crocodiles with a clear reduction in movements occurring as mass/length ratios approached 0·17 kg per cm snout–vent length. Reduced movement at that general size ratio probably indicated the onset of territoriality associated with maturity. Females usually remained near breeding sites even in years when they did not breed. Nomadic tendencies of pubescent males are probably associated with unsuccessful attempts at entering local dominance hierarchies. Linear home ranges were estimated to be 1·5–1·9 km for immature animals, 1·2 km for pubescent females, 30·3 km for pubescent males, 0·6 km for mature females and 1·6 km for adult males.

Introduction

Movement patterns are complex to resolve for Australian freshwater crocodiles, *Crocodylus johnstoni*, because their habits are strongly influenced by social hierarchies (Dunn 1980; Lang 1987), seasonal proximity to mating or nesting areas (Webb *et al.* 1983*a*), thermal conditions (Seebacher 1994) and seasonally fluctuating water levels (Webb 1991). Changes in each factor can facilitate or inhibit crocodilian movements. Movements by *C. johnstoni* are known primarily from locations recorded in mark–recapture studies as no telemetry studies of home range have been undertaken. *C. johnstoni* are thought to remain near the land–water interface, although this activity remains poorly documented, particularly for the wet season (Webb *et al.* 1983*c*). Movements of *C. johnstoni* have been studied at several locations in the Northern Territory (Webb *et al.* 1983*a*, 1983*b*, 1983*c*; Walsh 1989; Cooper-Preston 1992; Kennett and Christian 1993), yet limited information is available concerning effects of sex, size or maturity on movements because of short study duration or small sample sizes.

In this paper, we describe correlates of movement by *C. johnstoni* obtained during a mark–recapture study spanning 20 years, to provide comparative information for Queensland. The study objectives are to investigate movement patterns from a sample large enough to overcome potential biases from unequal capture probabilities of individual crocodiles. We adjusted for detection bias within the study site before determining whether directional biases exist for movement. We tested for different movement patterns in relation to sex, size and maturity. However, effects of size and maturity are confounded in crocodiles because crocodiles are sexually dimorphic and mature at a range of sizes. Therefore, it is sensible to ask whether maturity status, condition or scaled ratios of mass/length account for any sex differences in

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movement. We determined whether creche dispersal in the first year is random or current mediated. To characterise site fidelity, we established which animals move extensively and which are sedentary. We generated probability density distributions of annual movements to estimate composite home ranges. The findings provide new information on several poorly characterised aspects of crocodilian life history.

Methods

Study Area

Crocodiles from the drainage of the upper Lynd River and Fossilbrook Creek in north central Queensland (Fig. 1) were studied. The study site is at relatively high elevations (360–520 m) for the species' distribution and the region experiences an annual wet–dry cycle typical of tropical Australia (Fig. 2). Fossilbrook Creek is spring-fed and contributes the only surface waters to the drainage in the dry season. Proceeding downstream, the study site included 19·1 km of basaltic soils (including 8 km of shallow braided stream), 11·7 km of intergrading but predominantly basaltic soils and 30·8 km of granitic soil. Stream banks were either rocky, sandy or with sparse emergent vegetation because of heavy grazing pressure. *Callistemon*, *Casuarina*, *Melaleuca* and *Pandanus* trees grow along the river. Undercut banks beneath rocks or root masses were often used as refuges or enlarged into burrows by larger crocodiles.

Field trips were conducted during low water levels when *c.* 85% of the drainage consisted of pools 20–40 m wide, 100–800 m long and 0·5–3·0 m deep. Pools were connected by low-gradient rapids extending for 10–40 m or brief vertical cascades of 1–4 m, with a few isolated rapids extending up to 100 m. Conspicuous distinctions between pools and rapids disappear in the wet season when high surface runoff, narrow upstream drainage and a 3 m km^{-1} elevation gradient cause rapid flooding and ebbing. The narrow floodplain of the basalt region limited the availability of shallow-water habitat. Sandbanks suitable for nesting were adjacent to most but not all pools along the drainage. Pools favoured as breeding and nesting sites usually contained a single breeding male, one or more breeding females and an assortment of immature crocodiles.

A large-scale map (1 cm = 0·3 km) was created from aerial photographs (Lyndbrook 7762 series flown at an altitude of 530 m in 1978) and detailed field records. We determined distance between pool midpoints by tracing the mapped drainage with a map measurer. Errors of location were estimated to be ± 0·1 km. We numbered pools consecutively between Amber Hut Crossing and Springfield Camp (Fig. 1); within this section, the mean pool length was 0·72 km (s.d. = 0·40 km, n = 62). Upstream (Springfield Camp to Springfield Drains) and downstream (Amber Hut Crossing to the Pocket) of this main section, pools were longer (mean = 2·92 km, s.d. = 1·00 km, n = 6).

General Methods

The Queensland Department of Environment and Heritage conducted mark–recapture studies in 1976–82, 1984, 1986, 1989 and 1992–95 and a limited portion of the river was sampled in 1990–91. Sixteen sample trips occurred in the nesting season (August–September), 10 trips during the hatching season (December) and supplementary trips were made in March and June for three years. Sample efforts were roughly similar for 12 of 16 years. We captured crocodiles by several methods (Walsh 1987) to obtain a representative sample of all size-classes. After processing, crocodiles were released into the same pool where they were captured.

Crocodiles were placed on their back to measure snout–vent length (SVL) to the nearest 0·1 cm with a straightened steel tape. However, animals were classed into 10-cm SVL categories for statistical analyses. Crocodiles were weighed on a Pesola spring scale to the nearest gram if lighter than 2 kg or on a Salter scale to the nearest 0·5 kg if heavier than 2 kg. We did not adjust mass for (i) crocodiles that had fed recently, as it was impractical to stomach flush all animals, or (ii) gravid females, as we were unable to capture females before and after nesting to determine egg mass. Overestimates from (i) were probably negligible since crocodiles slow their feeding in the dry season (Cooper-Preston 1992), but overestimates from (ii) may account for *c.* 4–7% of body mass (T. Tucker, unpublished data). However, it is appropriate to include total mass as a movement influence in egg-bearing females since it is common for gravid reptiles to show decreased mobility.

Crocodiles were identified by notching their tail scutes and affixing small tags in their rear-foot webbing. We determined sex by visual examination of the genitalia (Webb *et al.* 1984) and assessed maturity for all animals longer than 70 cm SVL. Females were recorded as adults when eggs or vitellogenic follicles were

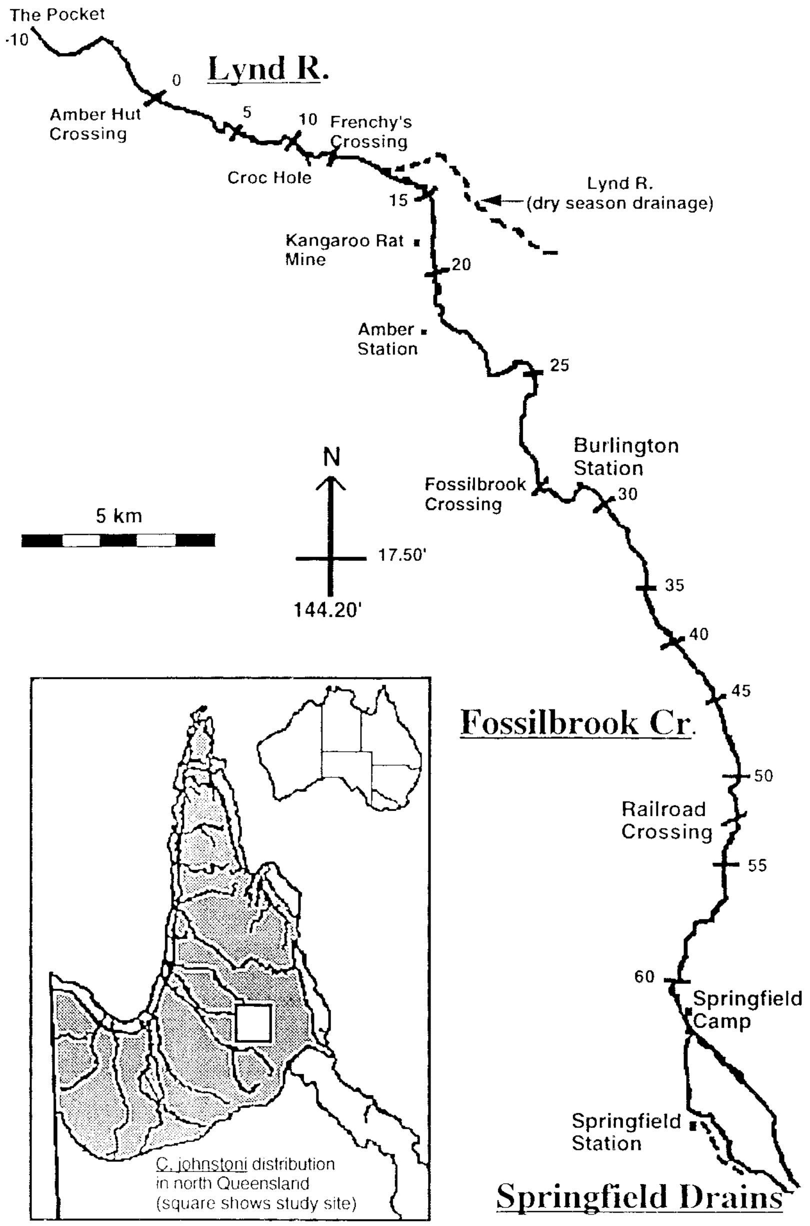

Fig. 1. Location of Lynd River study site. Numbers along drainage indicate pool locations.

detected by cloacal examination, or a fully convoluted mature oviduct, vitellogenic follicles or corpora lutea were visible by laparoscopy (Limpus 1984). Males were recorded as adults if microscopic examination of a sperm smear from the penile groove showed active spermatogenesis (Webb *et al.* 1983*a*), or the epididymis was convoluted and enlarged with sperm when viewed by laparoscopy (C. Limpus, unpublished data). We assigned immature or pubescent status to crocodiles if undeveloped or developing gonads were detected (C. Limpus, unpublished data).

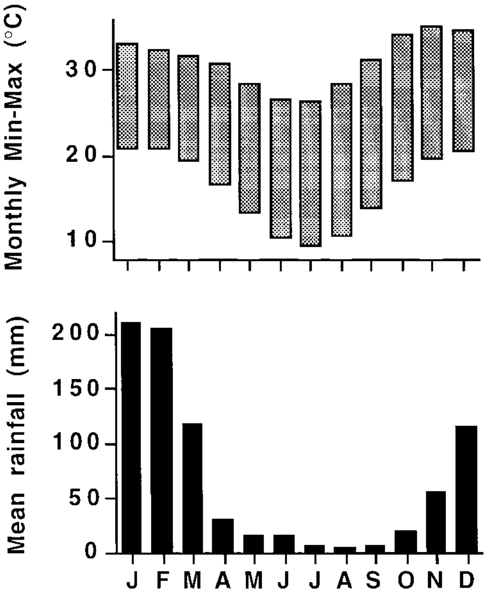

Fig. 2. Seasonal variation in mean monthly temperature (maximum and minimum) and mean monthly rainfall at the Lynd River study site (Australian Bureau of Meteorology, 65-year average for Station 30036, Mt Surprise, 32 km south-south-west of the study site).

Definitions and Selection of Data

In the entire study, 2138 individual crocodiles were captured, marked and released. Of these, 742 individuals were recaptured 1–8 times each, giving a total of 1365 recapture locations. Three components characterised changes of location: direction, distance and elapsed time between recaptures. To quantify directional bias and distance from an initial capture location, we assigned upstream movements as positive distances and downstream movements as negative distances. Animals recaptured in the same pool were assigned a zero distance.

Because the study contained recapture histories of variable length, we selected statistically independent subsets of data in addressing specific questions. The scope of the present study included only movements between successive years or within a year; long-term natal dispersals were addressed by a separate study. To attain independence among observations, we considered only the last recapture interval for each animal. We used recapture intervals that included only one phase of summer growth and extended from one nesting season to the hatching season of the following year (range 0·7–1·3 years). Annual growth rates of animals longer than 30 cm SVL were sufficiently low that few individuals changed size-classes in a single recapture interval. For crocodiles shorter than 30 cm SVL, we assigned the size at recapture.

Means with one standard deviation are reported. If assumptions of normality and homogeneity of variance were not met, we used non-parametric statistical tests or an appropriate transformation before statistical tests. Homogeneity of slopes in ANCOVA (analysis of covariance) was assessed by significance of the interaction term. Statistical tests used $\alpha = 0{\cdot}05$.

Movement Measurements asnd Estimates of Home-range Size

To study spatial heterogeneity in movement, recapture locations were plotted to determine detection biases within the study site (Fig. 3). Any movements beyond the confines of the study site were unrecorded, so we adjusted for this potential detection bias by considering movements only within a zone of equal detection (±10 km). As illustrated in Fig. 3, the adjustment gave a 20-km band across the study site within which to test for directional bias. We compared ratios of movements to non-movements in a log–linear model; we compared differences in up- or downstream distances by a Kolmogorov–Smirnov test.

Temporal variance in movement was examined at a coarse scale as there were no independent data from radio-telemetry for confirmation. We compared sequential capture locations up to two weeks later but within the same sample trip to estimate short-term movement rates. Direct seasonal comparisons between the middles of the wet and dry seasons were not possible for logistic reasons. Instead, we simply compared

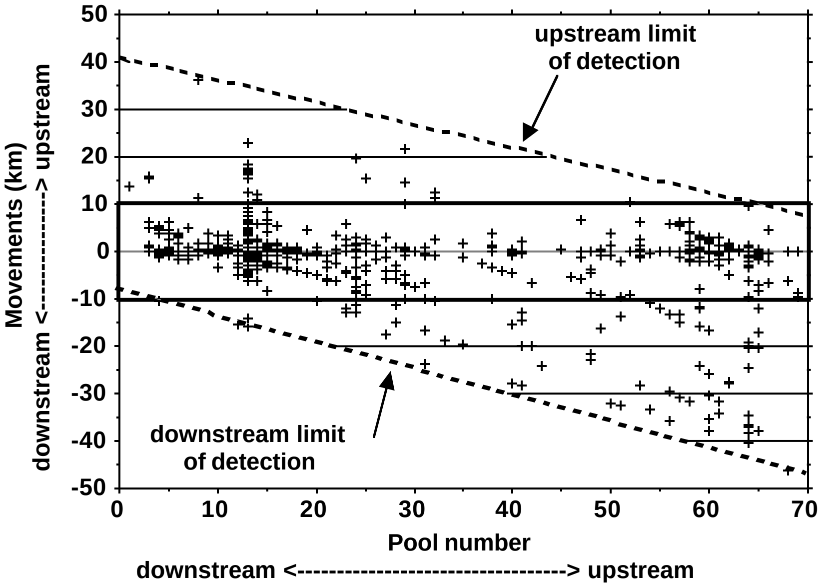

Fig. 3. Movements from pool of capture for 1514 recaptures of freshwater crocodiles in the Lynd River. Downstream movements are negative values and upstream movements are positive values, with dotted lines indicating the limits of movement detection for a pool. The box encloses a 20-km zone where the detection probability for recording upstream or downstream movements was equivalent; tests for directional bias included movements only from this zone.

recapture locations on successive field trips for intervals from nesting to hatching seasons (dry–wet) against those for intervals from hatching to nesting seasons (wet–dry).

To follow creche dispersal in the first year, we used hatchlings less than a week old (recognised by a protruding yolk scar, an intact egg tooth and visual confirmation of freshly excavated nests) to be certain of the natal site. To determine the timing of creche dispersal during early growth, we used multiple regression to examine relationships between movement distance versus age and standardised ratios of mass/length (kg per cm SVL). Recapture locations of crocodiles that were 0·5–1·0 years old were examined to determine whether creche dispersal was random or current-mediated, as a pronounced downstream bias would indicate the latter.

Two factors associated with wet-season rainfall can potentially influence creche dispersal. First, stream flow in wetter-than-average seasons might cause increases in downstream dispersal, particularly if narrow floodplains gave little escape from high current velocities. To test whether drainage structure affected dispersal distance, we compared sections of narrow drainage (the upstream basalt section) with wider floodplains (the downstream granite section). Records of hatchlings (n = 7) that crossed between substratum types or lived in a transition zone were omitted. Second, rainfall affects the density of small floating or streamside prey that young crocodiles eat (Cooper-Preston 1992) and small crocodiles might not travel far from successful foraging areas. As standardised ratios of mass/length present a reasonable reflection of crocodile foraging success, we looked for effects of substratum type on environmental ‘quality’ while accounting for variation in rainfall. We tested dispersal (number of pools travelled from natal site) on each substratum type (category) in an ANCOVA while adjusting for covariates of mass/length ratio and rainfall (total mm of rainfall recorded during November–March at Mount Surprise weather station, Australian Rainman software, Version 2.2).

In tests of correlates of sex and maturity on movement, untransformed means (± s.d.) are reported for distances. However, before statistical tests, we transformed distance data [ln(|x| + 0·01)] to minimise outlier influences of long but rare movements, to compare distances independent of direction and to include nil movements that indicated site fidelity. Distance rankings by combinations of sex and maturity were compared by a Kruskal–Wallis test. Effects of sex and maturity on ratios of movement to non-movements were tested by a generalised linear model with a binomial error structure and logistic link.

Movement tendencies were related to body size by three methods. We fit a least-squares quadratic equation to mean movements of size classes to identify groups that were prone to disperse for each sex. Next, a standard of body condition that was characteristic of the population was determined. Least-squares linear regression of ln(SVL) on ln(mass) ($F_{1,419} = 34\,354$, $r^2 = 0{\cdot}99$, $P = 0{\cdot}0001$) provided a size-independent measure of body condition (relatively superior condition indicated by positive residuals and poor condition by negative residuals). For each sex, residuals and SVL were plotted against movement distance to generate a trend response surface fitted locally by a cubic smoothing spline regression (Hastie and Tibshirani 1990). The vertical scale of the response surface shows zero as a weighted average movement, larger-than-average movements as positive and smaller-than-average movements as negative. Lastly, we detected changes in movement tendencies by plotting movement against scaled ratios of mass/length. This index provided a simple check for thresholds of body size correlated with territoriality by adult males or with residence near a breeding site by adult females.

Breeding dispersal by females was evaluated independently before estimating home ranges of all maturity classes. We tested for breeding dispersal by comparing sequential locations of females in breeding and non-breeding years in a paired *t*-test; a significant difference within subjects signified little site fidelity and was taken as evidence of breeding dispersal.

Conventional calculations of home-range size that require *x*–*y* co-ordinates were inapplicable for a linear habitat like a river drainage. We calculated linear home-range sizes, which simplified the estimation to a univariate probability distribution, because a density distribution of individual movement distances can be taken as a non-parametric estimate of composite home range (Ford and Krumme 1979; Worton 1995). One movement per crocodile contributed to a composite set of movements that was resampled by random permutation to generate a 95% confidence interval. The range bounded by upper and lower intervals was taken as an unbiased estimate of linear home range. Close convergence was obtained between parametric and bootstrap confidence intervals in empirical tests for immature categories (165 immature males, 155 immature females). To avoid problems associated with bootstrapping small samples (Efron and Tibshirani 1986), we used an equivalent number of permutations for distance data from adults (165 permutations for nine movements of adult males; 155 permutations for 17 movements of adult females). To compare our estimate with those from other studies, linear home-range sizes were multiplied by the average river width (30 m) to convert to home-range area (ha). Home-range size ratios were compared by sex and maturity (Stamps 1983).

Results

Spatial Heterogeneity in Movements

For 486 crocodiles recaptured one year later, 61% were within 1 km and 85% were within 5 km of the original capture site (Fig. 4); 94% were within 10 km of the previous capture site. Movement distances ranged up to 37 km but the modal movement was zero; 40% had not moved from the previous capture site. In comparisons of directional preference ($n = 535$) (Table 1), more upstream than downstream directions were observed (307 upstream, 228 downstream: $\chi^2 = 11{\cdot}67$, 1 d.f., $P = 0{\cdot}0006$) and more crocodiles moved than stayed in the same location (535 moved, 446 did not move: $\chi^2 = 8{\cdot}07$, 1 d.f., $P = 0{\cdot}0045$). No difference was found in the proportion of males or females that moved from a previous location ($\chi^2 = 1{\cdot}57$, 1 d.f., $P = 0{\cdot}21$) (Table 1), but more females than males stayed in the same location ($\chi^2 = 6{\cdot}06$, 1 d.f., $P = 0{\cdot}01$).

Before adjustment, movement detection was biased relative to the boundaries of the study site. Downstream movements were recorded predominantly for upstream pools with an opposite tendency for downstream pools (Fig. 3). The unadjusted mean movement vector calculated from all recaptures was 0·74 km upstream (s.d. = 5·64 km, $n = 486$), whereas after adjustment within a ±10-km zone of equivalent detection, the mean movement vector was 0·22 km upstream (s.d. = 2·61 km, $n = 457$). The upstream bias was caused by a higher frequency of upstream travel than of downstream travel, not by greater distances travelled in that direction (Kolmogorov–Smirnov statistic = 1·20, $P = 0{\cdot}23$). Biases were unrelated to movement toward deeper or more persistent pools as the drainage flowed all year and deep pools were distributed throughout the study site.

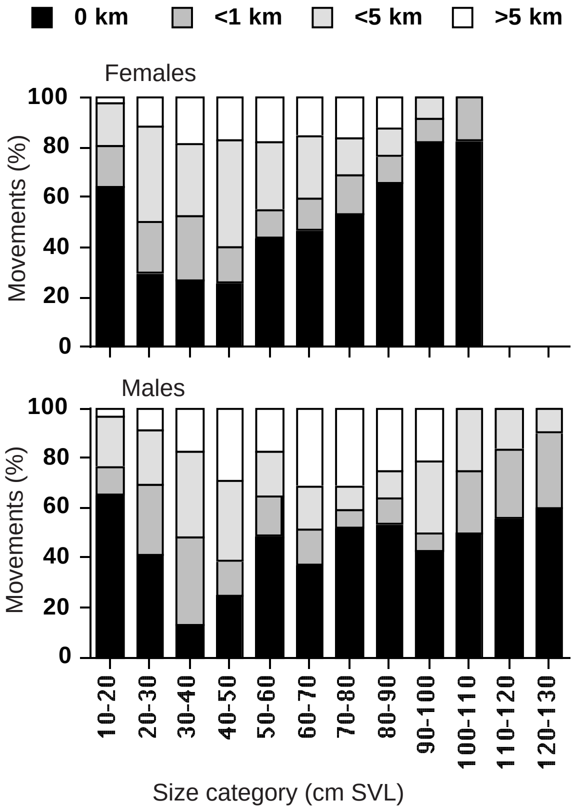

Fig. 4. Percentages of non-movements and movements shorter than 1 km, shorter than 5 km, or longer than 5 km from the original capture point by freshwater crocodiles in the Lynd River. SVL, snout–vent length.

Table 1. Movement preferences of freshwater crocodiles recaptured in the Lynd River

	n	Upstream movement	No movement	Downstream movement
Males	450	153	197	100
Females	531	154	249	128
Hatchlings	153	42	65	46

Temporal Heterogeneity in Movements

For recaptures within 14 days (n = 174), 59% of crocodiles did not move, 77% were found within 1 km and 97% were found within 5 km of the pool where captured. Average movement rate was 0·35 km day^{-1} for short-term movements (s.d. = 1·25 km day^{-1}, range 0–14·1 km day^{-1}) with a 95% confidence interval (CI) of 0·16–0·54 km day^{-1}. We were unable to detect a correlation between distance and time for recaptures between seasons (r = 0·10, P = 0·28). No significant difference (P = 0·98) was found between average movements spanning the dry–wet interval (mean = 1·15 km, s.d. = 6·5 km, n = 106) and those spanning the wet–dry interval (mean = 1·17 km, s.d. = 7·0 km, n = 161).

For recaptures more than six months apart (n = 340), there was a significant trend of increasing distance with time at an approximate rate of 360 m year^{-1} (y = 0·36x + 2·3, P = 0·0001, 95% CI for slope = 0·23–0·50), although the high variability (r^2 = 0·03) suggested that other influences were involved.

Creche Dispersal

For 153 captures of hatchlings during the first year, 30% moved downstream, 27% moved upstream and 43% did not move from the pool nearest their nest site (Table 1). The distribution of distances was highly leptokurtic (kurtosis = 8·30); that is, most hatchlings had not dispersed more than a pool away by end of the first year even though a minority did undertake long movements (range –15·5 to 16·3 km). The mean movement was 0·13 km upstream (s.e. = 0·26, 95% CI = –0·38 to 0·65 km), which corresponded to less than an average pool length.

Multiple regression of age and mass/length ratio against movement distance indicated that mass/length ratios (partial F = 4·60, P = 0·04) but not age (partial F = 0·02, P = 0·88) were significant in explaining creche dispersal. Hatchlings did not move far from the natal site until attaining a threshold mass/length ratio of *c.* 5 g cm^{-1} (Fig. 5). Colinearity between the two factors accounted for a lack of age significance in dispersal as all hatchlings attained the ratio threshold but at different ages because of individual growth trajectories.

Substratum type had no influence on dispersal distance (ANCOVA, $F_{1,95}$ = 0·83, P = 0·37) when adjusted for annual rainfall and the mass/length ratio of hatchlings that moved ($F_{2,95}$ = 2·02, P = 0·14). However, wet-season rainfall had a significant influence on mass/length ratios ($F_{7,95}$ = 8·92, P = 0·0001) that was independent of substratum ($F_{1,95}$ = 0·48, P = 0·49); no interaction was present ($F_{5,95}$ = 0·46, P = 0·81). A positive correlation between rainfall and mass/length ratio (r = 0·59, $F_{1,100}$ = 51·89, P = 0·0001) suggested that foraging opportunities of young crocodiles were linked with seasonal rainfall.

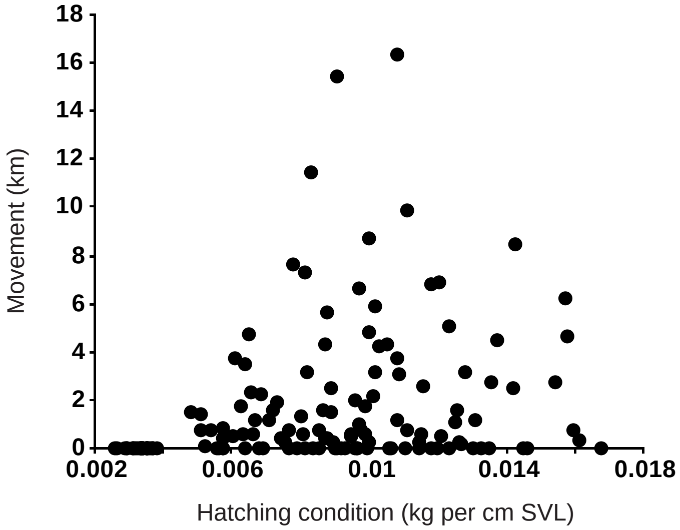

Fig. 5. Dispersal distances of hatchling freshwater crocodiles in the Lynd River from the nest site over the first year. SVL, snout–vent length.

Effects of Sex and Maturity

Significant variation in movement rankings was found among maturity categories (Kruskal–Wallis H = 13·29, P = 0·02), with adult females, pubescent females, adult males, immature females, immature males and pubescent males the order for movement frequency, ranked from lowest to highest (Table 2). Maximum-likelihood estimates for effects of maturity and sex on ratios of movement to no movements indicated no influence of sex (χ^2 = 0·003, 1 d.f., P = 0·96), but there was a significant effect of maturity after correction for sex (χ^2 = 49·13, 2 d.f., P = 0·002). However, the interaction between sex and maturity (χ^2 = 9·49, 2 d.f., P = 0·009) indicated that

Table 2. Movement propensity of crocodiles whose maturity status in both years was immature (I), pubescent (P) or adult (A)

Sex	Maturity	*n*	Movement (%)	No movement (%)	Distance moved (km)	
					Mean	s.d.
Male	I	162	62·3	37·7	0·80	6·39
	P	5	40·0	60·0	13·21	18·41
	A	9	44·4	55·5	0·12	1·25
Female	I	154	61·0	39·0	0·44	4·69
	P	4	25·0	75·0	0·29	0·58
	A	17	17·5	82·5	0·17	0·68

movements by each sex were not consistent across maturity categories. Given the simple factorial design, a coherent interpretation of the interaction was possible. Marginal frequencies indicated that immature crocodiles of both sexes were equally likely to move as not move, that pubescent males were over twice as likely to move as were pubescent females and that adult females were over three times more likely not to move as were adult males. The results were robust, as examination of the observed and fitted frequencies indicated no misfitted cells despite the small samples that resulted from rigorous selection criteria.

Influence of Size, Body Condition and Ratios of Mass/Length

A quadratic least-squares regression fitted for mean distance by each size category (Table 3) showed that on average the greatest movements were taken by females that were 40–50 cm SVL ($y = 1{\cdot}60 + 0{\cdot}05x - 0{\cdot}001x^2$, $r^2 = 0{\cdot}71$, $P = 0{\cdot}01$) and by males that were 60–70 cm SVL ($y = 0{\cdot}73 + 0{\cdot}10x - 0{\cdot}001x^2$, $r^2 = 0{\cdot}45$, $P = 0{\cdot}07$). For males, a marginal insignificance came from above-average residuals for the 60–80 cm SVL categories but from lower-than-average residuals for smaller or larger categories than these. In other words, the crocodile length categories that travelled most widely were preceded and anteceded by size-classes with reduced movement tendencies.

Table 3. Distance moved (mean ± s.e.) by size categories of male and female freshwater crocodiles between recaptures in successive years

SVL, snout–vent length

Size category (cm SVL)	Males		Females	
	Distance moved (km)	*n*	Distance moved (km)	*n*
10–20	1·6 ± 0·5	15	1·5 ± 0·5	16
20–30	2·6 ± 0·5	52	2·7 ± 0·5	68
30–40	2·6 ± 0·6	58	2·0 ± 0·5	29
40–50	2·8 ± 0·7	32	3·4 ± 0·9	31
50–60	2·0 ± 1·3	34	1·7 ± 0·6	30
60–70	6·0 ± 3·1	14	2·7 ± 1·3	16
70–80	5·3 ± 2·2	24	0·7 ± 0·4	23
80–90	2·2 ± 1·1	9	0·8 ± 0·6	25
90–100	0·2 ± 0·2	6	0·0 ± 0·1	3
100–110	0·7 ± 0·8	16	–	
110–120	0·7 ± 0·3	13	–	
120–130	0·5 ± 0·3	6	–	

Table 4. Characteristics of freshwater crocodiles that travelled the longest 5% of distances recorded among movements in the Lynd River
n = 65. SVL, snout–vent length

Characteristic	Percentage
Sex	63% male
	37% female
Maturity	87% immature
	5% adult
	8% hatchling
Size	31% 10–30 cm SVL
	35% 30–50 cm SVL
	25% 50–70 cm SVL
	9% >70 cm SVL
Direction	69% upstream
	31% downstream
Point of origin	65% Amber Station
	31% Burlington Station
	4% Springfield Station

Animals that undertook the longest 5% of movements (Table 4) were characterised as predominantly immature males of 10–50 cm SVL that dispersed upstream, and most had originated from an area of high crocodile density.

The trend surface response for females showed a moderate and steady decline in movement tendency with increased size, particularly in animals of above-average condition (Fig. 6*a*). In contrast, three dominant features appeared on the surface trend for movements by males (Fig. 6*b*). A peak in movement occurred for subadult males that were in below-average condition. Two features other than the peak indicated separate extremes in movement related to size. The steep descent surface of declining condition with increasing size indicates crocodiles that adopted subordinate status. Declines in movement by these males probably reflected a loss-minimising strategy. The other feature is declining movement associated with large crocodiles with positive residuals. This pattern presumably arises with the establishment of a male's territory.

The same interpretation was suggested by a pattern of movement plotted against ratios of mass/length, which indicated a dramatic threshold of change in movement tendency by both sexes near 0·17 kg cm^{-1} (Fig. 7). Although we considered movement as a dependent variable, it was equally conceivable that minimisation of movement or residency in a region of adequate resources actually promoted gains in condition. As a covariate in a two-way ANCOVA, ratios of mass/length had a significant influence on movement ($F_{1,\,340}$ = 6·12, P = 0·0001) regardless of sex ($F_{1,340}$ = 0·21, P = 0·65) or maturity ($F_{1,340}$ = 0·11, P = 0·90) and with no interaction between sex and maturity (P = 0·12–0·85).

Site Fidelity and Home Range

Little evidence was found for breeding dispersal in the Lynd River. For eight adult females recorded outside the breeding season, seven were recaptured in the same pool as during the breeding season. Accordingly, there was no difference in breeding and non-breeding locations (within subjects $F_{1,7}$ = 1·0, P = 0·36). Long-term residence near breeding locations was apparent from capture histories of breeding females. Eight of nine females with breeding histories ranging from 10 to 20 years had moved only 0–2 pools from where they were first captured when gravid; the remaining female moved four pools away from a pool that was abandoned by all inhabitants in a year when all available sand for nesting substratum near the pool was lost during the preceding wet season.

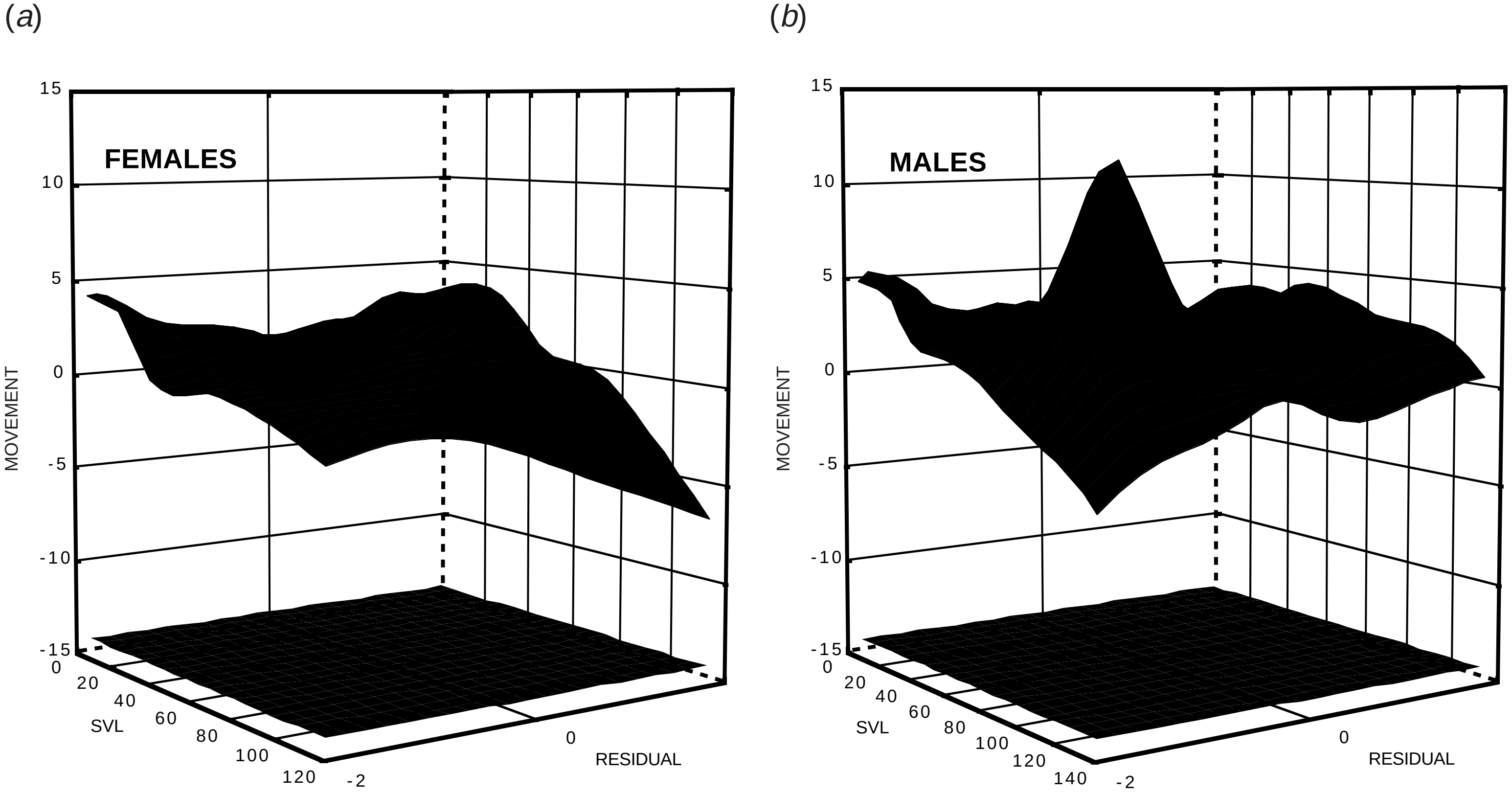

Fig. 6. Trend surface responses for (*a*) female and (*b*) male freshwater crocodiles for body length [cm snout–vent length (SVL)] and body condition [standardised residuals for regression of ln(mass) against ln(SVL)] on movement. Positive residuals indicate animals in superior condition and negative residuals indicate animals in below-average condition. Zero on the movement scale represents an average movement with values scaled as the number of kilometres more or less than an average movement. Shaded contours on the floor of the plot provide information about the hidden surface topography.

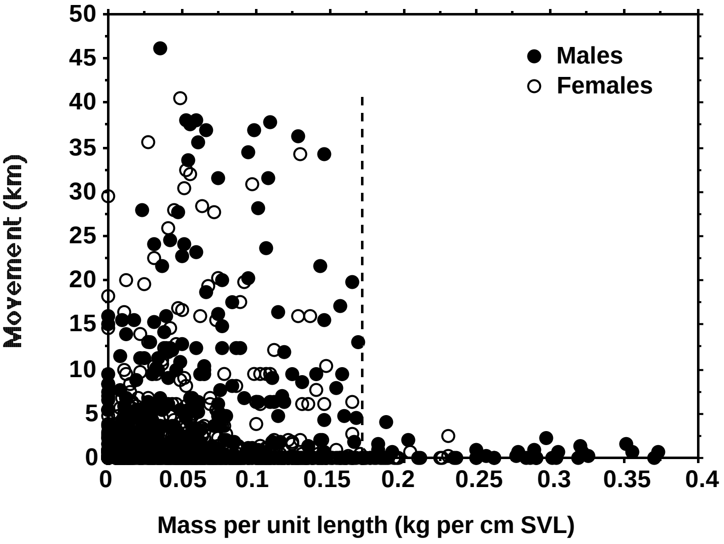

Fig. 7. Indication of thresholds for territoriality by freshwater crocodiles as interpreted from the influence of mass/length ratio [kg per cm snout–vent length (SVL)] on movement.

Immature crocodiles had larger home ranges than did adults, and males had larger home ranges than did females (Table 5). Pubescent females had home ranges closer in size to those of immatures than to those of adult females. The extensive travel of pubescent males (Table 5) probably indicated a nomadic phase before establishment of an adult home range rather than occupancy of a vast territory. Home-range ratios (male : females) indicated a minor bias towards males for immature crocodiles (1·3 : 1), a huge bias towards males among pubescent crocodiles (26 : 3 : 1), and a consistently larger home range among adult males (2·7 : 1).

Discussion

This study successfully determined several key components that characterise crocodile movements in the Lynd River. However, an obvious comparison with previous movement studies of *C. johnstoni* (Webb *et al.* 1983*a*, 1983*b*; Cooper-Preston 1992; this study) is among aquatic habitat types. We find that the following habitat ‘types’ are convenient but artificial

Table 5. Estimates of linear home-range size from parametric and bootstrapped 95% confidence intervals (CI) for annual movements by freshwater crocodiles in the Lynd River, Queensland

Home-range areas were the product of linear home-range sizes and average river width (30 m)

Sex and maturity	*n*	Parametric estimate		Bootstrapped estimate	
		Linear home-range size (km) (95% CI)	Home-range area (ha)	Linear home-range size (km) (95% CI)	Home-range area (ha)
Female immature	154	1·49 (–0·30 to 1·19)	4·47	1·54 (–0·28 to 1·26)	4·62
Female pubescent	4	1·83 (–0·63 to 1·20)	5·49	1·15 (0·00 to 1·15)	3·45
Female adult	17	0·69 (–0·17 to 0·52)	2·07	0·59 (–0·03 to 0·56)	1·77
Male immature	162	1·98 (–0·19 to 1·79)	5·94	1·93 (–0·17 to 1·76)	5·79
Male pubescent	5	45·70 (–9·65 to 36·08)	137·10	30·26 (0·00 to 30·26)	90·78
Male adult	9	1·92 (–0·84 to 1·08)	5·76	1·58 (–0·70 to 0·88)	4·74

categories that can be designated in the dry season: linear riverine habitats (Type I), broad expanses of wetland such as swamps, marsh and lakes (Type II), and isolated bodies of water such as ponds, waterholes or billabongs (Type III). Habitats of *C. johnstoni* that are representative of each type include the Lynd and Katherine Rivers (Type I), Lakes Argyle and Kununurra in Western Australia (Type II) and the McKinlay and Liverpool Rivers (Type III).

Fundamental differences in hydrology suggest that movement is more easily facilitated in Type I habitats with continuous stream flow than in seasonally restricted Type III habitats (recapture rates within 1 km of an original capture are 61% in the Lynd, cf. 83% in the McKinlay and 100% in the Liverpool). A contrasting view is that Type III habitats could cause greater movements if contracting water levels force crocodiles to move toward the remaining deep pools, yet the available evidence (Webb *et al.* 1983*a*, 1983*b*; Cooper-Preston 1992; this study) provides no support for the assertion.

Directional preferences of *C. johnstoni* may be evident in the dry season if movements are oriented toward burrows or deep pools (Webb *et al.* 1983*b*). However, dry-season refugia are probably less important in rivers with continuous flow such as the Lynd than for crocodiles that occupy Type III habitats. In our study, upstream movements were recorded more often (31%) than were downstream movements (23%), with 45% of crocodiles not moving, whereas in the McKinlay River 20% moved upstream to areas of deeper pools and 7% moved downstream but 73% remained in the same pool; the last category reflects the use of deep pools that remained in the dry season (Webb *et al.* 1983*a*, 1983*b*). Recaptures of *C. johnstoni* in the Northern Territory indicate high site fidelity to specific burrows or caverns for aestivation in the dry season (Walsh 1989; Kennett and Christian 1993). Additional evidence of site fidelity or homing by crocodilians is known from displacement experiments on *C. johnstoni* (Webb *et al.* 1983*b*) and *Alligator mississippiensis* (Chabreck 1965; Rodda 1984*b*, 1985), by breeding migrations of *C. niloticus* (Modha 1967), by relocations of problem *C. porosus* (Walsh and Whitehead 1993) and by dry-season migrations of *Caiman crocodilus* to permanent water (Staton and Dixon 1975; Gorzula 1978).

However, to discriminate between directional orientation and random walks requires reciprocal translocation both upstream and downstream (as in Chabreck 1965; Webb and Messel 1978). Until we accounted for the proximity of upstream or downstream boundaries in our study, potential directional biases were obscured by detection biases (see Fig. 3). A separate movement study of adult *C. johnstoni* recorded a downstream directional bias from an upstream release site as evidence for homing (Webb *et al.* 1983*b*). However, those results may simply indicate detection bias since capture efforts were concentrated downstream from the release site and fewer than half of the translocated crocodiles were recovered. Translocated crocodiles seldom linger in a release area (Webb and Messel 1978; Webb *et al.* 1983*b*), often because of aggressive interactions with resident crocodiles (Walsh and Whitehead 1993). Hence post-translocation movements may be unrelated to homing or orientation tendencies (Murphy 1981). Reciprocal translocation of both small and large crocodiles tracked by radio-telemetry would improve our comprehension of the strength and nature of homing in crocodilians.

Temporal Trends

There were several cases where short-term travel exceeded movement recorded over a yearly interval. Hence it is difficult to interpret whether our annual capture activities promoted short-term movements. Any disturbance from the brief field trips would appear minor and more likely to affect immature crocodiles because most adults were recaptured in the same pool in a following year.

Given that little evidence was found for seasonal movement, it is possible that confined movements are typical year-round. However, it is likely that infrequent field trips simply are unable to document seasonal movements. There are anecdotal accounts of crocodiles moving into and from small creeks that join the Lynd in the wet season but that are dry during the remainder of the year (K. McDonald, unpublished data). A thermal study of *C. johnstoni* in the Lynd River noted that crocodiles with implanted transmitters travel more often during the wet season (Seebacher 1994). Cooper-Preston (1992) reports seasonal movements for a *C. johnstoni* that travelled more than 80 km between dry seasons in the Katherine River yet the recapture location was within 400 m of the original capture site. Seasonal changes in density of *C. johnstoni* are interpreted as responses to rising and falling water levels (Webb *et al.* 1983*c*; Cooper-Preston 1992) and other crocodilians show similar movement patterns coinciding with seasonal flooding, for example, *C. niloticus* (Cott 1961), *Caiman crocodilus* (Staton and Dixon 1975; Gorzula 1978), *Crocodylus porosus* (Webb and Messel 1978) and *A. mississippiensis* (Chabreck 1965). Detailed accounts of seasonal movements will clearly require telemetry.

Creche Dispersal

Equivalent numbers of upstream and downstream dispersals of hatchlings were recorded despite differences in wet-season rainfall and drainage characteristics. The pattern suggests that creche dispersal is not current-mediated, or downstream movements would be expected to predominate. An overall upstream vector, even though minor, may reflect an underlying current orientation or rheotaxis by smaller crocodiles. The prospect deserves additional study as an instinct to head upstream can be vital to maintaining position despite strong currents in the wet season. Furthermore, more extensive creche dispersal seems to characterise crocodilians residing in river or tidal habitats [*C. acutus* (Mazzotti 1983); *C. porosus* (Webb and Messel 1978; Magnusson 1979)] than those inhabiting lentic habitats [*A. mississippiensis* (Chabreck 1965; Dietz 1979); *C. acutus* (Rodda 1984*a*); *C. niloticus* (Pooley 1969)].

Several factors are allied with the finding of an environmental influence on mass/length ratio and a correlation between mass/length ratios and creche dispersal. First, creche behaviour seldom lasts more than a month in *C. johnstoni* (K. McDonald, unpublished data) but can be highly variable among crocodilians, ranging from a few days to more than one year (Dietz 1979; Mazzotti 1983). The threshold in mass/length before wider movements ensue probably corresponds to the consumption of residual yolk mass (Fischer *et al.* 1991) and a subsequent need to forage (Cooper-Preston 1992). Similar foraging movements are thought to account for spacing behaviour among hatchling *C. acutusj* (Rodda 1984*a*), but it is pertinent to note that exceptional ‘poor’ or ‘good’ wet seasons may shift the timing of creche dispersal. Crocodiles that occupy rich foraging habitats might logically have little cause to move elsewhere (Tucker *et al.* 1996, 1997), but more data on habitat quality and hatchling mortality are required to accept this premise. A lack of effects from rainfall or drainage characteristics on dispersal suggests that biological factors within the Lynd River are more influential than are physical factors in terms of creche dispersal. Finally, greater dispersal with increasing body size is to be expected because physiological costs of locomotion in crocodilians are inversely related to size (Gatten *et al.* 1991).

Correlates of Sex, Size, Maturity and Body Condition

Size- and maturity-related movement patterns in the Lynd River appear to be consistent with behaviour of *C. johnstoni* in the McKinlay and Katherine Rivers (Webb *et al.* 1983*a*; Cooper-Preston 1992). Juvenile *C. johnstoni* vary widely in the extent and direction of movements, as reported for other juvenile crocodilians (McNease and Joanen 1974; Schaller and Cranshaw 1982; Ouboter and Nanhoe 1988), but as adults, movements become localised in areas that provide suitable food, proximity to mates, nesting banks and burrows. Population density will determine which pools are already occupied and levels of resource competition within pools, but adult females generally move to or remain near suitable nesting substrata while adult males occupy regions that overlap with females. There are no sex differences in proportions of movements directed either upstream or downstream, but substantially more females than males did not move at all. This difference probably results from adult females remaining near a nest location. Even though female *C. johnstoni* do not actively guard nests in the wild (Greer 1970), they remain nearby to excavate nests at hatching.

A wider variance in movements by adult males than by adult females may result from seeking access to females or territorial defence (Lang 1987; Drews 1990). Movements by pubescent males are possibly promoted by aggression from larger dominants (Dunn 1980) or if a pubescent seeks an unoccupied territory. Non-breeding or small adult males generally bear more scars from 'ritual' bites than do larger animals (Webb and Manolis 1983), and our observations of extensive movements by pubescent males (Table 2) are consistent with conventional wisdom on a polygynous mating system in a size-based hierarchy (Webb and Manolis 1983; Lang 1987).

Our perceptions of crocodile movement are largely shaped by when it is convenient to conduct field studies, namely in the dry season. However, as pool dimensions change seasonally, crocodiles are likely to perceive and use the aquatic habitat differently in response. Therefore, it may be difficult at first to attach biological significance to an average difference of a few pools because of the variance in movements by adult or immature animals. Yet movement to only one pool upstream or downstream can place an individual in an entirely different assemblage of crocodiles during the dry season when intense social interactions occur among breeding individuals (Dunn 1980; Lang 1987). Modest annual movements can thereby contribute to significant long-term dispersal with important consequences on reproductive fitness of parents and offspring. Male-biased dispersal is predicted for polygynous mating systems, but no studies have yet investigated natal dispersal in long-lived aquatic vertebrates such as crocodiles (Johnson and Gaines 1990).

Thresholds of decreased movement at similar body-size indices for each sex (Fig. 7) may reflect establishment of an adult home range. For females, the state is probably associated with the attainment of sufficient energetic stores for reproduction, but for males it probably represents a sufficient size to claim territory and breeding access to females. Crocodiles of average mass/length ratios are equally likely to move or remain in the same pool. While habitat quality cannot be inferred directly from movement inclinations, a lower probability of movement by animals in better condition (residuals >1) may reflect residency in a pool that provides adequate resource conditions. Likewise, it is difficult to understand why crocodiles in worse-than-average condition (residuals <–1) have low movement rates, unless poor condition affected movement abilities, as these individuals would presumably benefit from leaving a pool where they fared poorly.

Site Fidelity and Home-range Size

A few conclusions about home-range size restate the preceding discussion since estimates were derived from a probability distribution of distances. However, composite home ranges derived from independent movements contain no bias from serial autocorrelation as do home ranges derived from following a few animals in a limited range of habitat (Worton 1995). Consequently, probability distributions allow other studies of crocodilian movements to generate meaningful home-range estimates from many recapture records of individuals but few observations per animal.

Population density has an additional influence on home-range size of crocodiles (Webb and Messel 1978), although density was not quantified for the present study. We expect that individual variations in home-range size will be contingent upon size and maturity of each crocodile relative to the other conspecifics present. A lack of home range for pubescent males (Table 5) is probably promoted by larger conspecifics because once adult status was attained, males had characteristically low movement levels. Similar nomadic tendencies by pre-breeding males are reported for *A. mississippiensis* (McNease and Joanen 1974), *C. niloticus* (Hutton 1989) and *C. porosus* (Webb and Messel 1978).

Dispersal by females for breeding appears uncommon and because sandbanks of variable size are found near most pools along the Lynd River, there may be little cause for extensive travel to suitable nest areas. Female *C. johnstoni* often remain near a nest site until hatching occurs (Webb and Manolis 1989), but some crocodilians display a wider scope of movement by breeding females (Joanen and McNease 1970; McNease and Joanen 1974; Hutton 1989). For example, when nesting habitats are limited, female *C. acutus* travel to suitable nesting substrata for the season (Gaby *et al.* 1985). Home-range sizes of female crocodilians may fluctuate seasonally (Joanen and McNease 1970), but often shrink to the nest vicinity during the reproductive period (Goodwin and Marion 1979; Rootes and Chabreck 1993). Furthermore, not all females exhibit home-range shifts (Hutton 1989; Rootes and Chabreck 1993). The stability of nest-site preference over spans of up to 20 years by Lynd River females argues that there may be seldom cause to move far from an initial choice of nesting site.

Crocodile home-range sizes are described as being inversely correlated with habitat heterogeneity and resource richness (Rodda 1984*a*). In similar comparisons of habitat type, fish home ranges are larger in lacustrine habitats (Type II) than in continuously flowing habitats (Type I) than in seasonally constrained habitats (Type III) (Minns 1995). Related spatial influences on home-range size are posited to exist in other crocodile populations (Webb and Messel 1978; Hutton 1989), but to test the hypothesis for *C. johnstoni* requires additional data from Type II and III habitats. Such comparisons would clarify whether narrow drainages at higher altitudes impose different physical constraints on home-range size than do broader rivers of the coastal plains.

This investigation identified relevant questions for additional research. With baseline information now available from several recapture studies, future studies of *C. johnstoni* that incorporate radio-telemetry would advance our understanding of dynamic activity budgets and seasonal patterns of habitat use by different life-history stages. The possibility of sex-biased dispersal begs additional study because reptiles are poorly represented in studies of natal dispersal (Johnson and Gaines 1990). Such topics are excellent opportunities to relate field studies of crocodilians to questions of broad ecological scope.

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