

Movement and Dispersal Patterns of *Crocodylus porosus* in some Rivers of Arnhem Land, Northern Australia*

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Abstract

The dispersal of juvenile *C. porosus* hatched in the Liverpool River is described. Of those initially caught when hatchlings, 1-y-olds and 2-4-y-olds, and recaptured 1 year later, 93%, 73% and 57%, respectively were within 10 km of the original capture site. Movements of up to 21 km in one direction in 1 year could be followed by a similar movement in the opposite direction the following year. Relocated *C. porosus* demonstrated a homing instinct. A possible explanation for the long distances travelled by some juveniles (up to 81 km in a year), is that chance wandering placed them in the mouth of another stream, and attempts to 'home' in the new stream took them further away from their original capture site. The distribution of *C. porosus* in other rivers can be explained by dispersal patterns similar to those found in the Liverpool River. Some rivers seem to have supported successful *C. porosus* breeding for a number of years, others seem to have been sporadically successful, and still others unsuccessful. Movement of juveniles from 'successful' to 'unsuccessful' rivers could account for older juveniles found in the latter type of river.

Introduction

Although 28 species and subspecies of living crocodylians are currently recognized (Brazaitis 1973), *Alligator mississippiensis* appears to be the only one whose movements have been studied in detail. By mark-recapture methods (Chabreck 1965) and radio-telemetry (Joanen and McNease 1970, 1972; McNease and Joanen 1974), movement patterns of adult and subadult *A. mississippiensis* have been examined, and seasonal influences described. These studies have been fundamental to the formulation of a trial harvest program (Palmisano *et al.* 1973), and the development of a model for simulating a commercially harvested *A. mississippiensis* population (Nichols *et al.* 1976).

Crocodylus porosus, the saltwater or estuarine crocodile, is generally regarded as the crocodylian which most readily takes to the sea (Ditmars 1910; Smith 1931; Loveridge 1945; Wermuth 1964; Neill 1971; Guggisberg 1972; Brazaitis 1973). This reputation results from sightings of the animals travelling at sea (e.g. Hornaday 1926), and the appearance of individuals well away from known populations (Neill 1971); recently, a 3.8-m male *C. porosus* arrived at Ponape, Eastern Caroline Islands, 1360 km from the nearest known population (Allen 1974). Most of the above authors attribute the wide distribution of *C. porosus*, from India across to the

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Philippines and down to Australia (see Wermuth 1953; Neill 1971; Brazaitis 1973), to its 'not uncommon...long sea journeys' (Brazaitis 1973).

In Australia, *C. porosus* are restricted to the coastal regions of the far north (Cogger 1975). They are mostly found in rivers as far upstream as tidal influence extends, though populations exist in swamps, billabongs, lakes and non-tidal rivers (Webb *et al.* 1977a). In Papua New Guinea, and perhaps many other countries, *C. porosus* are now far more common in freshwater swamps than in tidal rivers (John Lever, personal communication), but this appears to be an artefact of selective hunting; crocodiles in tidal rivers are exposed on the edge of mudbanks at low tide and are more easily approached and shot than those in non-tidal, vegetated swamps.

Our early studies of *C. porosus* were mainly carried out in the Liverpool River system, on the north coast of Arnhem Land. Movement and dispersal were studied by annual recapture of marked individuals, between 1973 and 1975. Adults, which were extremely wary and few in number, were rarely caught, and consequently the study deals mainly with juveniles.

Some data on adult movements were obtained while testing development models of a new radio-tracking system (Brockelsby 1974; Yerbury 1977), and these are presented. Additional insights into *C. porosus* dispersal patterns have been obtained from examining the distribution of different-sized individuals in some northern rivers.

A preliminary discussion of *C. porosus* movement has been included in a popular publication (Webb 1977).

Methods

General

Snout-vent length (svl) has been used as the standard measure of *C. porosus* body size, total length [approximately twice svl (Webb and Messel 1978)] being rejected because of tail tip amputations (Webb and Messel 1977a).

For plotting *C. porosus* locations, maps were prepared from aerial photographs, and the accuracy of stated locations is ± 0.1 km.

Mark-Recapture

C. porosus were mostly caught with either handnet, harpoon or set of 'Pilstrom' tongs (Rogers, Arkansas) (Webb and Messel 1977b). Total length, svl and body weight were measured (complete list of measurements in Webb and Messel 1978), and sex determined by direct observation of the spread cloaca. Each animal was consecutively numbered by branding a sequence of scute whorls on the tail, and individuals were released at the site of capture within 24 h. Altogether, over 1500 *C. porosus* were caught, marked and released in 11 different rivers. To date, recapture efforts have been restricted to the Liverpool River system because crocodiles become shy and difficult to catch once they have been caught and handled [also found by Bustard (1968)], and long-term growth and movement studies are still in progress.

Catching was generally restricted to the dry season of each year (May–November; see later) and, though some individuals have been caught at other times, they are only briefly alluded to here.

Relocation Experiment

To obtain information on the effect of relocation on movement, 20 *C. porosus* (eight hatchlings and 12 1½-y-olds) were caught between 63.2 and 67.8 km upstream in the Tomkinson River and released on the shores of Bat I. (Fig. 1) in September 1973. Five have subsequently been recaptured.

Three other individuals, which were recaptured, had been released at sites more than 5 km from where they were originally captured.

Telemetry

Yerbury (1977) has discussed the high-frequency radio-tracking system (1.2 GHz) being developed. Seven experimental transmitter models have been tested on *C. porosus* in the field.

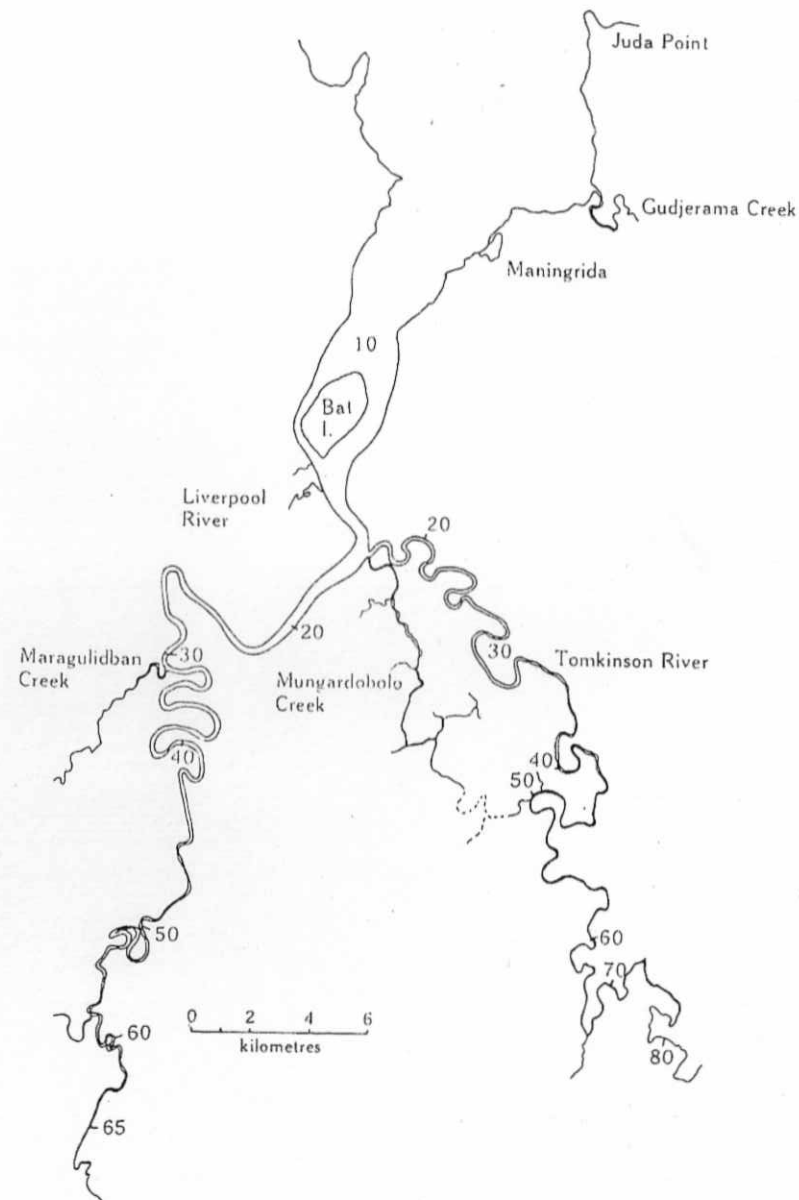


Fig. 1. The section of the Liverpool River system which is under tidal influence. Numerals, kilometres upstream; broken line, a seasonal channel.

The transmitters are attached to the cranial platform (Yerbury 1977), and, as at any one time there was often only one crocodile in the river with a transmitter attached, sightings of such crocodiles have given some information, even when the transmitter was not working.

River Surveys

General crocodile surveys were carried out at night from 5-m boats powered by 50-hp outboard engines (see Messel 1977). Crocodiles were located by the reflective tapetum of the eye: a red glow in the beam of a spotlight. In most cases, individuals were approached to within 3 m and body size estimated in 1-ft categories of total length. This measure was intuitively more familiar than metrics to the observers.

A comprehensive study aimed at explaining variation in *C. porosus* night survey counts is currently under way, but not yet complete. Indications are that variation in consecutive surveys is usually much less than 25%, and somewhere between 60 and 90% of juveniles in a section of river are seen during a night survey at low tide. Altogether, some 38 rivers and creeks have been surveyed at low tide; however, not all are discussed in the present paper.

The Study Area

Annual average rainfall at the mouth of the Liverpool River (Maningrida Settlement; 134°15'E., 12°2'S.) is 1141 mm; 83% falls between December and March (95% between November and April), giving distinct wet and dry seasons.

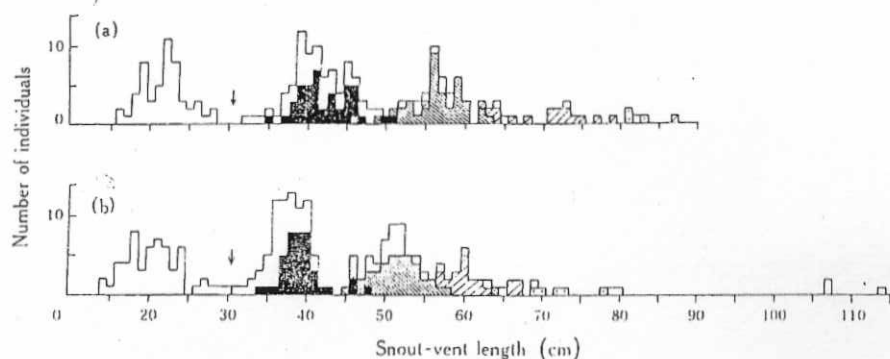


Fig. 2. Size-frequency histograms of male (a) and female (b) *C. porosus* caught during the dry season in the Liverpool River. Black, recapture size of crocodiles which were less than 31 cm svL when first caught. Light hatching, recapture size of crocodiles which were within the cohort typified by the black region, when first caught. Heavy hatching, group 4; dotted areas, group 5 (see Table 1).

Maximum air temperatures (at 0900 and 1500 h) range from monthly means of 32.7°C (November) to 30.0°C (July), and minimum air temperatures from 25.0°C (December) to 16.3°C (July) (means for 15–17 years from the Australian Bureau of Meteorology).

The sections of the Liverpool River system which are under tidal influence (Fig. 1) have muddy banks, are lined with either mangrove forest or flood-plain grasses and sedges, and contain water discoloured with suspended sediments. There are two tidal cycles each day and tidal range is about 3 m. During the dry season a salt wedge moves upstream, and by November mildly brackish water (<5‰) may be at the limit of tidal influence. During the wet season, extensive flooding can occur and zero salinity has been measured 10 km upstream in the Liverpool River.

Results

General

With the exception of five individuals, movements were explained by assuming travel was via the main streams. The five exceptions were originally marked and

released between 49.4 and 59.9 km upstream in the Tomkinson River, and recaptured in Mungardobolo Creek. A channel, which flows during the wet season, joins the upper reaches of Mungardobolo Creek to the 50.5-km mark in the Tomkinson (Fig. 1), and it was assumed that the five individuals travelled by this route. Unlike movement in the main stream, where water is always present, that by the channel could reflect a short movement to get into the channel, then a continued movement as water levels recede. In most of the following analyses, these five have been excluded.

The size-frequency histograms of juveniles caught during the dry season (Fig. 2) shows some distinct age-size groups or cohorts. It was assumed that all *C. porosus* less than 31 cm svL were between 0.1 and 0.8 years of age (hatchlings from the previous breeding season), and from the size of these individuals, when recaptured after 1 y, the size of *C. porosus* when 1.1–1.8 years of age was determined.

Table 1. Age-size groups of *C. porosus*

N, the number recaptured which were in the specified size group when first caught

Group No.	svL (cm)	<i>N</i>	Males		Females	
			Age composition (years; percentage)	svL (cm)	<i>N</i>	Age composition (years; percentage)
1	10–30	53	0.1–0.8; 100	10–30	40	0.1–0.8; 100
2	32–50	43	1.1–1.8; 95 2.1–2.8; 5	31–43	37	1.1–1.8; 100
3	51–63	38	1.1–1.8; 2 2.1–2.8; 85 3.1–3.8; 13	45–56	41	1.1–1.8; 7 2.1–2.8; 93
4	64–80	14	2.1–2.8; 2 3.1–3.8; 85 4.1–4.8; 13	57–67	23	2.1–2.8; 14 3.1–3.8; 86
5	81–90	5	3.1–3.8; 20 4.1–4.8; 70 5.1–5.8; 10	68–78	5	3.1–3.8; 14 4.1–4.8; 86
6	—	—	—	79–120	3	5.1–5.8; 33 7.1–7.8; 67

By repeating this process with *C. porosus* caught when between 1.1 and 1.8 years old (i.e. those within the size range determined above) and recaptured 1 y later, the size of 2.1–2.8-y-olds was estimated. Table 1 was derived in this manner: the overlap of age classes results from variations in growth rate and time of hatching (February–June; Webb *et al.* 1977a).

Movement of *C. porosus* Hatchlings from Nest Sites

Hatchlings ($n = 52$) from three nests in the Tomkinson River (53.9, 59.7 and 65.1 km upstream) were marked within a week of hatching (June 1974); 43 were recaptured 2–2½ months later, and 19, 13–13½ months later. Their recapture locations relative to the nest sites are shown in Table 2. As described elsewhere (Webb *et al.* 1977a) the hatchlings formed crèches with an adult (presumed to be the female) for at least 2 months.

After 13–13½ months, 19 of the hatchlings were recaptured: 11 of the males had moved downstream and one upstream of the nest site; two females had moved downstream and five upstream. These proportions were significantly different

($P = 0.009$; Fisher's exact probability test), indicating that more males moved downstream from the nest site than females. Maximum downstream movement was 38.9 km from the nest, though the remainder of the sample were within 14 km of the nest site (mean \pm SD = 3.3 ± 4.8 km; range from 15.6 km downstream to 6.8 km upstream; $n = 18$).

Table 2. Dispersal of *C. porosus* hatchlings from nests in Tomkinson River

	2-2½ months after hatching	13-13½ months after hatching
No. of hatchlings	43	19
Percentage recovered at distance of:		
50-11 km downstream	0	11
10-6 km downstream	0	26
5-2 km downstream	2	26
1 km each way	91	26
2-5 km upstream	2	0
6-10 km upstream	5	11

Movement of Juvenile *C. porosus* where Nest Site is Unknown

Seventy-nine males and 90 females which had been caught, marked and released during one dry season, were recaptured the following dry season. The recapture locations relative to the initial capture locations are shown in Fig. 3. Clearly, there is a nearly normal distribution around the initial capture site, with a tail of long-distance movers, especially downstream.

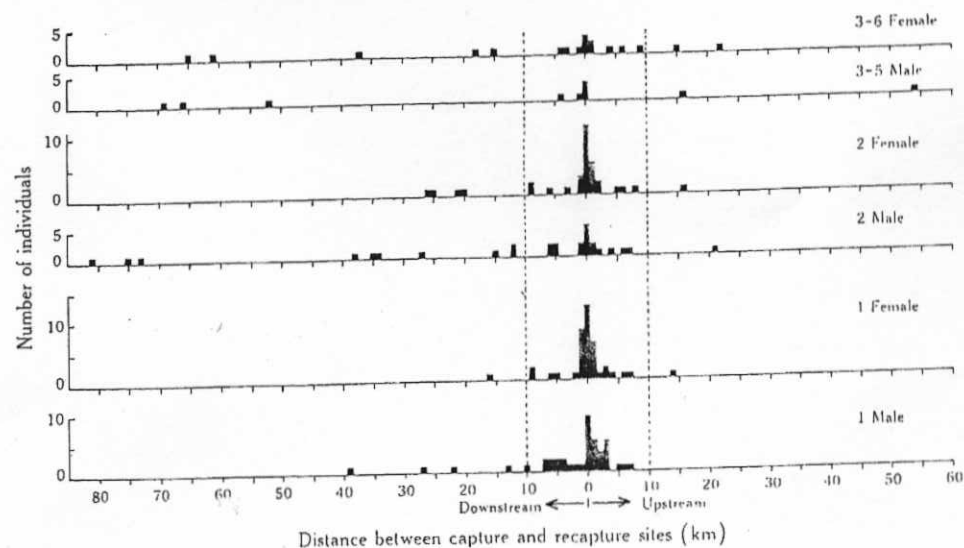


Fig. 3. Recapture location relative to capture location for male and female *C. porosus* recaptured after approximately 1 year. Numerals refer to groups in Table 1.

To facilitate comparison of groups (Table 1), animals which had moved more than 30 km from their initial capture site were termed 'long-distance movers' (LDM)

and those which had moved less, 'short-distance movers' (SDM). In Fig. 4, the percentage of SDMs in each group is plotted against the mean svL of the group for both males and females. The proportion of SDMs decreases with increasing body size. Numbers of individuals in groups 1 and 2 were sufficient for a meaningful comparison between sexes, and it was found that the proportion of SDMs in group 2 males was significantly less than in group 2 females ($P = 0.024$; Fisher's test), i.e. more males than females moved more than 10 km from their original capture site. The apparent greater mobility of females over 50 cm svL (Fig. 4) was not significant.

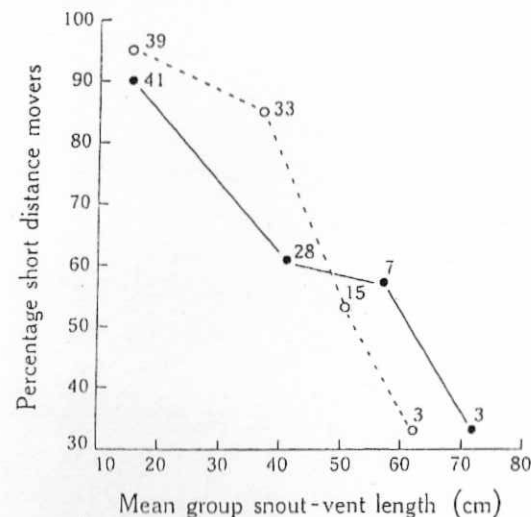


Fig. 4. The percentage of *C. porosus* that were caught less than 10 km from their original capture site (SDM). Mean group snout-vent length refers to the midpoint of the svL ranges in Table 1. ● Males. ○ Females. Numerals are sample sizes. The lines joining points are to distinguish sexes and are of no statistical significance.

Table 3. Distances between capture and recapture sites of *C. porosus*

For definition of groups, see Table 1. Interval between captures approximately 1 year. Values are percentages of captures in each group at each distance. D, downstream; U, upstream

Distance from initial site (km)	Males			Female			Male + Female		
	Group 1	Group 2	Groups 3-5	Group 1	Group 2	Groups 3-5	Group 1	Group 2	Groups 3-5
100-51 D	0	11	30	0	0	11	0	5	18
50-11 D	10	25	0	3	12	17	6	18	11
10-6 D	12	7	0	8	9	0	10	8	0
5-2 D	15	7	10	5	3	11	10	5	11
1 D-1 U	36	32	40	66	55	33	52	44	35
2-5 U	22	7	0	10	9	6	16	8	4
6-10 U	5	7	0	5	9	11	5	8	7
11-50 U	0	4	10	3	3	11	1	4	14
51-100	0	0	10	0	0	0	0	0	0
No. of captures	41	28	10	39	33	18	80	61	28

In the Liverpool River system, nests upstream of the 30-km mark tend to be on the riverside, whereas those downstream are in freshwater swamps (Webb *et al.* 1977a). Hatchlings from the upstream nests often form crèches, while those from the swamps seem to enter the river in ones and twos and have not been observed to form riverside crèches. As it is possible that crèche formation and differences in the currents between the river mouth and further upstream could both influence movement patterns, group 1 animals from above and below 30 km were compared. The proportions of SDM and LDM (66 : 5 above 30 km; 11 : 1 below 30 km) were nearly

identical. The males and females (group 1) showed no significant differences in the proportion which moved upstream or downstream, in either the above- or below-30-km sections. However, when males and females from each region were grouped, there was a significant difference ($P = 0.008$; Fisher's test) between those above and those below 30 km; 10 of the 12 group 1 *C. porosus* from below 30 km moved upstream, whereas only 28 of the 67 from above 30 km moved upstream.

With group 2 individuals, there was no significant difference in the proportions from above and below 30 km which moved either upstream or downstream; however, when all were lumped, there was a significant difference between the proportion of males and females which moved upstream or downstream ($P = 0.05$; Fisher's test); more males moved downstream. The proportion which moved downstream was significantly greater than would have been expected by chance (19 out of 26; 2 remained at zero; χ^2 , $P = 0.05$). If the males in groups 3 and above were added

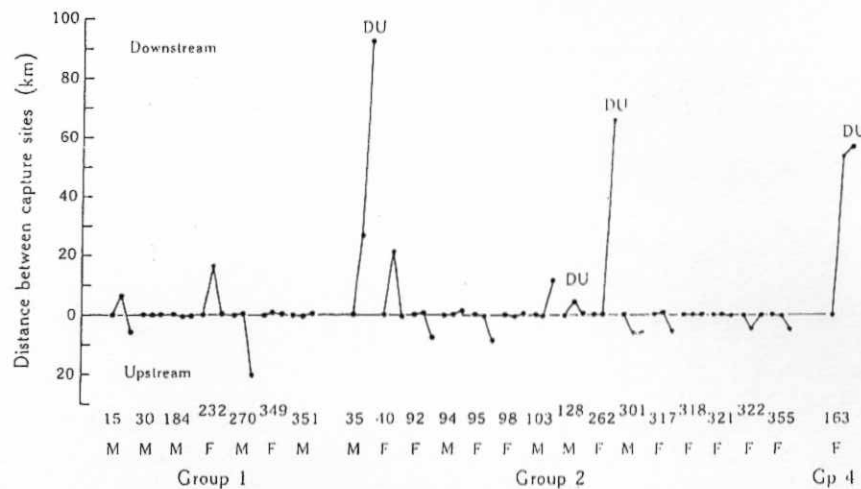


Fig. 5. Recapture locations of *C. porosus* juveniles relative to initial capture location: 1 year between captures. DU, movement down one stream and then up another. Numerals and letters below graph are the individuals' numbers and sex; groups are those in which the crocodiles were first captured (see Table 1).

to the group 2 males, the downstream shift was highly significant (χ^2 , $0.01 > P > 0.001$; 25 out of 34 moved downstream). With the females (both group 2 and group 2+ larger size classes) there was no significant deviation from an expected 50% upstream and 50% downstream.

Table 3 summarizes the distances travelled by the juvenile *C. porosus*; sexes are treated both separately and together.

Movement as Shown by Multiple Recaptures

Twenty-three juveniles were recaptured twice, and their recapture locations relative to the initial capture locations are shown in Fig. 5. Of the seven group 1 animals, two moved more than 3 km in the first year, and both had moved in the opposite direction the following year. Of the 15 group 2 individuals, five moved more than 3 km in the first year, and four had moved in the opposite direction the following year: for No. 301, movement in the second year was 0.1 km—probably negligible.

The single group 4 individual (No. 163), moved 53.2 km in the first year, and 3.3 km in the second year.

That there were movements of up to 21.1 km downstream in one year (No. 40), followed by a return towards the initial capture site the following year, suggests that some of the *C. porosus* classed as LDM's could be in fact moving back and forth from a centre of activity.

Relocated *C. porosus*

Seven of the *C. porosus* juveniles which had been relocated by more than 5 km when released after their initial capture, were recaptured. Their movements are shown in Table 4. Nos 91 and 110 were used in drugging experiments prior to release, and although No. 91 remained in the general vicinity of the release site, No. 110 travelled 101.8 km.

Table 4. Details of the movements of relocated *C. porosus*

No.	Sex	svt. (cm)	Capture in 1973	Recapture	Movement (km)	Direction	Days
91	M	48	27 July, Liverpool, 44.4 km, released 65.2 km, 1 Aug. (drugging experiment)	9.vii.1974 Liverpool 58.6 km	8.6	Downstream	347
110	F	52	28 July, Liverpool, 40.9 km, released 65.2 km, 1 Aug. (drugging experiment)	25.vii.1975 Tomkinson 70.4 km	101.8	Downstream upstream	727
324	M	38	17 Sept., Tomkinson, 63.2 km, released Bat I., 13.4 km, 18 Sept.	28.viii.1974 Tomkinson 24.9 km	11.5	Upstream	345
325	M	38	17 Sept., Tomkinson, 63.3 km, released Bat I., 10.5 km, 18 Sept.	29.viii.1974 Tomkinson 18.8 km	8.3	Upstream	346
328	F	34	17 Sept., Tomkinson, 63.9 km, released Bat I., 12.6 km, 18 Sept.	26.vii.1975 Tomkinson 62.1 km	49.5	Upstream	677
331	M	39	17 Sept., Tomkinson, 65.7 km, released Bat I., 13.5 km, 18 Sept.	15.vii.1975 Liverpool 45.2 km	37.7	Upstream	666
339	M	42	17 Sept., Tomkinson, 67.3 km, released Bat I., 10.8 km, 18 Sept.	18.viii.1974 Tomkinson 70.0 km	59.2	Upstream	335

Nos 324–339 were group 2 animals caught between 63.2 and 67.8 km in the Tomkinson River and released on the shores of Bat I. in the mouth of the Liverpool River (Fig. 1). All had moved upstream, and four of the five were LDM's. Seven group 2 *C. porosus* which were not relocated (and had been caught and released less than 30 km upstream) were also recaptured; none of these were LDM's and only three of the seven had moved upstream. The difference in the proportion of LDM's was significant ($P = 0.01$; Fisher's test); more relocated *C. porosus* were LDM's. The difference in the proportion which moved either upstream or downstream was not significant. That four of the five relocated specimens found the mouth of the Tomkinson River and entered it, and that Nos 328 and 339 returned to 1.8 and 2.7 km from their original capture site, strongly suggests a homing instinct.

Individual Case Histories

Our records of adult movements are from four *C. porosus*, three of which were fitted with development models of the 1.2-GHz radio transmitters. The case histories

transmitter was attached and one juvenile which moved from the Blyth River system to the Liverpool River system. Locations can be seen on Fig. 1.

Number 3 (Male; 111 cm SVL; immature). Caught on 9 July 1973, 49.9 km upstream in the Liverpool River; transmitter attached. Recaught on 21 July 1973 at 43.0 km in the Liverpool River and faulty transmitter replaced. Between 25 and 31 July 1973, was watched daily; remained between 44.8 and 45.5 km in the Liverpool River.

Number 363 (Male; 192 cm SVL; mature). Caught on 26 January 1974 at 35.4 km in the Liverpool River; no transmitter attached. Recaught 11 May 1977, 28.2 km upstream in Liverpool River; transmitter attached. After release, moved downstream to 26.5 km, then upstream to 27.3 km.

Number 365 (Male; 160 cm SVL; mature?). Caught on 27 March 1974 in the mouth of the Liverpool River (5.6 km upstream); transmitter attached. On release, moved to 8.5 km and remained there in a small creek for 7 days. Moved further upstream and was sighted at 10.5, 17.4 and 18.5 km in the Liverpool River. Appeared in Gudjerama Creek and remained there for most of May and June. Recaught in Gudjerama Creek on 4 July 1974; released on 5 July 1974 with new transmitter which failed shortly afterwards. Sighted at Juda point (mouth of Liverpool River; east bank) and at Maningrida (5.5 km). Recaught on 1 January 1975, 31 km upstream in Liverpool River, and third transmitter fitted. Upon release moved downstream to 25.7 km. Remains of transmitter found next to a trap set for *C. porosus* at 9.0 km in the Liverpool River in January 1976.

Number 837 (Female; 46 cm SVL; immature). Caught on 30 October 1974 at 28.2 km upstream in the Blyth River; no transmitter attached. Recaught 4 January 1976, 0.6 km in the mouth of Mungardobolo Creek. This represents a movement of at least 90 km, 90 km of which was around the coast from the mouth of the Blyth River to the mouth of the Liverpool River.

Number 889 (Male; 195 cm SVL; mature). Caught on 8 January 1975 at 24.1 km upstream in the Tomkinson River; transmitter fitted. Signal picked up between 25 and 30 km in the Tomkinson River over the next 2 weeks. Recaught 13 May 1977 at 33.6 km in the Tomkinson River. Following release on the same day with new transmitter, moved to 36.4 km, then downstream to 20.1 km, then back upstream to 24.1 and 27.8 km.

Number 1300 (Male; 184 cm SVL; mature). Caught on 10 December 1975 at 49.9 km in Tomkinson River; transmitter fitted. Upon release, moved upstream and on 12 December 1975 was at 54.5 km. Between 12 December and 16 January 1975, remained between 53.1 and 56.2 km. Sighted on 11 April 1976, when attacked investigators (Webb *et al.* 1977b) at 54.7 km; not sighted, nor transmitter signal received, since a few days after this; another large *C. porosus* was frequently seen at 53.1 km after April 1976. A letter from Dr J. P. Reser (dated 26 August 1976) informed us that he and a group of Aborigines had clearly seen a 10–12 ft crocodile with a transmitter attached to its head, at the mouth of Dharbila Creek, Millingimbi. As No. 1300 was the only crocodile with a transmitter on at this time, it was assumed that Dr. Reser had seen it. This movement would represent a total of at least 130 km, some 80 km being around the coast.

Interpretation of General River Surveys

In general river surveys, the location of each crocodile sighted was noted to the nearest 0.1 km, and total length was estimated in 1-ft categories (Messel 1977). Because surveys were carried out in a few days, hatchlings and 1-y-old crocodiles (noted as H and 2–3 ft) were distinct from the older groups: catching in the Liverpool River system was over a period of months and size-age classes tended to merge. Most crocodiles noted in surveys as 3–4 ft would be 2-y-olds; however, those estimated as 4 ft and above should be considered as being ± 1 ft, and no firm year classes can be assigned.

The Blyth and Cadell Rivers, some 45 km east of the Liverpool River system, were surveyed in November 1975; the results are shown in Fig. 6. The Blyth is a

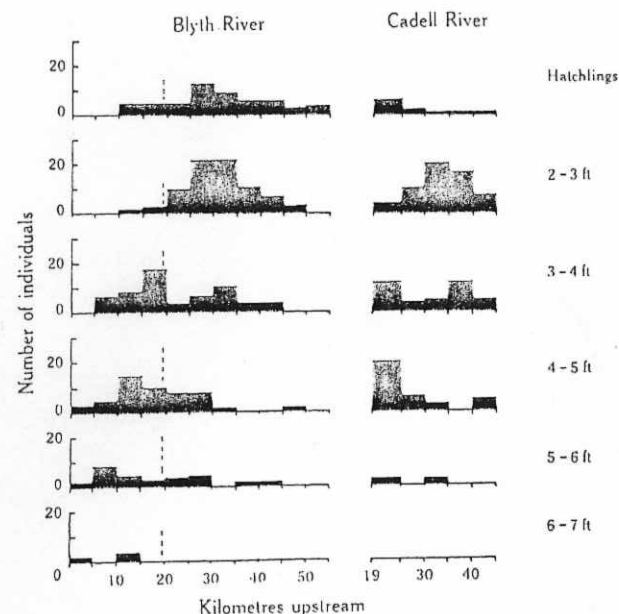


Fig. 6. Site-frequency histogram of different size groups of *C. porosus* sighted in the Blyth and Cadell Rivers in November 1975. The dashed line represents where the Cadell River enters the Blyth River.

long meandering river in which the meanders abruptly reach the sea, without a conspicuous estuary. This contrasts to the Liverpool River in which the mouth region appears to be a drowned river valley (Fig. 1). The Cadell River enters the Blyth River 19 km from its mouth.

Successful breeding in the 1974–75 wet season is evidenced by hatchlings distributed between 10 and 55 km, with a slight peak between 25 and 35 km. In the Liverpool River (Table 2) we found that after 2½ months, 95% of hatchlings were within 5 km of the nest site, and after 13½ months, 42% were. If the movements of the crocodiles in the Blyth River system are similar to those in the Liverpool, the nesting area could be considered as being at least between 15 and 50 km. In the Cadell River, there may have been a nest near the mouth, or alternatively, the hatchlings near the mouth (Fig. 6) could have come from the Blyth River.

The distribution of 2-3-ft crocodiles (1.4-1.8 y old) in the Blyth River is similar to that of the hatchlings, though the peak between 25 and 35 km is more pronounced. In the Liverpool River, group 1 animals (1.1-1.8 y old) near the mouth showed an upstream movement, whereas those further upstream showed no significant directional movement; the combined data showed a normal distribution around the previous year's capture site, 93% of individuals being within 10 km of that site (Table 3). If, in the Blyth River, the same basic nesting areas were used in the 1974-75 and 1973-74 seasons, the distribution of 2-3-ft *C. porosus* in 1975 would be consistent with the Liverpool River results. The distribution of 2-3-ft crocodiles in the Cadell River indicates successful nesting between 25 and 40 km, during the 1973-74 season.

The 3-4-ft crocodiles in the Blyth River (mostly 2.4-2.8 years old; compare with group 2 from the Liverpool River) show minor peaks in the 25-35-km section of the Blyth River and the 30-40-km section of the Cadell; both are regions which appear to be nesting areas. In addition, there is a peak between 15 and 20 km in the

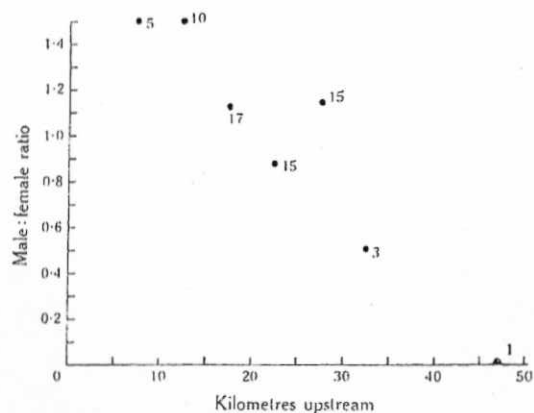


Fig. 7. Sex ratio of *C. porosus* of >50 cm SVL caught in the Blyth River in November 1974. Numerals on graph, number of crocodiles in 5-km segments of river.

Blyth, which tails to 5 km in the Blyth and back to 25 km in the Cadell. Such a distribution is consistent with a downstream movement of group 2 animals. In the Liverpool River there was a significant downstream movement of males, and from Table 3 it can be seen that the distribution of group 2 individuals as a whole was bimodal.

The distribution of 4-5-ft and 5-6-ft crocodiles in the Blyth and Cadell Rivers could be explained by a further downstream movement relative to the nesting areas, again consistent with the movement of group 3-5 crocodiles in the Liverpool River. The peak of 4-5-ft crocodiles in the mouth of the Cadell River could represent those which have moved downstream in the Cadell, or alternatively, crocodiles from the Blyth River which are moving upstream in the Cadell (see discussion, p. 280).

The Liverpool River results indicated that more males than females (of group 2 and above) moved downstream. The sexes of the crocodiles in Fig. 6 were unknown; however, in 1974, 191 *C. porosus* were caught, marked and released in the Blyth River. Fig. 7 contains the sex ratios of those over 50 cm SVL (i.e. 3-4-ft and above), plotted against kilometres upstream; the trend towards downstream movement of males is

evident, though sample sizes were small and significance could not be demonstrated.

The Goromuru River in Arnhem Bay was surveyed in October 1975, and the results are shown in Fig. 8. It appears there was successful breeding in the 1974-75 and 1973-74 seasons, both in the main stream and in Creek C. As in the Blyth River, little dispersal of 1-y-olds is apparent. The 3-4-ft crocodiles are more dispersed, though some remain in what is presumed to be the nesting area (20-30 km and further upstream). The 4-5-ft, 5-6-ft and 6-7-ft crocodiles are mostly nearer the mouth, consistent with a downstream movement from the nesting areas. The 7-9-ft crocodiles, some of which could well be adult females, are both at the mouth and well upstream.

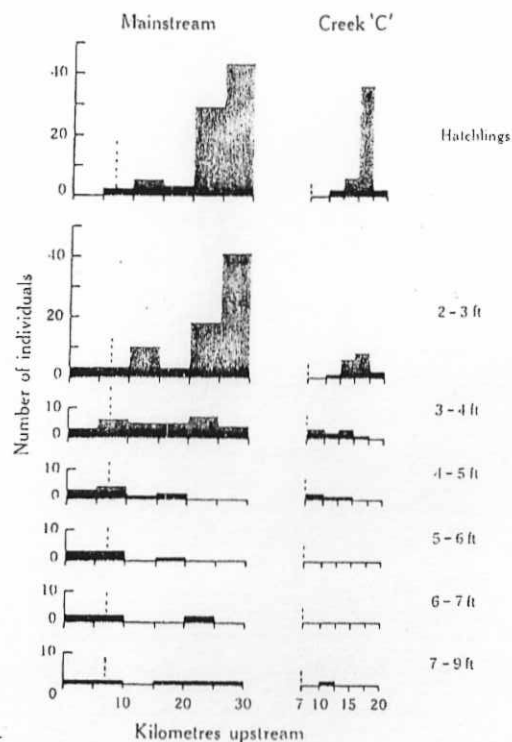


Fig. 8. Site-frequency histogram of different size groups of *C. porosus* sighted in the Goromuru River in October 1975. The dashed line represents where the major tributary enters the mainstream.

The rather startling decrease in the number of crocodiles of more than 3 ft could reflect the end of hide hunting in 1972.

A complex of four rivers and a creek in the western corner of Arnhem Bay were also surveyed in October 1975, and the results are shown in Fig. 9.

The Habgood River contained representatives of at least five year groups, and thus appeared to be a successful river for *C. porosus* breeding. The hatchlings and one year olds were abundant in the same regions of the river (10-20 km), again suggesting little dispersal of 1-y-olds, and possibly localizing a nesting region. The 3-4-ft, 4-5-ft and 5-6-ft crocodiles were more widespread in the river and extended to the mouth. The 6-10-ft crocodiles were between 10 and 20 km upstream. This distribution is similar to that found in the Blyth, Cadell and Goromuru Rivers, and is consistent with the dispersal of crocodiles described in the Liverpool River.

The distribution of crocodiles in the adjoining rivers is not as easily explained.

There were only two hatchlings sighted, both in the Gopalpa River, and a single 2–3-ft crocodile in the Darawarunga River. Crocodiles of more than 3 ft were scattered throughout the rivers, but showed no obvious dispersal pattern comparable with that described above.

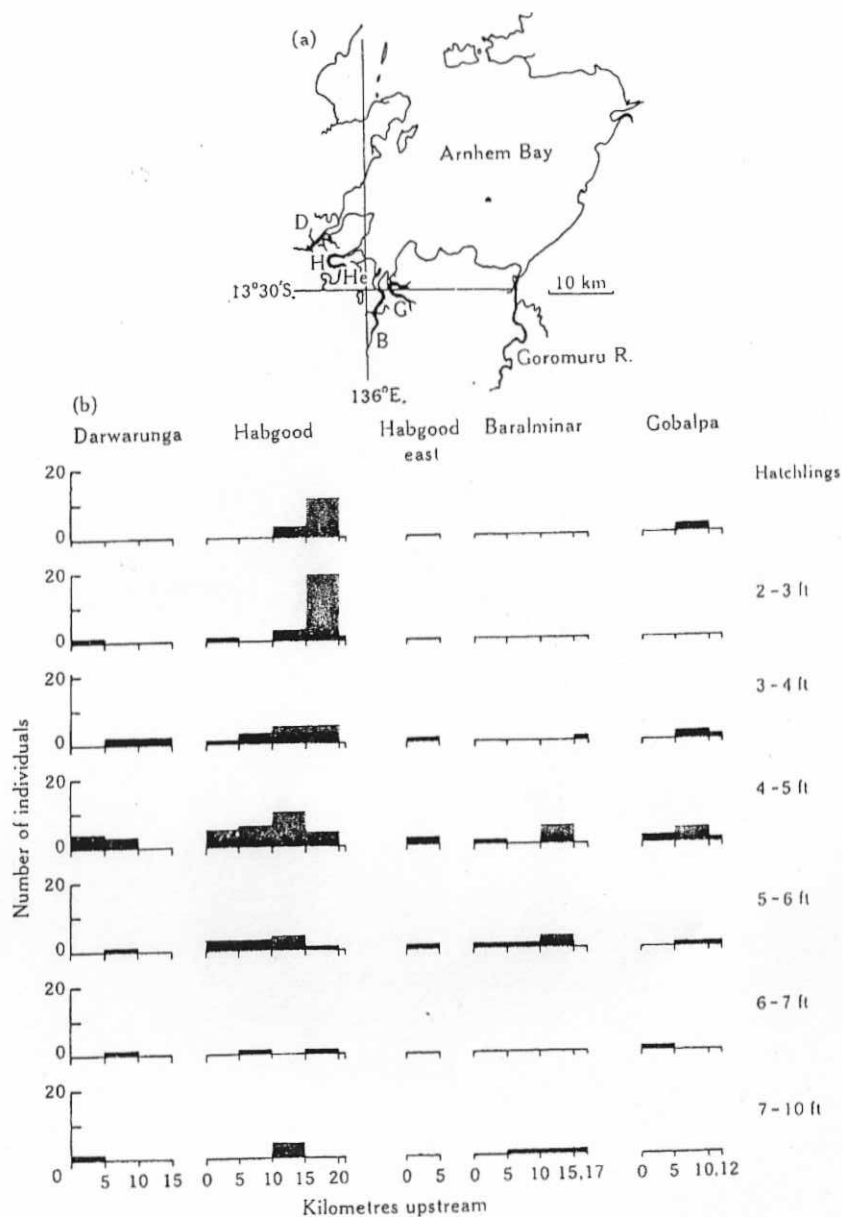


Fig. 9. (a) Map of Arnhem Bay. (b) Site-frequency histograms of different size groups of *C. porosus* sighted in the complex of rivers in the western corner of Arnhem Bay. Letters on (a) refer to rivers on (b).

It is possible that many of the crocodiles in these rivers represent juveniles from nests well upstream (out of tidal influence), or from swamps away from the river's

edge. The 3–4-ft and 4–5-ft crocodiles in the Darawunga River could be demonstrating a downstream shift from further upstream: the hatchlings in the Gopalpa River indicate at least a partly successful nest in the 1974–75 wet season. It is equally possible, however, that the rivers on each side of the Habgood collect crocodiles which move out of the mouth of the Habgood, and possibly even the Goromuru River, which is only 20 km to the east.

Although quite clearly both possibilities could account for the proportions of crocodiles sighted in the rivers on each side of the Habgood, if the hypothesis is made that all crocodiles originate from the Habgood, and the assumption accepted that the same proportion of crocodiles was seen in the surveys of each river, the number of crocodiles outside the Habgood can be considered as a percentage of those within. By assuming a mean distance necessary to bring the crocodiles to the mouth of the Habgood River, and by calculating the percentage of crocodiles in the Liverpool which travelled further than this, we can compare the Habgood and Liverpool Rivers (Table 5). Clearly a large proportion of the crocodiles outside the Habgood

Table 5. Numbers of *C. porosus* within and outside of the Habgood River, compared to those in the Liverpool River
See text for explanation of categories

	Values for Habgood R. size class:			
	2–3 ft	3–4 ft	4–6 ft	6–9 ft
No. in Habgood River	24	12	29	5
No. outside Habgood River	1	9	29	7
Percentage outside Habgood River	4	42	50	58
Mean distance from river mouth (km)	17.5	17.5	12.5	—
Equivalent Liverpool River group	1	2	3–5	—
Equivalent percentage outside Liverpool River	4	18	41	— ^A

^A No comparable data.

River could be accounted for by movement of juveniles from the Habgood, if the crocodiles dispersed in a similar manner. It must be remembered that the Liverpool River results are underestimates, as the proportion which left this river system altogether is unknown.

Discussion

Alligator mississippiensis is the only other crocodylian in which movement has been studied in detail (Chabreck 1965; Joanen and McNease 1970, 1972; McNease and Joanen 1974) and which can be compared with *C. porosus*. In such a comparison, basic differences between the two species and their habitats must be recognized. In the region where *A. mississippiensis* was studied (Louisiana), the terrain was low marshland with a network of bayous, canals and shallow ponds (Chabreck 1965); movement was not restricted to a main river channel as was usual with *C. porosus*. In addition, *A. mississippiensis* experiences a period of winter dormancy (during which movement is severely restricted), which does not occur in *C. porosus*.

In Chabreck's (1965) study, he found that two *A. mississippiensis* nesting situations influenced juvenile movement patterns. Some adult females occupied dense marsh in which they made several dens, and nested nearby. Hatchlings from such nests

moved into one of the dens and remained there throughout the winter. The following spring, their movements were restricted to between 6 and 15 m, and the next winter was spent in the same den, with the new batch of hatchlings. In the second spring they tended to disperse, and in floods they all left; however, in drought many remained in the den, so that in some dens females were found with three year classes of juveniles.

In contrast to those *A. mississippiensis* nesting in dense marsh, other females nested on the edge of larger bodies of water and excavated a den under the bank. In these situations, hatchlings moved more than when in dense marsh, though seldom venturing over 60 m from the den, to which they returned periodically. The following spring, they all departed from the nest area, seeming to swim aimlessly in search of food.

As with *A. mississippiensis*, there are two basic nesting situations in *C. porosus* which could affect movement patterns. Some females nest in freshwater swamps, back from the river's edge, and others nest on the riverside (Webb *et al.* 1977a). In the Liverpool River system, the freshwater swamps are in the mouth region, where no riverside nests are made. It is not known whether hatchlings from swamp nests form crèches in the swamp; however, at least in the Liverpool River swamps, the hatchlings seem to disperse soon after hatching, and many reach the river, via small creeks, in a few days. We have no evidence that these hatchlings form crèches in the river. On the other hand, hatchlings from riverside nests often form crèches.

A comparison of hatchling movements from above and below 30 km [the dividing line between swamp and riverside nests in the Liverpool River system (Webb *et al.* 1977a)], demonstrated no significant difference in the distances travelled by hatchlings, but a significant difference in the direction of travel. Hatchlings from above 30 km moved either upstream (42%) or downstream (58%) whereas those from below 30 km mainly (83%) moved upstream.

This difference could in part reflect an unequal probability of catching the 'less than 30 km' hatchlings which moved downstream, because they may have left the river. However, searches were made to at least 5 km downstream of the capture location of the hatchlings closest to the mouth, without success. Of 115 hatchlings marked in 1973 (99 from above 30 km and 16 from below), recapture percentages were 49% and 31% respectively. This suggests a greater loss of the 'less than 30 km' hatchlings, which could be accounted for by movement from the mouth, selection of habitats back from the river's edge, or a difference in predation pressure in the above- and below-30-km sections.

Differences in direction of movement of hatchlings from above and below 30 km would be expected if the direction of flow of the river influenced movement. In the dry season, tidal influence extends to the limits of the area shown on Fig. 1, the water flowing alternately downstream and upstream with ebbing and flooding tide. During the wet season, the influx of fresh water pushes the limit of tidal influence toward the mouth, and above this the water may flow downstream continuously for as much as months at a time. If movement was passively related to the direction of flow, one would expect hatchlings downstream of 30 km to move both upstream and downstream (with a downstream bias dependent on the proportionally greater time of flow downstream) and hatchlings upstream of 30 km to move downstream. That we find the opposite suggests that hatchlings move against the flow. It is possible that crèche formation in upstream areas results in the establishment of a centre of activity,

which tends to keep upstream hatchlings in the same general area. Unfortunately, we have no way of testing this at present. Preliminary results from the Blyth River suggest that crèche formation in upstream regions is not as common there as in the Liverpool River system.

The distribution of crocodiles in the rivers surveyed demonstrated little dispersal of 1-y-olds, which was consistent with the recapture results and with Chabreck's (1965) data on *A. mississippiensis*. In addition, the apparent normal distribution of 2-3-ft crocodiles (1-y-olds) in the Blyth River (when compared to the hatching distribution; Fig. 6) would be expected if downstream hatchlings did in fact have a tendency to move upstream.

Chabreck (1965) found no significant male:female differences in movement patterns of juvenile *A. mississippiensis*, and lumped all animals under 2 m total length together. Mean movement after 6-12 months was 1.0 km (range 0-5.6 km; $n = 19$); that after 12-24 months was 2.4 km (range 0.2-11.3 km; $n = 21$); that after 24-36 months was 1.6 km (range 0.2-4.0 km; $n = 8$); that after 36-48 months was 4.8 km (range 1.2-16.9 km; $n = 3$). After 12-24 months, 37% of recaptured *A. mississippiensis* had travelled less than 0.8 km, 21% between 0.8 and 1.6 km, and 42% between 1.6 and 11.3 km. It is not possible to compare our results directly with these, because our animals were more likely to be long-distance movers as they grew larger (see Fig. 4), and therefore we cannot 'lump' the data. Clearly many more *C. porosus* than *A. mississippiensis* travelled long distances, and the 58% of *A. mississippiensis* which travelled between 0 and 1.6 km is similar only to *C. porosus* hatchlings (group 1); 52% travelled between +1.4 and -1.4 km (Table 3).

The question of male-female differences in juvenile *A. mississippiensis* patterns was reinvestigated by McNease and Joanen (1974), using tracking transmitters on 17 males and 13 females. They found that male and female mean home ranges and daily distances travelled were not significantly different. However, 46% of males had two or more widely separated centres of activity, whereas only 27% of females did. In addition, 54% of males had no clear centre of activity whereas 73% of females 'showed considerable movement in one concentrated activity centre'. A further difference was found in the selection of habitat, which in part determined the size of home ranges. Females showed a preference for natural marsh, and males for deep water areas and impoundments; movement was more difficult in the marsh areas.

In the Liverpool River *C. porosus* does not have the variety of habitats available to *A. mississippiensis*. However, the possibility of juvenile females having a centre of activity could well explain the male-female differences observed in the Liverpool and Blyth Rivers, namely that: after 13½ months, more males than females had moved downstream of the nest site; more group 2 males than females were long-distance travellers; in the groups above 2, more males than females moved downstream, and the downstream shift was significantly different from an expected 50% upstream and 50% downstream; more males of more than 50 cm SVL were near the mouth than further upstream in the Blyth River.

The concept of long- and short-distance movers was one of convenience, yet one which appears to have biological significance. Unfortunately it is not possible to fully assess whether or not many long-distance movements were the result of interference; however, we have assumed that they indeed were natural movements. Multiple recaptures of marked *C. porosus* indicated that a movement of over 3 km in one year

was usually followed by a movement in the opposite direction in the following year (Fig. 5). Some animals, however, continued to move away from the original capture site. From Fig. 3 it can be seen that nine *C. porosus* travelled between 50 and 100 km from the original capture site (seven males; two females). Eight moved downstream of their original capture site, and each of these then moved upstream in another main channel. If the finding by a crocodile of the mouth of another stream is opportunistic, it is possible that if it found no other stream its subsequent upstream movement could have brought it back to where it originally came from. For example, No. 35 (see Fig. 5) was caught in 1973 at 50.2 km in the Liverpool River. In 1974 it was caught at 36.4 km in Maragulidban Creek, having moved at least 20.3 km downstream and 6.4 km upstream. In the following year it was caught at 63.0 km in the Tomkinson River; a downstream shift of 19.5 km to the mouth of the Tomkinson, then an upstream movement of 46.1 km. Had it not found the mouth of the Tomkinson and travelled the same distance back upstream in the Liverpool River, the 1975 capture site would have been at 63 km; i.e. 12.8 rather than 79.4 km from the 1973 site.

The opportunistic movement into the mouth of another stream, which could equally be out of the mouth of a river onto the coast, could be responsible for many of the long distances travelled in the Liverpool River system, and, as pointed out previously, could explain the distribution of crocodiles in and around the Habgood River in Arnhem Bay. It is interesting to note that in the Liverpool River there were 10 *C. porosus* which moved between 20 and 40 km from their capture site and seven between 60 and 80 km: only two moved between 40 and 60 km. This bimodal distribution could be reflecting a tendency to keep moving once a certain distance has been covered.

To be consistent with the idea of chance placement in another stream leading to long-distance travel, a homing instinct needs to be hypothesized, at least whether 'home' is upstream or downstream. The results from the relocation experiments support the notion that such an instinct exists in juvenile *C. porosus*. Chabreck (1965) arrived at a similar conclusion with *A. mississippiensis*: of 29 (recaught) which were relocated, 59% travelled in the direction of the original capture site, 21% within 45° of it, and 17% within 90° of it. The relocated *A. mississippiensis* travelled further than those not relocated, and after 2-4 years, 83% of the relocated *A. mississippiensis* had moved more than 8 miles, whereas only 27% of those not relocated had moved more than 2 miles.

Joanen and McNease (1970, 1972) studied the movements of adult *A. mississippiensis*. Their results were expressed in terms of daily distances travelled and home ranges [the area enclosed by connecting the outside points of an animal's plotted movement (McNease and Joanen 1974)]. For *C. porosus* such areas must be limited to the river, and problems arise when, for example, No. 1300 moved around the coast—this region obviously cannot be included in a home range. To gain some idea of the areas in which adult male *C. porosus* travel, the mean width of the river was multiplied by the maximum distance between sightings for the animals whose case histories are given (p. 271). No. 363 moved within 130 ha between captures, and number 889 moved within 120 ha. No. 1300 remained within approximately 9 ha for nearly 3 months, then moved out of the river system. No. 365, which may or may not be mature (sizes of males at maturity are not definitely known, but believed to be around 160 cm SVL), moved within 1500 ha (if the eastern bank

of the mouth region was included to 1 km out). Such areas are generally less than those (890-332 ha) reported for *A. mississippiensis* when not dormant (Joanen and McNease 1972); however, the methods of determining range could account for this difference.

In a previous study (Webb *et al.* 1977a), indirect evidence was presented which suggested that adult females remain in the vicinity of the nest site for most of the year. Such a finding is consistent with Joanen and McNease's (1970) study of adult female *A. mississippiensis* and consistent with the trends exhibited by juvenile females in the present study. Unfortunately we have no additional data.

Similarly, we cannot throw much light on the phenomenon of sea travel by *C. porosus*. The trends in juvenile dispersal patterns suggest that juvenile males reach the sea before females; however, the age of the crocodiles which reach the sea would seem to depend at least on the distance between the nesting areas and the sea. The single juvenile marked in the Blyth River and recaptured in the Liverpool River was a group 2 female.

No. 365 was frequently sighted in and around the mouth of the Liverpool River, though never more than 1 km offshore. No. 1300 moved at least 80 km around the coast. Whether such movements by larger crocodiles are the result of aimless wandering is unknown.

There are many factors which could presumably affect movement and dispersal patterns of both adult and juvenile *C. porosus*. Flooding during the wet season could be expected to enhance movement, both from its effect on river flow and the making available of cross-country routes which could allow a crocodile to reach a different drainage system (e.g. the juveniles which moved from the Tomkinson River to Mungardobolo Creek). Cott (1961) found that flooding could result in *C. niloticus* moving out across flood plains and becoming marooned in temporary ponds. Chabreck (1965) discussed how *A. mississippiensis* were 'swept northward...for distances ranging from 3 to 10 miles' by flooding and high winds associated with a hurricane in 1957. He also pointed out that high-water conditions in general were normally associated with increased movement, especially by immature alligators.

Another factor which could well influence patterns of movement is a response by crocodiles to handling. No. 110, used for an experiment while in captivity, moved 102 km in 2 y. No. 365, released with a transmitter, remained in a small tidal creek for 7 days. Joanen and McNease (1970) found that movements of adult females in the first week after release were generally greater than at other times; the longest daily movement (1500 ft) they recorded for a female occurred the day after release. It seems likely that a response to being caught and handled is reflected in increased or decreased movement by at least some *C. porosus*; however, it is not yet possible to quantify that effect.

Taken together, the results of the present study demonstrate general trends in the dispersal of juvenile *C. porosus* in tidal rivers. Combined with the results from the nesting study (Webb *et al.* 1977a), there is now a considerable amount of data which can be used to interpret general night survey results. The management implications of such interpretations are obvious, especially whether a river is a successful, marginal or unsuccessful *C. porosus* breeding area. Radio-telemetry will eventually give more detailed information on *C. porosus* movement; however, the general picture of juvenile dispersal would not be expected to change considerably.

Acknowledgments

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Note

The following correction should be made to the authors' paper: 'Morphometric analysis of *Crocodylus porosus* from the north coast of Arnhem Land, northern Australia'. *Aust. J. Zool.* (1978), 26, 1-27.
p. 18, Table 4, column 8, heading:
For 'With two protruding' read 'With teeth protruding'.

Corrigendum

Aust. Wildl. Res., 1978, Vol. 5, No. 1, p. 148

The reference to the paper by Gooding and Harrison (1964) should appear at the end of line 1 and should be deleted from line 11. The reference is:

Gooding, C. D., and Harrison, L. A. (1964). 'One shot' baiting. *J. Agric. West. Aust.* 5, 12-15.