Movements and home ranges of radio-tracked *Crocodylus porosus* in the Cambridge Gulf region of Western Australia

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Abstract.   VHF radio-tags were attached to 16 estuarine crocodiles that were tracked between October 2001 and May 2003. Male ($n = 12$) and female ($n = 4$) crocodiles exhibited distinctly different patterns of movement. Females occupied a small core linear range (1.3 ± 0.9 km) on the main river channel during the dry season and moved up to 62 km to nesting habitat during the wet season, returning to the same core area the following dry season. They occasionally made excursions away from their core areas during the dry season. Males moved considerable distances along the Ord River throughout the year. The largest range recorded was 87 km for a 2.5-m juvenile male. However, ranges of males did not appear to be related to body size, with the largest two ranges being recorded for the smallest (2.5 m) and largest (4.3 m) males tagged. Rates of movement of males did not differ significantly between three size classes of males but there were significant seasonal differences, with the highest mean rates of movement occurring during the summer wet season (4.0 ± 5.4 km day^{-1}). However, males were quite mobile during the dry season and the highest rate of movement detected was 23.3 km day^{-1} for a 4.3-m male at the end of July. The highest rate of sustained movement was 9.8 km day^{-1} for a translocated 2.6-m juvenile male, which travelled 118 km in 12 days to return to the area of its capture. Neither males nor females showed exclusive habitat preferences for any of four broad riverine habitats identified on the Ord River. However, the three largest males had activity centres that they returned to frequently despite numerous excursions throughout the year, both up- and downriver. Males had substantial range overlaps with no obvious spatial partitioning, suggesting that territoriality is not an important behavioural characteristic of free-ranging male crocodiles along the Ord River.

Introduction

Crocodylus porosus is the most widely distributed crocodilian species, occurring throughout south-east Asia and ranging from northern Australia to southern India and Palau (Ross 1998). It is regarded as the crocodilian that most readily takes to the sea because it is extremely euryhaline and can maintain homeoosmotic conditions over a broad range of salinities (0–60 ‰: see Taplin 1988; Taplin and Grigg 1989). There are numerous reports of individuals undertaking ocean voyages over hundreds of kilometres (e.g. see Bustard and Choudhury 1980) and Allen (1974) gives an account of a 3.8-m male that arrived at the eastern Caroline Islands, >1300 km by sea from the nearest known population. While this species is obviously capable of very large-scale movements, these are likely to be atypical. Most studies indicate that crocodilians move around little for most life-history stages (Webb and Messel 1978*b*; Magnusson 1979; Webb *et al*. 1983*a*; Taylor 1984; Hutton 1989; Rootes and Chabreck 1993; Tucker *et al*. 1997; Muñoz and Thorbjarnarson 2000). However, Tucker *et al*. (1997) found that pubescent male *Crocodylus johnstoni* were essentially nomadic and had much larger home ranges than other life stages.

Patterns of animal movement must be known in order to understand basic population processes and may themselves be important demographic parameters (Hutton 1989). Movement, home-range behaviour and dispersal have received careful examination only in *Alligator mississippiensis* despite their potential importance to crocodilian life histories (Hutton 1989). Radio-telemetry has been used successfully to track *A. mississippiensis* (Joanen and McNease 1970, 1972; McNease and Joanen 1974; Goodwin and Marion 1979; Rodda 1984*a*; Taylor 1984; Rootes and Chabreck 1993), *Crocodylus acutus* (Rodda 1984*b*), *Crocodylus niloticus* (Hutton 1989; Hocutt *et al*. 1992), *Crocodylus intermedius* (Muñoz and Thorbjarnarson 2000), *Paleosuchus trigonatus* (Magnusson and Lima 1991) and *Melanosuchus niger* (Martin and da Silva 1998).

Surprisingly, there are no published tracking studies for either species of crocodilian found in Australia. All data on movements of *C. porosus* have been determined by mark–recapture studies (e.g. Webb and Messel 1978*b*; Messel and Vorlicek 1987; Walsh and Whitehead 1993). Early attempts to radio-track *C. porosus* were unsuccessful, perhaps due to the limitations of prototype equipment or attachment difficulties (see Webb and Messel 1978*b*;

Yerbury 1980). Signal attenuation in brackish or salty water may also have been a contributing factor (Kenward 2001). Webb and Messel (1978*b*) discussed radio-tracking *C. porosus* and described the movements of five animals with attached transmitters although it appears that much of the information presented on their movements was derived from resightings and it is unclear how often animals were radio-located. While recapture studies have provided baseline information on the movements of *C. porosus*, telemetry is more suitable for clarifying theories about patterns of movement and advancing our understanding of dynamic activity budgets and seasonal patterns of habitat use by different life-history stages (Tucker *et al*. 1997). This is the first study reporting the movements of *C. porosus* using telemetry data.

Methods

Study area

The bioclimate of the Cambridge Gulf region (Fig. 1) in Western Australia (WA) is classified as Dry Hot Tropical and is characterised by summer rainfall with a long dry season. More than 80% of rain falls between December and March and precipitation is insufficient to sustain plant growth for eight months of the year (Beard 1990). The seasonal alternation of flood and drought is a highly predictable and dominant feature of the climate (McDonald and McAlpine 1991). Average annual rainfall at Wyndham is ~700 mm and humidity ranges from 32% in July to 68% in February (Bureau of Meteorology 1996). Mean daily maximum temperatures range from 31°C in June/July to 40°C in November with >45 days per annum exceeding 40°C. Minima range from 17°C in July to 27°C in November.

Five major rivers flow into Cambridge Gulf and stream flows peak in February after a corresponding peak in mean monthly rainfall. The riparian vegetation of freshwater reaches is dominated by *Eucalyptus camaldulensis*, *Melaleuca leucadendra* and *Pandanus aquaticus* (Beard 1990). Fringing mangrove communities occur on tidal mud in the more sheltered bays and inlets of the coast. Mangrove species richness in the gulf reaches a maximum for WA, with 15 species documented, which may occur in pure stands or form mixed associations (Thom *et al*. 1975; Beard 1990). The region is macrotidal, with spring tidal amplitudes of up to 8 m.

The Ord River is one of the major rivers in WA and has a catchment area of 50 000 km². The largest recorded instantaneous flow on the Ord River was ~30 800 cumecs in February 1956 (Ruprecht and Rodgers 1999). Since then, the construction of two dams to service an irrigation scheme has reduced the average annual river flow at the mouth from ~4500 GL to 3200 GL (Ruprecht and Rodgers 1999). Overflow and discharge from the dams has transformed the flow regime from seasonal to perennial and there has been a substantial reduction in the magnitude of floods. The suppression of large flood events has resulted in appreciable siltation within the lower Ord estuary where the cross-sectional area of the river has decreased by ~50% over the last 30 years (Wolanski *et al*. 2001) and there have been considerable changes to riparian vegetation in the freshwater reaches (Start and Handasyde 2002).

The climate favours grassland vegetation so most of the region is covered by tropical savannas, which are utilised primarily for grazing cattle (Beard 1990) but there are 12 000 ha of irrigated farmland surrounding Kununurra. Most of the lower Ord estuary is gazetted as nature reserve (Fig. 1) although small areas in the east are within Carlton Hill pastoral lease or are Unallocated Crown Land. The Ord River Nature Reserve was declared primarily to protect *C. porosus* after

the recommendations of Bustard (1970), who felt that the area was ideal for a crocodile reserve because it contained excellent habitat and still held a number of crocodiles, which could repopulate the area if rigidly protected (Burbidge *et al*. 1991).

Tracking methods

Crocodiles were caught either by means of the harpooning technique described by Webb and Messel (1977) or with baited cage traps (see Walsh 1987). VHF radiotags (150 MHz) manufactured by Sirtrack Ltd (http://sirtrack.landcareresearch.co.nz) were attached to the nuchal scales of 16 animals using the techniques described by Kay (2005). Initially, tags were attached to three crocodiles caught on the King River and one to a problem animal caught at Wyndham Port (Fig. 1) in a pilot study that commenced in October 2001. The remaining 12 tags were attached to animals caught on the Ord River during April and May of 2002. Eleven of the 12 Ord River crocodiles were caught within a 7-km reach of river and all were caught within a 13-km reach. By the end of the study, the Ord River animals had dispersed over a 108-km section of river. Most tracking was undertaken on the Ord River because large sections contain fresh water due to perennial discharge from Lake Argyle which made locating tags on submerged animals more likely (see Kenward 2001).

Animals were tracked manually, mainly from a boat and occasionally from a variety of aircraft, using a point-sampling approach (Kenward 2001). Only one location per tracking day was recorded for each crocodile. When tracking from a boat, signals were initially detected using a scanning receiver (Telonics TR2) connected to an omnidirectional antenna. Under optimal conditions, such as with a crocodile basking on the bank and an unobstructed line of sight, signals were discernible from 2–3 km. Mostly, however, signals were detected from 0.2–0.5 km, particularly when animals were submerged. Signals were perceptible at depths of 4–5 m in fresh water. Once detected, a portable three-element Yagi antenna was used to pinpoint the location of a crocodile. Animals were routinely located to within a few metres, especially in fresh water, and their position was recorded to the nearest second of latitude and longitude (40 m) with a GPS receiver (Lowrance GlobalMap 100). Tracking in brackish or saline water was much more difficult because signals were lost as soon as animals submerged. Crocodiles could still be located to within 50 m, depending on behaviour, but some animals no doubt evaded detection.

Not surprisingly, animals that had been trapped were more tolerant of being approached by a boat than those that were harpooned. Crocodiles responded to an approaching boat by submerging and utilising prevailing currents to move to deeper water away from the vessel. While all animals showed avoidance behaviour as they were being approached, this is unlikely to have had a major influence on long-term patterns of movement because boats are common along the Ord River and most crocodiles are accustomed to seeing them as well as being approached by curious fishermen and tourists. Furthermore, all tagged females inhabited a small section of river for many months, despite being tracked regularly. Three of the females were harpooned in the same section of river that they occupied during the dry season.

Aerial tracking was occasionally used to find missing animals and during the wet season when access to the river became difficult. Under optimal conditions, signals were detectable over ~10 km at an altitude of 750 m. Judging by signal behaviour, crocodiles reacted to aircraft flying at altitudes below 750–900 m by submerging. Altitude was not a critical factor over fresh water but became an important consideration when tracking over brackish–saline water. Locations were recorded with a GPS receiver. The accuracy of aerial fixes depended on the type of aircraft, its speed and altitude. Signal propagation is greatest immediately overhead when tags are submerged (Kenward 2001). Helicopters enabled the most accurate fixes because they could hover over a location at low altitude to pinpoint the strongest signal. They also had the added advantage of being able to land nearby so that tracking

could be undertaken on foot if necessary. The accuracy of locations obtained from fixed-wing aircraft was variable and ranged from 40 m, based on known locations, to ~400 m. Obvious errors, such as a terrestrial location, were identified and corrected using geographic information system (GIS) software by recalculating the position at the shortest straight-line distance to the river.

Ord River crocodiles were tracked during the day for logistical reasons. A routine tracking run involved searching a 60–70-km reach of river (120–140-km round trip). Crocodiles were tracked for 5–15 days per month between April and September. Thereafter, they were tracked for 2–6 days every 2 months from October 2002 until the study ended in May 2003. King River animals were mostly tracked at night on an irregular basis. Crocodiles are probably more active at night, so diurnal tracking would bias estimates of short-term daily movements. However, diurnal tracking was considered sufficient for estimates of space use and home range over the longer term. Patterns of movement were consistent between Ord and King River crocodiles, although sample sizes were small.

Time tabling was a minor issue while tracking on the Ord River. There were a limited number of locations from which the boat could be launched and the linear habitat meant that some animals were often encountered at similar locations at similar times on consecutive days. From April to October 2002, the boat was launched at a location that enabled an upstream and a downstream tracking run that could be varied between morning and afternoon to reduce this effect though the choice was sometimes made with respect to tidal movements on any particular day. The locations recorded were sometimes varied between forwards and return runs as well; however, the logistics of manually tracking in this region imposed a significant constraint on sampling strategy.

Analysis of home range

Most telemetry studies of animal movements have been of mammals and birds (Millspaugh and Marzluff 2001). Consequently, much of the literature describes the analysis and interpretation of data from species whose movements are largely unrestricted in two-dimensional space. One of the simplest ways to measure movements and home ranges of animals that are geographically restricted to a drainage channel is to measure linear river distances. This approach has been used to quantify home ranges for Australian freshwater crocodiles (Tucker *et al*. 1997) and river otters (Melquist and Hornocker 1983). Linear home ranges have also been used to describe the movements of rats in farmland (Hardy and Taylor 1980). Kenward's (2001) definition of home range as an area traversed repeatedly by an animal is particularly apt for a river-dwelling animal such as a crocodile, because, given any two points along the river, the path the animal traversed to travel between them is known at the broad scale.

Tucker *et al*. (1997) regarded conventional calculations of home-range size that required *x–y* coordinates as inapplicable for linear habitat such as a river. However, a straight line can be described by an infinite number of *x–y* coordinates since both are continuous variables. More importantly, the range and variance of the coordinates is determined by the length, orientation and shape of the line. Provided the locations obtained from the movements of an animal are representative of the shape of the river section over which it traverses, any of the conventional algorithms could be used to calculate a home range that is then corrected by subtracting encroaching terrestrial habitat. This approach is relatively straight-forward with the use of GIS software. The advantages of using one of the conventional methods include a standardised approach for greater comparability between studies and relatively objective criteria for identifying 'normal' movements and activity centres (see Kernohan *et al*. 2001).

If locations are not representative of river shape, which will be a consequence of the sampling intensity/interval, many of the conventional methods result in a disjointed utilisation distribution. Disjointed utilisation distributions are not uncommon when using methods such as the 95% home range of a fixed-kernel estimator, which is one of the shortcomings of this method (Powell 2000). The problem becomes untenable in linear habitat (such as a river) because the interpretation of a disjointed 100% utilisation distribution is that the probability of finding an animal in a section of river that it used to travel between two areas is zero, which is biologically dubious.

Unfortunately, none of the conventional methods could be used in this study because sampling intensity was insufficient for locations to be representative of the shape of the river section inhabited by a crocodile. Consequently, two measures of home range were used: midstream linear range (MSLR) and river channel area (RCA). MSLR was the mid-stream linear distance in kilometres between the most upstream and downstream locations for a particular crocodile and RCA was the river area in hectares encompassing the MSLR, which was effectively a minimum convex polygon (MCP) approach within the river channel. Many of the conventional methods used for home-range analysis assume independence between successive locations. Home-range size will tend to be underestimated when data are serially correlated (Swihart and Slade 1985) but minimum area techniques are not affected in this way (Harris *et al*. 1990). Therefore, all locations collected for each animal were used to calculate MSLRs in this study. Many authors now consider that strict adherence to the 'time to independence' concept in movement studies is ill advised (Otis and White 1999; Kenward 2001; Kernohan *et al*. 2001).

Spatial analyses were performed using ArcView GIS software (ver. 3.3; ESRI, Redlands, California) in conjunction with the animal movement analyst extension (AMAE ver. 2.0: Hooge and Eichenlaub 2001) and 1 : 50 000 scale geo-referenced topographic data as base layers. Area–observation curves were plotted to determine whether an animal's home range had stabilised for the number of locations collected, using the MCP sample-size bootstrap function of AMAE (see Hooge 2002). This function bootstraps an MCP home range for a user-specified number of iterations and observation interval. Obviously, an MCP home range is only an index of the true home range for a crocodile inhabiting linear habitat such as a river.

It was not possible to objectively identify centres of activity using conventional methods such as the 50% utilisation distribution of a fixed-kernel estimator. This was because serially correlated data would have resulted in the erroneous identification of activity centres, as animals were often detected close to their previous location on consecutive days. Therefore, activity centres are reported for individual animals, where considered appropriate, based on knowledge of movements from tracking experience and visual inspection of data using GIS.

Habitat selection

Four broad habitat types were recognised on the basis of water chemistry and knowledge of the river: (1) macrotidal brackish-saline (MTBS) reaches; (2) macrotidal freshwater (MTF) reaches; (3) tidal freshwater (TF) reaches and (4) non-tidal freshwater (NTF) reaches. Tracking data were insufficient to make quantitative assessments of habitat selection (see Alldredge and Ratti 1986; White and Garrott 1990; Samuel and Fuller 1996) so qualitative assessments of habitat preference were made for individual animals, based on the frequency of occurrence in a particular habitat and knowledge of movements. Furthermore, while boundaries of the habitat types were relatively static during the dry season, they became dynamic during the wet season as a result of floods so interpretations should be treated cautiously. For example, the salinity at Adolphus Island (Fig. 1) ranges from 24‰ on neap tides to 30‰ on spring tides during the dry season yet can be as low as 5‰ during the wet season (D. Palmer, Water and Rivers Commission, Kununurra, personal communication).

Analysis of movements

Crocodile movements showed distinct sexual differences, so movements of males and females were analysed separately. Movements of females were analysed using simple descriptive statistics and GIS. Those of males were analysed using data from Ord River males only, but interesting records are presented for Males 146 and 350. No data are presented for Male 147 from King River owing to the small number of locations recorded.

Rates of movement of males

Rate of movement (ROM) was calculated as the ratio of distance travelled (in kilometres) to the time interval (in days) between successive locations. Histograms were constructed to investigate the frequency distribution of ROM. Due to the shape of the distribution, Kruskal–Wallis tests were used to determine whether ROM varied between male size classes, season or tidal phase. Three size classes were

used: males between 50 and 100 kg ($n = 3$), males between 100 and 140 kg ($n = 3$), and males >140 kg ($n = 3$). Categorical variables used for season were: wet (December–March), post-wet (April–May), dry (June–August), and late dry (September–November). Those for tidal phase were: neap first quarter, neap last quarter, spring full moon, and spring new moon. Only rates of movement where the time interval between successive locations was <8 days were used in analyses. Analyses of ROM were performed using R software (ver. 1.6.2: R Development Core Team 2004).

Interactions between males

Static interaction between Ord River males was measured using a simple percentage MSLR overlap. This measure of space sharing was calculated as:

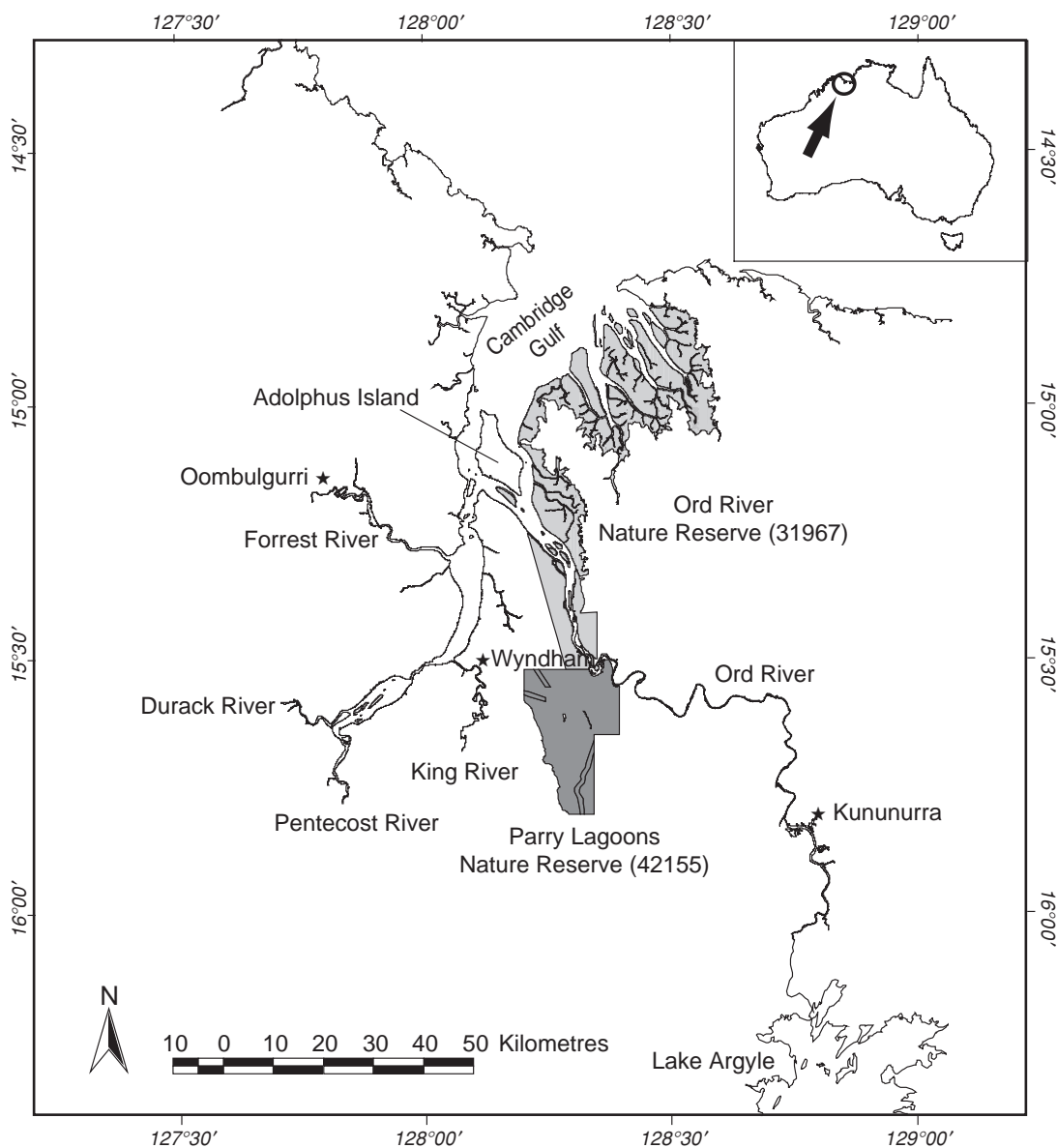$$HR_{1,2} = A_{1,2}/A_1 \quad \text{and} \quad HR_{2,1} = A_{1,2}/A_2,$$

Fig. 1. Cambridge Gulf region of Western Australia.
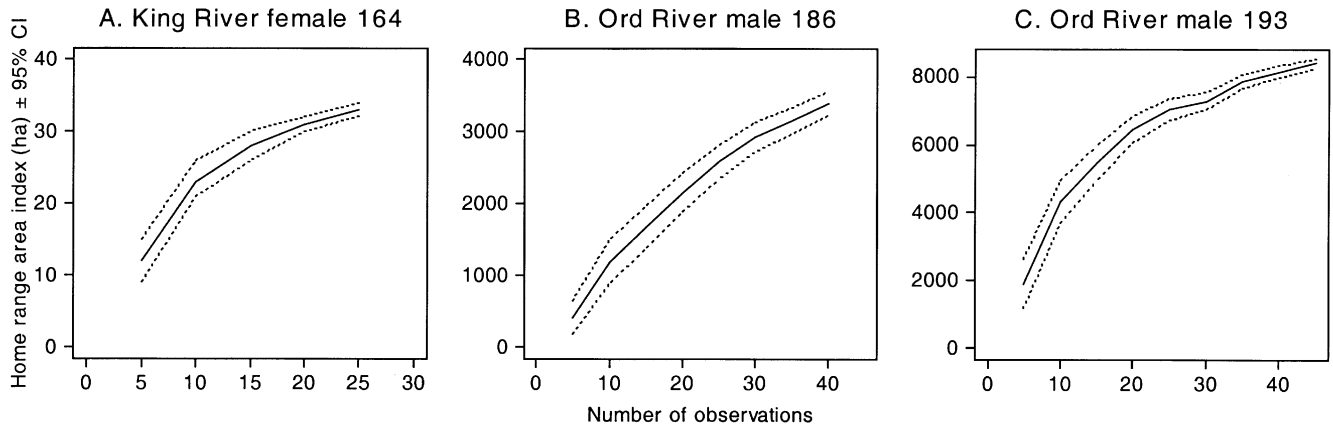
Fig. 2. Area–observation curves for three crocodiles radio-tracked from October 2001 to May 2003. The home-range area index is a minimum convex polygon area bootstrapped for 500 iterations at intervals of five observations. All observations were used for males but only dry-season core-area observations were used for females. The axes are not to uniform scale.

where $HR_{1,2}$ is the proportion of Animal 1's home range overlapped by Animal 2's home range, $HR_{2,1}$ is the proportion of Animal 2's home range overlapped by Animal 1's home range, and $A_{1,2}$ is the area of overlap between HR_1 and HR_2 (Kernohan *et al.* 2001).

Directionality of movements of males

Chi-square tests were used to evaluate whether the cumulative distance travelled up- or downstream by Ord River male crocodiles was biased in either direction. Tests were performed using R.

Results

Area–observation curves suggest that dry-season core areas of females (see below) approach an asymptote between 30 and 40 locations (e.g. Fig. 2*a*), whereas home ranges of males probably asymptote at between 40 and 50 locations (Fig. 2*c*). Estimates of the size of core areas of females (Table 1) are considered reliable but home ranges appear to have stabilised

only for Males 184, 188 and 193 (e.g. Fig. 2*c*) with MSLRs for other males likely to be underestimates (e.g. Fig. 2*b*).

Movements of females

All females studied inhabited different core area habitats although they showed consistent patterns of movement: all occupied a small core area on the main river channel during the dry season and moved to areas of suitable nesting habitat at the beginning of the wet season where they remained until the following dry season (Fig. 3, Table 1). Dry-season core areas ranged from 0.3 to 2.5 km (mean ± s.d.: 1.3 ± 0.9 km) and encompassed an RCA of 5–20 ha (15 ± 7 ha). Females occasionally made excursions away from their core areas during the dry season and the maximum excursion distance detected was 15 km. Mean rates of movement for females were generally low (<1 km day^{-1}) because they occupied

Table 1. Summary statistics for four mature *Crocodylus porosus* females radio-tracked between October 2001 and May 2003

	Crocodile No.				Mean ± s.d.
	164	183	185	189	
Date captured	25.x.2001	11.iv.2002	24.iv.2002	07.v.2002	
Total length (m)	2.72	3.08	2.74	2.72	
Body mass (kg)	76	103	76	82	
Study interval (d)	412	384	370	360	
Total number of locations (*n*)	30	37	44	41	
Max. rate of movement detected[A] (km day^{-1})	−1.1	−2.4	<1	10.1	
Dry season core area					
MSLD[B] (km)	1.5	2.5	1.0	0.3	1.3 ± 0.9
Area (ha)	17	20	17	5	15 ± 7
Number of core area locations (*n*$_c$)	27	32	41	33	
Core area habitat[C]	MTBS	TF	NTF	MTF	
Max. excursion distance detected[A] (km)	7	4	0	−15	
Wet season movement[A] (MSLD[B] km)	15	± 21	−62	−15	28 ± 22.7

[A]Negative values indicate downstream movement and positive values indicate upstream movement.
[B]MSLD = mid-stream linear distance.
[C]MTBS = macrotidal brackish-saline reach; TF = tidal freshwater reach; NTF = non-tidal freshwater reach; and MTF = macrotidal freshwater reach.

small core areas during the dry season. The maximum ROM detected was a 10.1 km day^{-1} upriver movement by Female 189 when she was returning to her core area after a downriver excursion. Females moved 15–62 km from their dry-season core areas to nesting habitat during the wet season (Fig. 3, Table 1). Two of the four females returned to the same core area after the wet season. Female 183's tag detached at her wet season habitat and Female 189 was not known to have returned to her previous core area when the study ended in early May 2003.

All female *C. porosus* tagged during this study were quite large (Table 1) and thought to be reproductively mature. Female 164 had a swollen abdomen when she was caught in October 2001 and was thought to be gravid although palpation of the abdomen was inconclusive. She was not detected moving from her dry-season core area from December 2001 to March 2002 (*n* = 6) and either nested nearby or did not nest that season, possibly due to the stress of capture in late October (see Seymour *et al.* 1987; Elsey *et al.* 1991; Rooney and Guillette 2000; Jessop *et al.* 2003). She was detected 15 km upriver from her dry-season core area in December 2002 where most nesting activity is reported for the King River. Female 189 was tracked to a recently constructed nest in December 2002 and all females moved to what were pre-

sumably nesting habitats during the 2002–03 wet season. Females were tracked exclusively from the air during the wet season and all but Female 189 were detected near or under canopy, which made it difficult to confirm the presence or absence of a nest.

After the wet season, both Females 164 and 185 returned to the same core area they occupied the previous dry season. In April 2003, Female 189 was still on the floodplain of the lower Ord on the opposite bank to the one on which she had constructed a nest in December 2002. Inspection of the nest mound in April 2003 failed to detect any egg-shell residue and she may have abandoned the site due to below-average rainfall during the previous the wet season. By May 2003, she had moved back to the main channel of the Ord River and may have returned to the core area she inhabited the previous dry season. Unfortunately no funds were left to continue the tracking study.

Female 183 moved between the main Ord channel and a small backwater during the 2002 dry season. Signals were reliably detected in the main channel yet disappeared when approaching her in the backwater. The backwater was tidally influenced although the water was fresh. Maximum depth was ~2–3.5 m, depending on tide, and the signal should have been detectable. One possible explanation was that she was
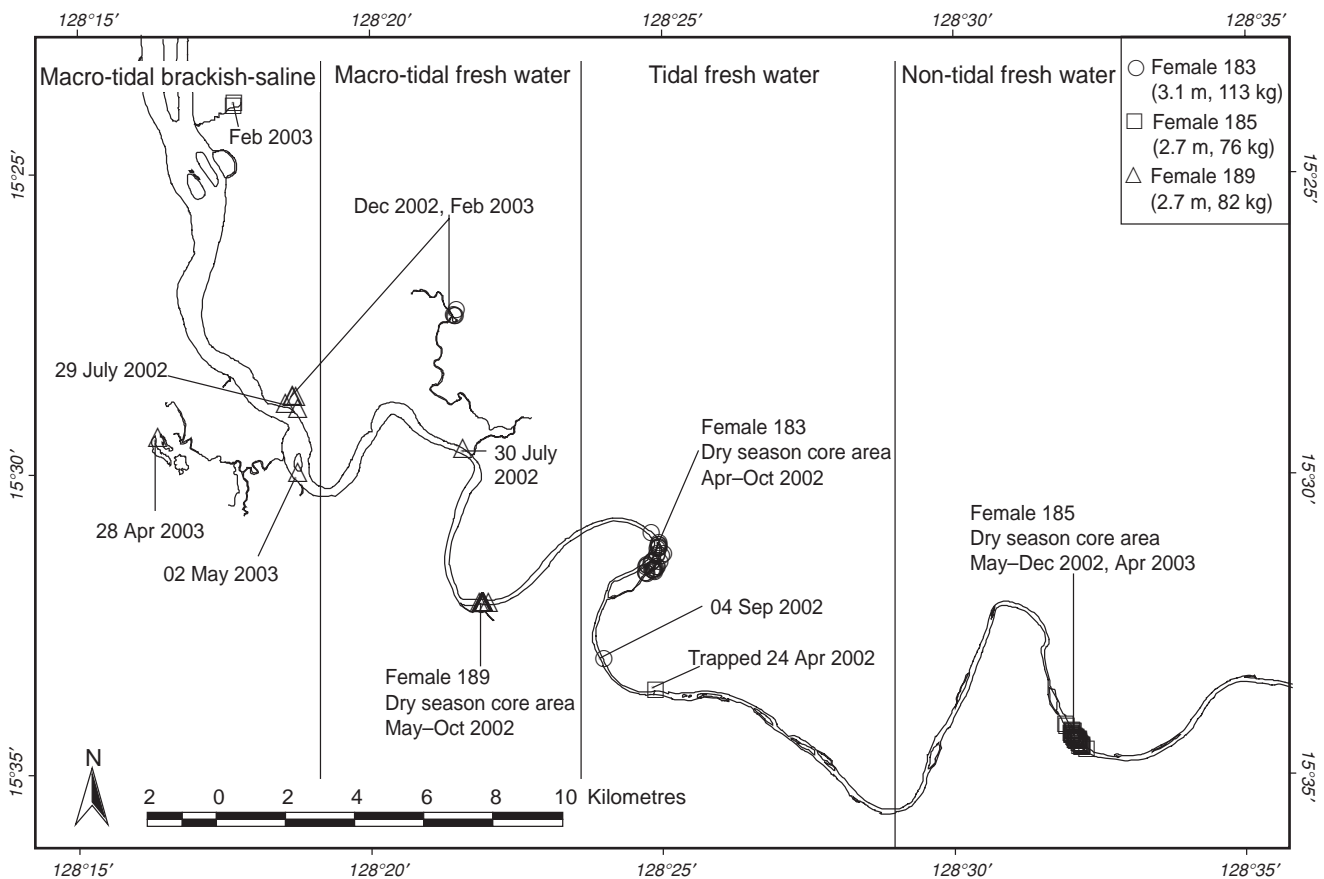

Fig. 3.   Movements of three mature female *Crocodylus porosus* within the Ord River system between April 2002 and May 2003.

using an underwater den for refuge, which formed a physical barrier to the tag's signal. Between October and December 2002, Female 183 moved 21 km from her dry-season core area up a tributary to a non-tidal pool that was possibly spring-fed and where crocodile nests had been seen previously. Her tag was recovered in April 2003 and had detached between October 2002 and April 2003. Signals had been detected from the air in December 2002 and February 2003. Preliminary inspection of the tag indicated damage consistent with a bullet hole. Subsequent examination in Perth by a forensic chemist confirmed that the damage and hole dimensions were consistent with calibres commonly used in the region, indicating that Female 183 had probably been shot.

Movements of males

Patterns of movement of males were substantially different to those of females (Table 2). Males traversed large sections of river and had MSLRs of 11–87 km. The size of the MSLR or RCA appeared to be unrelated to body size and the smallest male tagged (195) had the largest MSLR (87 km), which had not stabilised by the end of the study. The second largest MSLR was 67 km, for the largest male tagged (191), which also had not stabilised. MSLRs were 33–44 km for the three animals with stabilised estimates (Table 2). It was unclear whether river area was important for crocodiles and the large RCAs observed for Males 191, 192 and 194 may reflect a

habitat preference for the lower Ord estuary where the river channel was broad.

Most males did not appear to have site fidelity to particular sections of river or exclusive habitat preferences based on tracking experience and GIS analysis. The MSLR of most males encompassed three or four different habitats (Table 2). However, the three largest males had centres of activity that comprised 4–16% of their MSLR. They moved away from, and returned to, these centres throughout the year. The largest male (191) may have had multiple centres of activity as he was thought to have spent much of the dry season in 2002 on the lower reaches of the Ord River well outside the routine tracking section. Therefore, his habitat preference was thought to be MTBS despite the recorded centre of activity being in a TF reach (Table 2). There did not appear to be strong seasonal patterns of movement for most males however the four largest animals tended to make more excursions to the upriver sections of their MSLR during the late dry and wet seasons.

Rates of movement of males appeared to be bimodally distributed (Fig. 4). This was consistent with observations while tracking. Most males tended to occupy a small section of river for a period of days or weeks where ROM was low. They then moved to another section of river, often with a high ROM, where they would spend a variable period of time. There were no significant differences in ROM between three size classes of males ($H = 0.71$, $P > 0.70$) or between

Table 2. Summary statistics for nine *Crocodylus porosus* males radio-tracked between April 2002 and May 2003

Crocodile	Crocodile No.								
	195[A]	190[A]	184	194[A]	192[A]	193	186[A]	188	191[A]
Date captured	26.v.2002	9.v.2002	22.iv.2002	25.v.2002	16.v.2002	21.v.2002	24.iv.2002	07.v.2002	12.v.2002
Total length (m)	2.53	2.63	3.25	3.07	3.12	3.17	3.27	3.53	4.34
Body mass (kg)	62	62	91	103	111	116	141	151	337[B]
Study interval (d)	341	67	377	195	352	348	375	361	287
Total number of locations (n)	34	19	44	18	22	45	43	38	26
Mid-stream linear range (km)	87	11	36	62	51	44	29	33	67
River channel area range (ha)	1734	127	985	6427	4160	626	416	658	4988
Mean (± s.d.) rate of movement (km day^{-1})	0.7 ± 0.6	0.6 ± 1.0	2.1 ± 2.2	1.2 ± 1.6	1.8 ± 1.4	1.3 ± 2.6	1.2 ± 1.6	2.0 ± 4.0	3.3 ± 6.5
Max. rate of movement detected[C] (km day^{-1})	–2.1	3.6	–9.5	4.6	–4.5	–13.1	5.4	19.4	–23.3
Cumulative distance travelled (km)	215	19	207	158	131	138	136	193	190
Centres of activity[D]									
n	0	0	0	0	0	0	1	1	1
% locations	NA	NA	NA	NA	NA	NA	84	68	62
MSLD[E] (km)	NA	NA	NA	NA	NA	NA	4.6	2.6	2.4
Habitat type	NA	NA	NA	NA	NA	NA	TF	MTBS	TF
Habitats utilised[F]	1, 2, 3, 4	3	1, 2, 3	1, 2, 3	1, 2, 3	2, 3, 4	3,4	1,2, 3	1, 2, 3, 4
Habitat preference[F]	NTF	NA	NA	MTBS	MTBS	NA	TF	MTBS	MTBS

[A]Home ranges for these individuals are likely to be underestimates (see Fig. 2).

[B]Body mass was estimated from skull dimensions and total length using equations from Webb and Messel (1978*a*).

[C]Negative values indicate downstream movement and positive values indicate upstream movement.

[D]NA = not applicable.

[E]MSLD = mid-stream linear distance.

[F]1 = macrotidal brackish-saline reach (MTBS); 2 = macrotidal freshwater reach (MTF); 3 = tidal freshwater reach (TF); and 4 = non-tidal freshwater reach (NTF).

different tidal phases ($H = 0.88$, $P > 0.83$) but there were significant differences between seasons ($H = 13.10$, $P < 0.005$). Mean (±s.d.) rates of movement were highest during the summer wet season (4.0 ± 5.4 km day^{-1}), followed by late dry (1.6 ± 2.3 km day^{-1}), dry (1.3 ± 3.3 km day^{-1}) and post-wet (1.1 ± 1.4 km day^{-1}) seasons. However, males were still quite mobile during the dry season and the highest rate of movement detected was a 28-km downriver movement in 1.2 days by Male 191 during neap tides at the end of July 2002 (Table 2). Conversely, the second highest rate of movement detected was a 19-km upriver movement in one day by Male 188 during spring tides in December 2002. The highest detected rates of movement were for the two largest males (Table 2) despite there being no significant differences in ROM for different size classes.

Interactions between males

There was substantial overlap of MSLRs for most Ord River males, with no obvious exclusion or spatial partitioning evident (Fig. 5).

Directionality of male movements

Males moved both up- and downstream within any given period and throughout the year. Only Male 195 showed significant directional movement ($\chi^2 = 6.97$, $P < 0.01$) during the study. He reached Skull Rock at the end of July 2003 and was tracked over the next 10 weeks moving between Skull Rock and Tarrara Bar (Fig. 6). Tarrara Bar appeared to act as a natural physical barrier to further upstream movement. The lower section of Tarrara Bar had a small gorge where the water was much deeper and slower-flowing than in the adjacent upstream section. Male 195 was often detected at the upstream limit of the gorge in an eddy near a small sandbank that was used for basking. However, he negotiated this section of river between late February and early May 2003, most likely when river levels were elevated during the wet

season, and was detected 12 km further upstream in May 2003 (Fig. 6).

Movement upstream through the TF and NTF reaches required animals to traverse numerous sand, gravel or rock bars with sections of shallow, fast-flowing water, especially upstream from Carlton Crossing (see Fig. 6) where tidal movements no longer provided any assistance. Four of the nine Ord River males (including two of the three largest males) were detected upstream from Carlton Crossing at some point during the study.

Males 146 and 350

Male 146 was a 2.6-m problem male that was translocated from Wyndham Port to the Ord River (Fig. 7). He showed the highest rate of sustained movement detected during the study by travelling 118 km in 12 days at an average rate of 9.8 km day^{-1} to return to the area of capture. This is likely to be a conservative estimate because it assumes that he entered a trap set on the King River immediately on return, having overshot the original site of capture.

Male 350 was the only crocodile detected moving to another river system during the study (Fig. 7). He was caught and tagged in the King River in October 2001. From October to December 2001, he spent most of his time near the mouth of the King River and was not detected in the river in January or February 2002. In March 2002 he was detected in the Durack River, approximately 44 km from the mouth of the King River. He returned to the King River in June 2002 and was detected in Cambridge Gulf in July 2002, 14 km from his previous location.

Discussion

Interspecies comparisons

Data on home ranges and movements of crocodilians are scarce for all species other than *A. mississippiensis*, providing limited opportunities for making comparisons within and
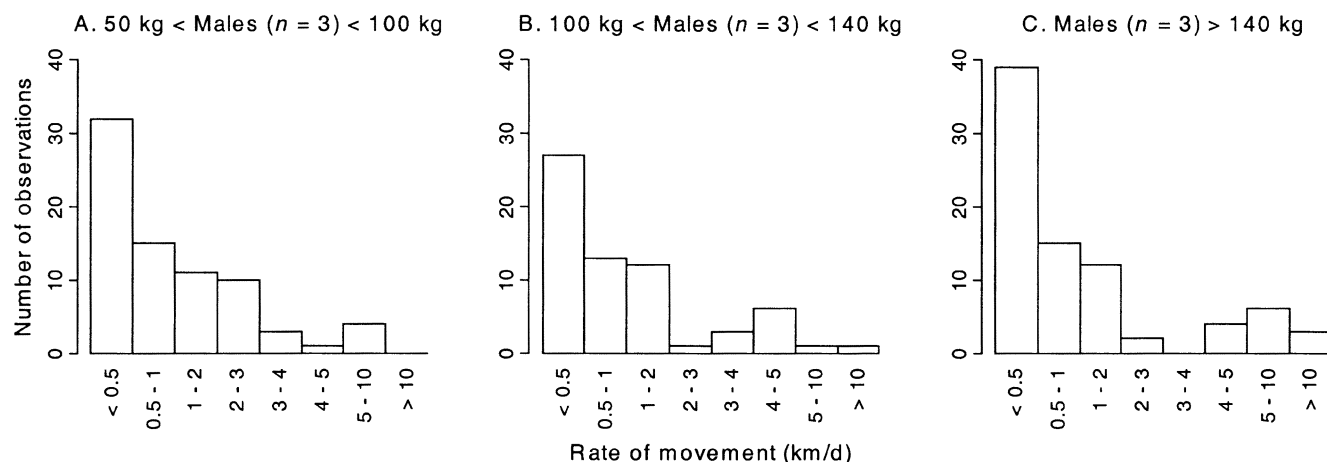

Fig. 4. Frequency histograms of rates of movement (km day^{-1}) for three size classes of Ord River male *Crocodylus porosus*.

among species. Furthermore, all movement studies of *A. mississippiensis* and *C. niloticus* have occurred in lacustrine systems whereas the present study investigated movements of *C. porosus* in riverine environments. Nevertheless, comparisons across habitats are informative for examining broad differences between species. Home ranges and rates of movement found for *C. porosus* in this study are generally greater than those reported for other species of crocodilian but, even so, are thought to be conservative. The highest ROM detected was 23.3 km day^{-1} for the largest male (4.3 m) tagged and a translocated juvenile male (2.6 m) travelled 118 km in 12 days. In comparison, the highest ROM reported for *A. mississippiensis* and *C. niloticus* was 8.5 km day^{-1} (Joanen and McNease 1972) and 2.9 km overnight (Hocutt *et al*. 1992) respectively, both by large (>3 m) males. However, Bustard and Singh (1983) have reported adult gharials travelling distances of 12 km in two hours.

Male and female *C. porosus* showed distinctly different patterns of movement, as do male and female *A. mississippiensis* and *C. niloticus*. Male *C. porosus* had linear ranges of between 33 (smallest stabilised estimate) and 87 (largest estimate, unstabilised) km (RCA: 626–4988 ha). However,

MSLRs had stabilised for only three of nine males, with stabilised estimates of 33–44 km. Mean ROM for male *C. porosus* was 0.6–3.3 km day^{-1} but ROM appeared to be bimodally distributed and maximum rates were much higher. There were significant differences in rates of movement of males between seasons, with the highest ROM occurring during the summer wet season.

Stabilised MSLRs for *C. porosus* males are comparable with linear ranges reported for gharials, which ranged from 23 to 44 km (Bustard and Singh 1983). Australian freshwater crocodiles have much smaller linear ranges. Tucker *et al.* (1997) found that pubescent male *C. johnstoni* were probably nomadic and had linear ranges of ~30 km yet all other life stages had small (<2 km) linear ranges. Home ranges of male alligators vary from 183 to 5083 ha (Joanen and McNease 1972; Goodwin and Marion 1979), which are comparable with RCAs found in this study for male *C. porosus*. The mean daily movement reported for male alligators by Joanen and McNease (1972) was 0.7 km day^{-1}, which is also comparable with that of the smaller *C. porosus* males. Mature male *C. niloticus* had distinct home ranges, the largest of which was 80 ha (Hutton 1989), which was considerably
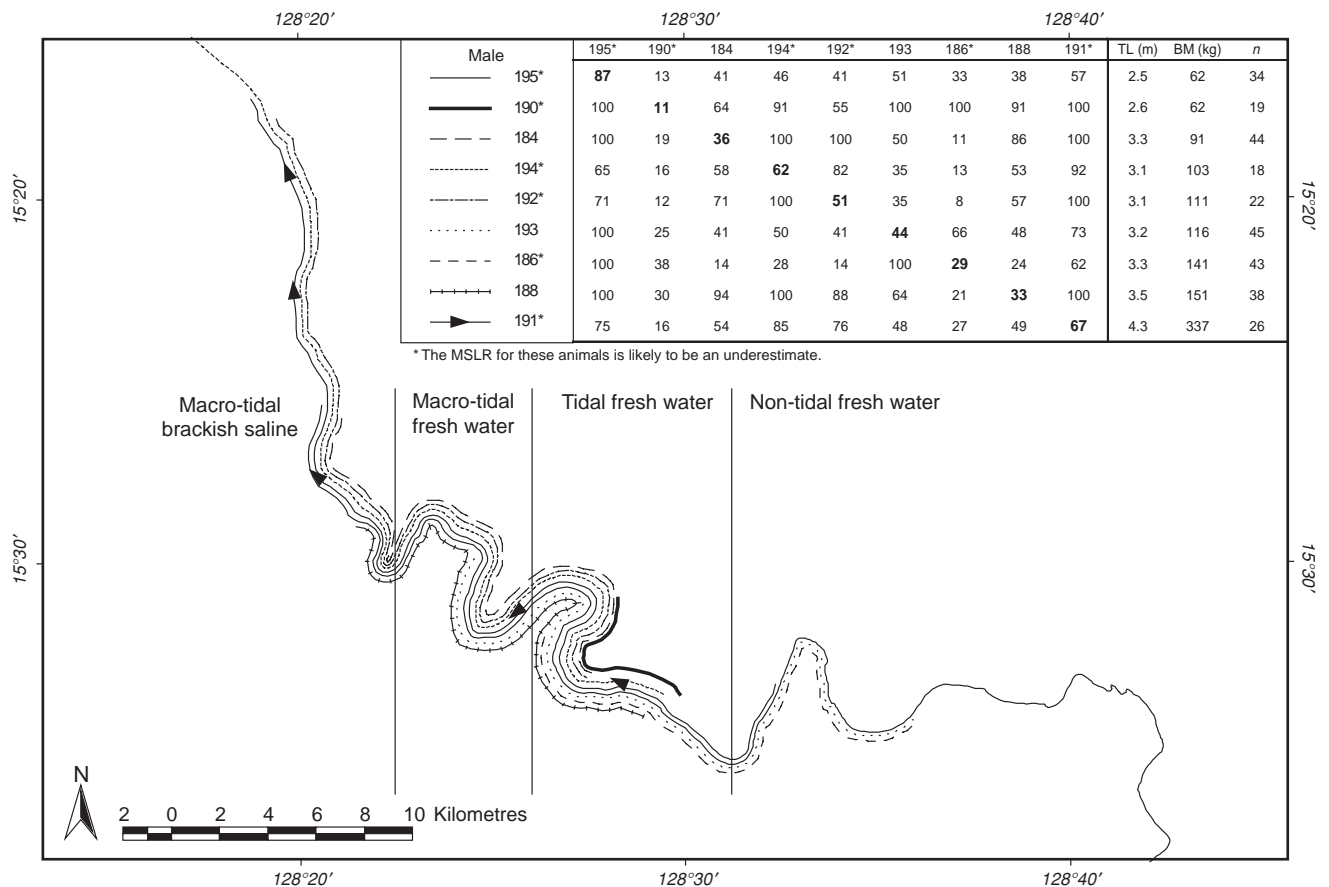

Male		195*	190*	184	194*	192*	193	186*	188	191*	TL (m)	BM (kg)	*n*
——————	195*	**87**	13	41	46	41	51	33	38	57	2.5	62	34
——————	190*	100	**11**	64	91	55	100	100	91	100	2.6	62	19
– – –	184	100	19	**36**	100	100	50	11	86	100	3.3	91	44
··········	194*	65	16	58	**62**	82	35	13	53	92	3.1	103	18
–·–·–	192*	71	12	71	100	**51**	35	8	57	100	3.1	111	22
··········	193	100	25	41	50	41	**44**	66	48	73	3.2	116	45
– – –	186*	100	38	14	28	14	100	**29**	24	62	3.3	141	43
⊢⊣⊢⊣	188	100	30	94	100	88	64	21	**33**	100	3.5	151	38
⟶	191*	75	16	54	85	76	48	27	49	**67**	4.3	337	26

* The MSLR for these animals is likely to be an underestimate.

Fig. 5. Mid-stream linear ranges (MSLR) of, and static interactions between, nine Ord River male *Crocodylus porosus*. Bold values on the diagonal in the table are the MSLR for each male in kilometres. The other values are the percentage of MSLR overlap between males.

smaller than those found for *C. porosus*. *C. niloticus* also showed seasonal patterns of activity and were more active during the warmer months (Hutton 1989; Hocutt *et al*. 1992).

Female *C. porosus* occupied small core areas during the dry season (1.3 ± 0.9 km, 15 ± 7 ha) where mean daily movements are generally <1 km day⁻¹. However, movements of 10.1 km day⁻¹ were detected during excursions. Females travelled up to 62 km to nesting habitat during the wet season. Female *A. mississippiensis* also show distinct seasonal patterns of movement. A number of authors have reported female activity being greatest during the spring breeding season (Joanen and McNease 1970; Goodwin and Marion 1979; Rootes and Chabreck 1993) although Taylor (1984) found that females were most active during summer. Mean home ranges for mature female alligators range from 8 (Joanen and McNease 1970) to 56 ha (Taylor 1984) and are quite variable (1–256 ha) between individuals (Taylor 1984). They are generally larger than the dry-season core areas of female *C. porosus* found in this study but daily movements reported for female alligators are very low. Most studies report movements of <0.06 km day⁻¹ for mature female alligators (Taylor 1984; Rootes and Chabreck 1993). The maximum daily movement reported was 0.46 km day⁻¹ by Joanen and McNease (1970). In contrast, female *C. porosus*

tracked during this study were usually quite mobile within their core areas and movements of up to 10.1 km day⁻¹ were detected. Hutton (1989) found that mature female *C. niloticus* had home ranges of about 15 ha, which are comparable to the dry-season core areas found for female *C. porosus* in this study. However, *C. niloticus* females maintained their home ranges near prime nest sites, whereas *C. porosus* females moved considerable distances to nesting habitat during the wet season.

Movements, territoriality and mating systems of males

Ord River males were very mobile and showed no consistent pattern of movement. There were no obvious patterns of seasonal site selection although the four largest males tended to make more excursions to the upriver sections of their MSLRs during the late dry and wet seasons. ROM increased during the late dry season and was greatest during the wet season. However, the highest ROM detected was 23.3 km day⁻¹ downriver during the dry season. Crocodiles are probably more active at night but Ord River males were quite mobile during the day. They were often observed utilising prevailing currents to move with minimal effort, especially making upriver movements on flooding tides. Despite this observation, no significant differences in ROM were found between different tidal phases. However, a more intensive
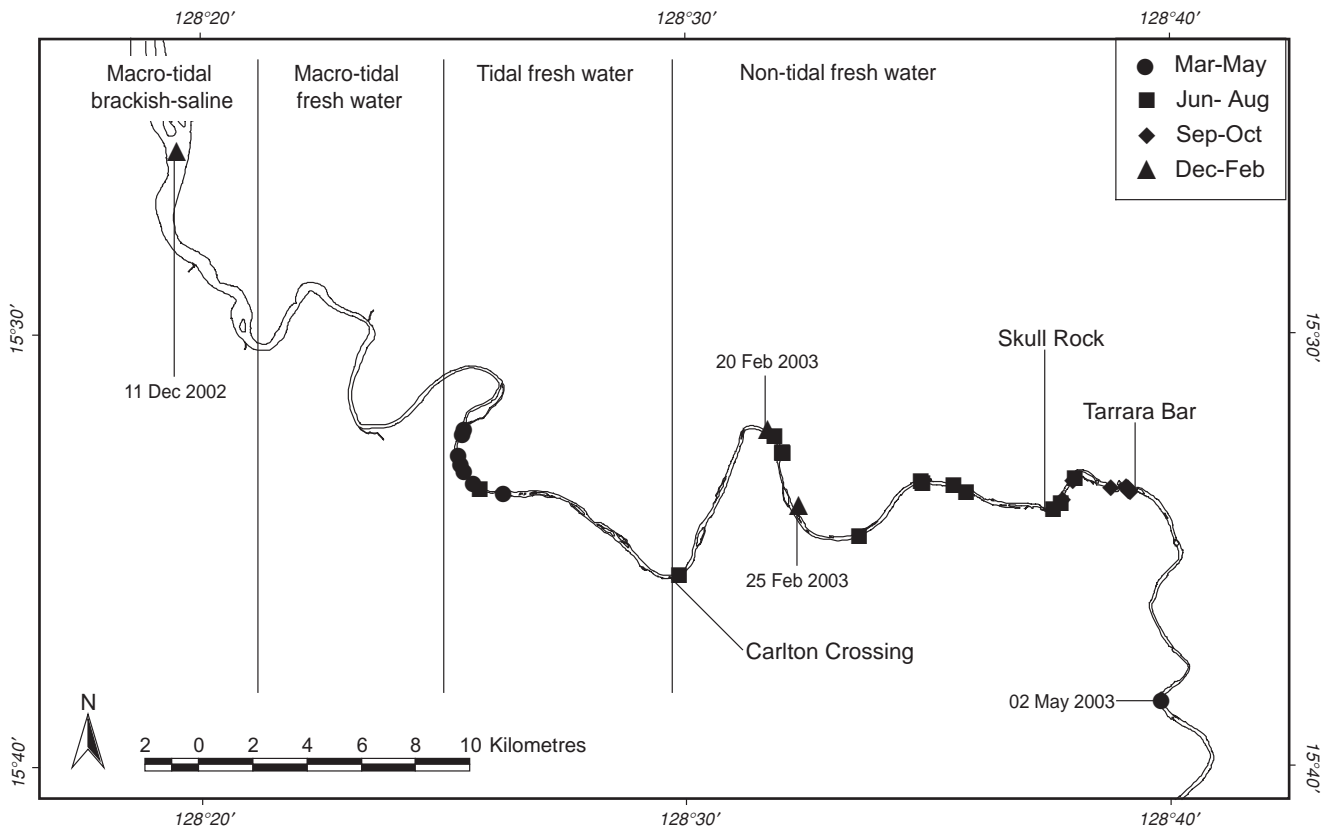

Fig. 6.   Movements of Ord River Male 195 (2.5 m, 62 kg) between May 2002 and May 2003. There was significant directional movement upstream (*P* < 0.01) but both up- and downstream movements occurred within any given period.

investigation would be desirable to analyse whether there was differential use of tidal cycles.

Of all crocodilian species, *C. porosus* is thought to be the least tolerant of conspecifics (Lang 1987). No convincing evidence was found of exclusive territories held by Ord River males. MSLRs overlapped substantially and there was no obvious exclusion or spatial partitioning of home ranges (Fig. 5). The three largest males had centres of activity but made numerous excursions away from these areas throughout the year both up- and downriver. Their MSLRs included the activity centres of the other largest males except for Male 186, whose MSLR did not include Male 188's activity centre. Nevertheless, Males 186 and 188 had >20% overlap of MSLRs. Many other large untagged males were often seen in the routine search area and had obviously overlapping MSLRs with the tagged males without any indication of the tagged animals being displaced or receiving injuries. It also seems unlikely that a large crocodile could successfully exclude all other males from MSLRs that mostly exceed 30 km.

Bi-modality of male movements may indicate dynamic interactions (see Kernohan *et al*. 2001) between males, where a male spends time in a particular section of river until provoked into moving by another male, but it is also difficult to

reconcile male territoriality with patterns of female movement. *C. porosus* are thought to have a polygynous mating system where dominant males mate with multiple females (Lang 1987). However, multiple paternity has been demonstrated in *A. mississippiensis* (Davis *et al*. 2001) and, more recently, genetic studies have found evidence of multiple paternity in captive *C. porosus* (Jamerlan 2003). Ord River females in this study occupied small sections of river from May to October, which included part of the courtship and mating season. A 2.7-m female dissected on 18 September 2002 had abundant mature follicles and oviducal eggs (plasma oestradiol = 683 pmol L^{-1}, testosterone = 0.7 nmol L^{-1}). A 3.4-m male dissected on 9 September 2002 had enlarged testes and appeared to be in full spermatogenesis (plasma testosterone = 17 nmol L^{-1}) (see Lance 1987, 1989; Kofron 1990; Coutinho *et al*. 2000; Guillette and Milnes 2000). Females were detected making excursions during the dry season though these were uncommon. While it remains possible that females move in search of males during the mating season, it seems more likely that males move in search of females occupying dry-season core areas. Mean male ROM increased during the late dry season and reached a maximum during the wet season. Additionally, the four largest males
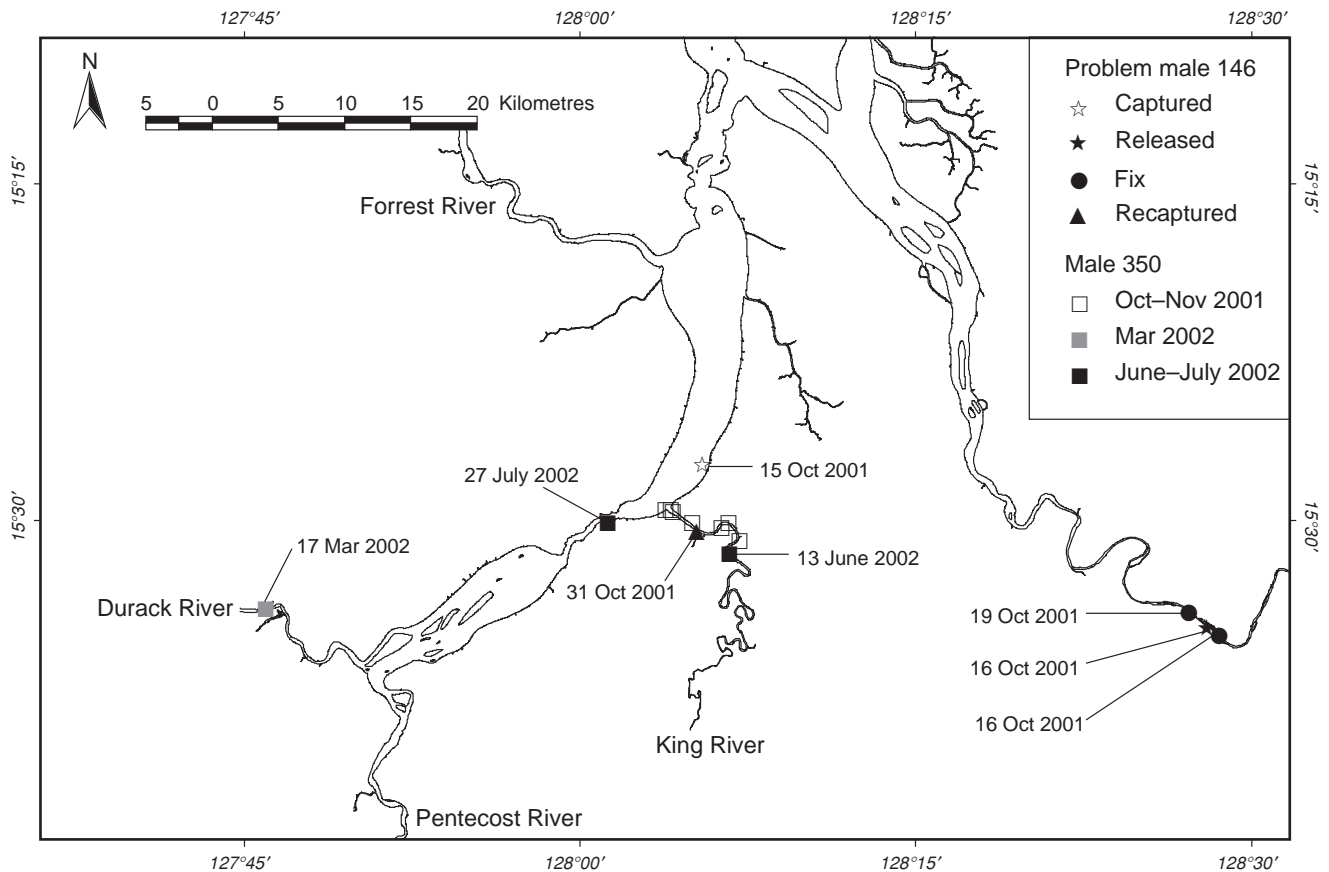

Fig. 7.   Movements of immature *Crocodylus porosus* Males 350 (2.1 m, 32 kg) and 146 (2.6 m, 59 kg). Male 146 was a problem male that was translocated from Wyndham port to the Ord River.

tended to make more excursions to the upriver sections of their MSLRs during the late dry and wet seasons. These patterns of movement were consistent with males actively seeking females during the breeding season. High mobility would be advantageous for males, enabling them to search for females occupying small core areas and would also facilitate multiple paternity in wild populations. This would make defending territories from rival males unnecessary. Size-based dominance hierarchies were clearly evident while observing interactions among Ord River crocodiles. Therefore, aggressive interactions among crocodiles are probably more likely to occur between evenly matched individuals.

Site fidelity

Most crocodiles remained within the river in which they were caught and only one animal showed any significant directional movement during the study. Furthermore, Male 350 was the only animal detected moving into another river system yet returned to the King River. These patterns of movement suggest at least some site fidelity, which is corroborated by genetic data. There are highly significant differences in allele frequencies between the King and Ord River populations and >74% of individuals were correctly designated to their source population using assignment tests (Kay 2004). Three Ord River males (191, 192 and 194) were thought to have spent much of the dry season in 2002 in the lower Ord estuary outside the routine search area. It is possible they moved into Cambridge Gulf and beyond. However, they were all detected further upriver during the late dry and wet seasons. Male 350 had been scute-marked previously but, unfortunately, no records were available to confirm his previous capture history and point of origin. It was assumed that he was an escapee from the crocodile farm in Wyndham.

Translocation and homing

The tendency for translocated animals to home has been reported for a number of crocodilian species, including *C. porosus* (e.g. Gorzula 1978; Webb and Messel 1978*b*; Webb *et al*. 1983*b*; Rodda 1984*a*). Translocated Male 146 travelled 118 km in 12 days (9.8 km day^{-1}) to return to the area of capture. He was blindfolded and chemically sedated at the site of capture and was still quite heavily sedated when released. He was quite likely disorientated after release but took only a few days to recover and returned rapidly to the area of capture. This would seem to have required good navigational ability as the return path was by no means obvious (see Murphy 1981; Rodda 1985; Phillips 1996). However, Walsh and Whitehead (1993) found that <50% of problem crocodiles translocated from Nhulunbuy in the Northern Territory returned to the original site of capture. It is unknown whether the remainder were translocated successfully and/or were killed by conspecifics and/or returned but were trap shy. Only 4 of 23 recaptured individuals had injuries attributable to other crocodiles and some were

recaptured up to eight times. The probability of recapture could not be related to distance and direction of release, nor to size or sex of the released animal. Frequency of recapture of individual crocodiles was also unrelated to these variables. The time between consecutive recaptures of the same crocodile was highly variable, ranging from 10 days to >3.7 years (Walsh and Whitehead 1993). The highest ROM detected between recaptures was 3.9 km day^{-1} (Walsh and Whitehead 1993), which was quite low when compared with rates of movement detected in this study. Homing may well be density-dependent for translocated problem animals but the data are equivocal (see Walsh and Whitehead 1993). Reciprocal translocations of electronically tagged animals from similar size and sex classes over different spatial scales would clarify the effectiveness of translocation as a possible solution to problem animals (see Tucker *et al*. 1997).

Conclusions

Estuarine crocodiles are large, mobile and long-lived animals that interact with their environment over large spatial and temporal scales. This study has provided an insight into their movements though the sample size and period of study were small. Data are needed from more animals of both sexes, over a more complete size range, in different geographic regions and habitat types and over a longer period to establish whether the patterns that have emerged are typical. It has become increasingly apparent from a number of simulation studies that large sample sizes are required to define the home range of an individual animal reliably, and that large numbers of animals from a particular class must be studied in order to make inferences about movements at the population level (see White and Garrott 1990; Garton *et al*. 2001; Kernohan *et al*. 2001). Automated telemetry systems using satellite tracking technology would be the most efficient and cost-effective approach for collecting the large amount of data required for analysing the movements of *C. porosus* in any future studies, especially in remote areas, and would be less likely to influence animal behaviour than manual tracking techniques.

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