

Estuarine crocodiles ride surface currents to facilitate long-distance travel

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Summary

1. The estuarine crocodile (*Crocodylus porosus*) is the world's largest living reptile. It predominately inhabits freshwater and estuarine habitats, but widespread geographic distribution throughout oceanic islands of the South-east Pacific suggests that individuals undertake sizeable ocean voyages.

2. Here we show that adult *C. porosus* adopt behavioural strategies to utilise surface water currents during long-distance travel, enabling them to move quickly and efficiently over considerable distances.

3. We used acoustic telemetry to monitor crocodile movement throughout 63 km of river, and found that when individuals engaged in a long-distance, constant direction journey ($> 10 \text{ km day}^{-1}$), they would only travel when current flow direction was favourable. Depth and temperature measurements from implanted transmitters showed that they remained at the water surface during travel but would dive to the river substratum or climb out on the river bank if current flow direction became unfavourable.

4. Satellite positional fixes from tagged crocodiles engaged in ocean travel were overlaid with residual surface current (RSC) estimates. The data showed a strong correlation existed between the bearing of the RSC and that of the travelling crocodile ($r^2 = 0.92$, $P < 0.0001$).

5. The study demonstrates that *C. porosus* dramatically increase their travel potential by riding surface currents, providing an effective dispersal strategy for this species.

Key-words: behaviour, *Crocodylus porosus*, migration, telemetry, zoogeography

Introduction

Of all the amazing things animals can do, the ability of certain species to migrate significant distances across formidable geographical barriers is one of the most remarkable. Mountain ranges, deserts, ice-fields and oceans generally obstruct long-distance animal movement because they are largely absent of the food and water necessary to replenish energy stores. Individuals which utilise wind and water currents to facilitate a reduction in the use of their endogenous energy supply during travel increase their chances of success, and consequently, the flight path of many migrating birds follows wind direction and strength (Gill *et al.* 2009), and the long-distance trajectory of marine animals often reflects residual

current drift (Gaspar *et al.* 2006; Metcalfe, Hunter & Buckley 2006).

If a group of individuals are geographically separated from their parent stock and no travel occurs between the divided populations, species diversification will occur. However, high levels of gene flow between isolated populations may homogenize the genes responsible for divergence and constrain the force of natural selection. Land-based animals will often show diversification from the parent stock if they become separated by an ocean barrier (Mayr 1963), but if mixing between island populations is supported through ocean currents, the spatial and temporal patterns of these phenomena might have important consequences for the evolution and adaptive radiation of these populations (Calsbeek & Smith 2003).

The geographical range of the estuarine crocodile (*Crocodylus porosus*) spans over 10 000 km² of the South-East Pacific; from East India and Sri Lanka throughout Southern

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China to Thailand; the Philippine and Sunda islands (including Sumatra, Java, Borneo, Celebes, and Timor); to North Australia, Vanuatu, Fiji and the Solomon islands (Webb & Manolis 1989). It is a semi-aquatic reptile, primarily inhabiting rivers, mangrove swamps and estuaries. Although not considered a marine reptile, breeding populations are isolated by significant marine barriers (Allen 1974) and the distribution of *C. porosus* demonstrates high trans-oceanic vagility (Taplin & Grigg 1989). Many anecdotal accounts exist of large crocodiles being sighted in open-ocean, and on islands hundreds of kilometres from the nearest known population (Ditmars 1957; Allen 1974; Webb & Manolis 1989), yet their capacity for long-distance ocean travel remains poorly understood and it is unknown if ocean voyages form part of their ecological repertoire or merely represent occasional mishaps of navigation.

Only three estuarine crocodiles have ever been tracked whilst undertaking ocean travel; attached satellite transmitters showed that they could travel more than 30 km in a single day and were able to sustain consecutive daily movements of over 20 km (Read *et al.* 2007). This level of sustained swimming seems astonishing for a reptile with such a limited aerobic capacity (Pough 1980; Elsworth, Seebacher & Franklin 2003), and suggests, that similar to other migrants, estuarine crocodiles take advantage of current systems to facilitate long-distance journeys. Adopting such a behavioural strategy would enable individuals to regularly travel between island populations, homogenizing the gene pool, and helps to explain why island speciation has never occurred throughout this vast geographical range.

We tested the hypothesis that *C. porosus* utilise water current flow to assist in horizontal movement (selective-stream-transport) by acoustically tracking their movements and associated behaviours throughout a tidal river system. Here the association between crocodile movement and current flow could be examined at a finite scale in both space and time, and associations would be simplified because the direction of flow would be either completely in support of or against the crocodile's direction of travel. In addition, we assessed if selective-stream-transport explained the horizontal movement in ocean travelling *C. porosus* by correlating satellite derived positional fixes from ocean travelling crocodiles (Read *et al.* 2007) with archived residual surface current data obtained by satellite and surface marker buoys.

Materials and methods

STUDY SITES

The acoustic tracking component of this study was undertaken on the Kennedy River, North Queensland in Australia. This river was chosen as it contains a healthy population of estuarine crocodiles, has limited boat traffic, and no urban development exists along its length. The acoustic receiver array was placed throughout 63 km of the river's tidal length (N-14-68768: E144-097373 to N-14-558771: E143-963074; WGS84, decimal degrees). The river at the furthest upstream extent of the array was *c.* 35 m wide and 3–5 m deep, increasing to 58 m wide and 5–7 m deep at the furthest

downstream receiver. The times of the tidal cycles at the mouth of the Kennedy River were obtained from the Australian National Tide Centre, and the timing of the ebb and flow tidal pulse through the receiver array were determined by depth loggers deployed throughout the extent of the array (sensitive to 0.1 m, Star-Oddi, Reykjavik, Iceland). The semidiurnal tidal range was 2.4 m at the furthest downstream receiver and 1.8 m at the furthest upstream receiver. The tidal pulse of the flood took 2.2 ± 0.1 h to travel through the array, whilst the ebb tide pulse took 1.8 ± 0.1 h. The river water temperature was recorded every hour at the location of each receiver by a data-logger attached to the anchor line (ibutton Thermocron; Dallas semiconductor, Dallas, TX, USA).

The satellite study was undertaken along the east and west coast of Cape York Peninsula, Northern Queensland, Australia. Data was only used from satellite tagged crocodiles once they had left the confines of the estuary and entered into open sea.

ACOUSTIC TAGGING

Twenty-seven adult estuarine crocodiles (18 males, 9 females; 2.1–4.86 m length) were captured by baited traps in August 2007 from along the North Kennedy River, North Queensland, Australia. The traps were either floating in the river or located on the river bank. The trap was sprung by the crocodile pulling a trigger pin attached to a bait line (details in Walsh 1987). The animals were manually restrained and 10 ml of local anaesthetic (Lignocaine, Troy laboratories, Smithfield, Australia) injected into the area of soft skin and muscle immediately behind the left forelimb. An 8-cm lateral incision was made using a scalpel and the skin teased apart from the muscle by blunt dissection. The sterilized transmitter was inserted into the created pocket, and the wound closed by 4–6 interrupted sutures (cat-gut suture; Ethicon, NJ, USA). The total procedure was completed in less than 20 min and the crocodiles were released at the point of capture. All surgical procedures were carried out using an aseptic technique.

The implanted transmitters were VEMCO V-16 (Nova Scotia, Canada) coded acoustic transmitters (length 98 mm, diameter, 16 mm, weight in air 36 g), fitted with either a pressure (rated to a maximum depth of 34 m, resolution, 0.1 m) or temperature sensor (temperature range 0–40 °C, resolution 0.3 °C) encased in a biologically inert PVC. The sensor data and the transmitter unique ID code were acoustically transmitted on 69 kHz at a power output of 158 dB, approximately every 12 s. The transmitters had a battery life of *c.* 12 months.

To detect the acoustic signal an array consisting of twenty separate listening receivers (VR2-W; Vemco, Nova Scotia, Canada) was deployed along a 63-km tidal stretch of the Kennedy River. Each receiver was attached to a cement anchor, moored to a fixed structure on the river bank. The anchors were deployed between 5 and 20 m from the river bank in 4–9 m of water. They floated in the water column on a subsurface buoy 1.5 m above the river substratum. A total of 14 receivers were placed *c.* 1 km apart to provide an area of near continual coverage with the remaining receivers spaced more sparsely. To determine the detection range, an activated tag was towed behind a boat in a predetermined pattern around each receiver. The detection range was generally 400–600 m, and therefore, a crocodile could not pass along the river without the implanted transmitter being detected. A total of 1 236 867 data packets were recorded over 12 months. Purpose designed software was implemented in the Microsoft Visual Basic language for analysis (the V-TRACK software, written by M. Watts and H.A. Campbell, University of Queensland, Brisbane, Australia). The data from each of the twenty receivers were

colated into a single data matrix. The data matrix was subjected to procedural event log analysis in order to extract and summarize events. These were movement between adjacent receivers, residence within a receiver's detection range, period of submergence, and interval out of the water.

Direction of movement was determined by the order of transmitter detection throughout the receiver array. Rate of movement was determined by two separate methods and compared for consistency; (1) the distance between the detection limits of two adjacent receivers divided by the time that a crocodile took to move between them, (2) the width of the detection field of a single receiver divided by the time that a crocodile took to pass through. Body temperature and depth of the crocodile in the water column were determined by sensors within the transmitters. All variables were compared between favourable (moving in the same direction as crocodile) and unfavourable (moving in the opposite direction to crocodile) directional tidal flow. The crocodiles' movement patterns were divided into two distinct behavioural modes. (1) Short-range movement; these movements were typically only 1–3 km day⁻¹ in a constant direction but for analysis all movements < 10 km day⁻¹ in a constant direction were grouped as short-range movement. (2) Long-range movement; these movements were typically > 25 km day⁻¹ in a constant direction but for analysis all movements > 10 km day⁻¹ in a constant direction were grouped as long-range movement. To test for significance in movement and behavioural parameters between short and long-range movement each crocodile was examined using nonparametric two-sample tests with normal approximation (Mann–Whitney *U*-test). For testing for significance between temperature of the water and that of the crocodiles a Wilcoxon two-sample test was used (Zar 1999). All statistics were undertaken using Statgraphics 5.0. The direction of tidal flow was determined from tide tables and the tidal pulse through the receiver array. The effect of tide was deemed significant upon the observed parameters if $P < 0.01$.

SATELLITE TRACKING

The consecutive fixes from satellite tracked *C. porosus* which had undergone movement in ocean water (Read *et al.* 2007) were correlated with residual surface current estimates for the same location and time period.

Briefly, the crocodiles were captured using the same methods as described for the acoustic study. The satellite transmitters were a KiwiSat101 platform with a duty cycle of 24 h on, 72 h off and a repetition rate of 60 s. The overall dimensions for each PTT were approximately 120 mm (L) 632 mm (W) 624 mm (H) and had a mass of 300 g. Satellite transmitters were attached between the nuchal scutes with plastic-coated braided stainless steel wire threaded through small holes drilled horizontally through the osteoderms of the nuchal shield. The locations of the crocodiles after release were recorded by the Argos satellite system. Positions with Argos accuracy Classes 1, 2 or 3 were used within this study, as this provided data with suggested accuracy of less than 1 km (Argos User's Manual 2000). Further details of tagging methodology are described in Read *et al.* (2007).

We sourced the information on surface water current estimates from the Bluelink Reanalysis Version 2.1 project conducted by CSIRO Division of Marine and Atmospheric Research (Hobart, Australia). Surface water current estimates were derived from satellite and drifter buoy data, and provided velocity and direction estimates at 1 km intervals across the study region. Data available from <http://www.marine.csiro.au/remotesensing/occurrents/DIY.htm>. The association between crocodile movement and residual surface

current was examined using linear (Pearsons) correlation comparing the bearing of the crocodile between successive satellite fixes and the bearing of the residual surface current. A correlation was deemed to be significant if $P < 0.01$.

Results

SHORT-DISTANCE MOVEMENT

A total of 27 (18 males, 9 females) crocodiles were implanted with acoustic transmitters in August 2007. The process of crocodile capture and receiver deployment resulted in abnormal human disturbance along the river during August 2007, and therefore, only data collected from September 2007 through until August 2008 was used in the analysis. This resulted in received transmitter detections from twenty crocodiles (13 males, 7 females). All these crocodiles exhibited short-distance movement (> 10 km day⁻¹) for the majority of their daily travel. These movements were generally < 3 km day⁻¹ in a constant direction and movement throughout the year by all crocodiles was concentrated within discrete sections of the river not more than a few kilometres in river distance (Fig. 1). This type of short-range travel comprised 97.4% of the total receiver to receiver movements from tagged *C. porosus*.

LONG-DISTANCE RIVER TRAVEL

Of the twenty tagged crocodiles which remained in the river throughout the year, only eight exhibited long-distance travel (6 males and 2 females, mean number of long-distance journeys/animal = 5.0 ± 0.4). Forty-two long-distance journeys were recorded and these moved the crocodile from their home-area to the river-mouth, a distance of > 50 km. Once the crocodiles travelled beyond the river-mouth they were outside the detection range of the receiver array and their movements were not recorded. All crocodiles returned to the river after a period of absence between 2 and 64 days. Once they returned to the Kennedy River they moved back up the river and remained at the original site of capture. In March 2008, a crocodile (M7) left the river-mouth and did not return again during the study. A similar disappearance occurred in May 2008 (M3). The transmitter detections from these eight crocodiles form the basis of the statistical analysis between long- and short-distance movements.

The North Kennedy is a tidal river, and each tidal cycle resulted in a 180° directional shift in current flow through the listening array. This occurred approximately every 6 h, and the tidal pulse through the array, from the furthest upstream to downstream receiver was 2.2 h. Long-distance travel was always initiated within an hour of the tide changing after its highest or lowest period – depending on the direction of travel. This allowed the crocodile 6–8.2 h travel time with a favourable current direction. The direction of crocodile movement (detected as movement between adjacent receivers) was strongly associated with current direction, < 4% of all movements between receivers occurred in the

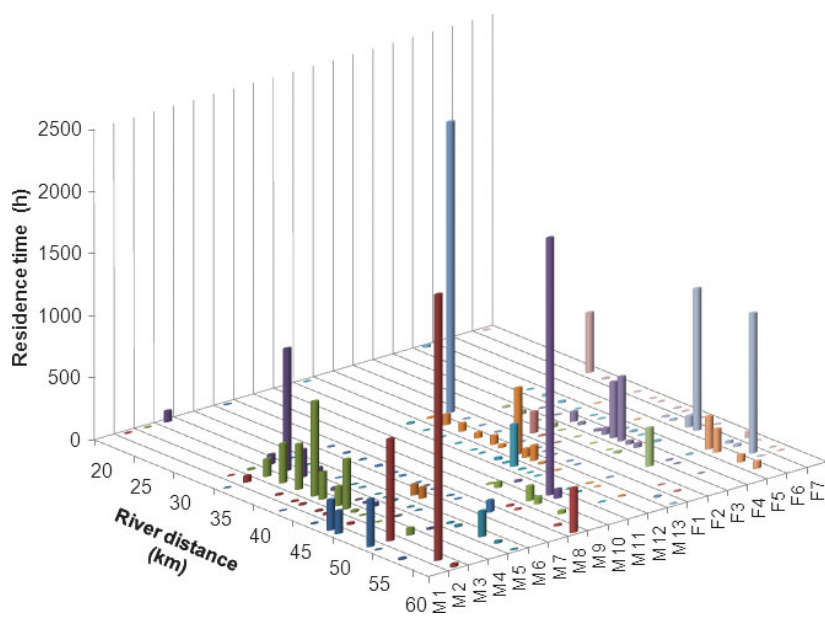


Fig. 1. The amount of time (h) that each acoustically-tagged *Crocodylus porosus* ($n = 20$) spent at discrete locations along the Kennedy River. River distance is expressed km from the River-mouth. Crocodile ID is on the z-axis (M, male; F, female), Crocodiles M2, M3, M5, M7, M11, F4 & F7 all undertook long-distance journeys beyond the river-mouth.

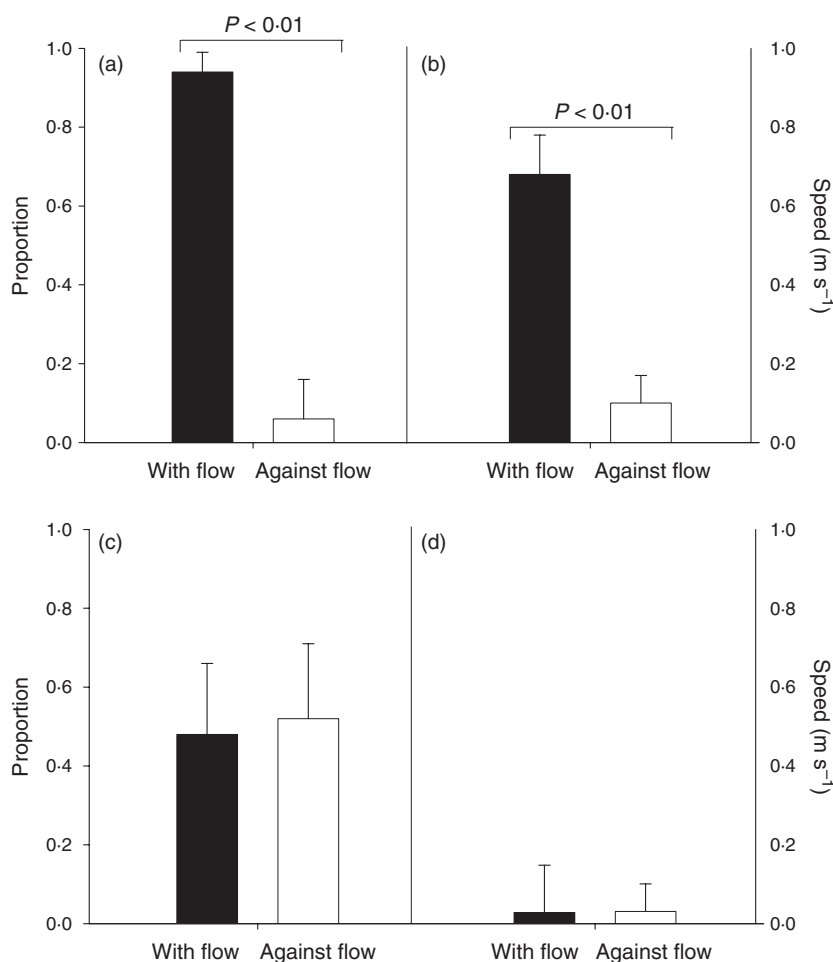


Fig. 2. The effects of current directional flow on movement during long- and short-distance travel in *Crocodylus porosus* ($n = 8$). The black bars show movement when the current was flowing in the same direction as the travelling crocodile and the clear bars demonstrate movement when the current was flowing opposite to the crocodiles' direction of travel. (a) The distribution of crocodile movement between adjacent underwater listening receivers when engaged on journeys when the daily distance travelled was > 10 km in a constant direction. (b) The rate of crocodile movement when engaged on journeys when the daily distance travelled was > 10 km in a constant direction. (c) The frequency distribution of crocodile movement between adjacent underwater listening receivers when engaged on journeys when the daily distance travelled was < 10 km in a constant direction. (d) The rate of crocodile movement when engaged on journeys when the daily distance travelled was < 10 km in a constant direction.

opposite direction to current flow (Fig. 2a, $Z > 18.9$, $P < 0.01$). Although a large size difference existed between tagged individuals (total body length = 2.6–4.9 m) there was no significance difference ($Z > 0.8$, $P = 0.87$) in the rate by which the crocodiles travelled along the river. The

mean rate of movement downstream was $0.68 \pm 0.10 \text{ m s}^{-1}$ and the rate of movement upstream was $0.58 \pm 0.05 \text{ m s}^{-1}$. Moreover, individuals showed similar changes in swimming speed between specific stretches of the river, demonstrating that the speed of crocodile movement was largely determined

by the rate of current flow ($Z > 18.2$, $P < 0.01$). When the crocodiles travelled against the current flow, their rate of movement was dramatically reduced compared with periods when they travelled in the direction of the current (Fig. 2b, d.f. = 23, $Z > 18.5$, $P < 0.01$). In contrast, short-distance movement did not exhibit a strong association with current direction (Fig. 2c, d.f. = 440, $Z > 0.9$, $P = 0.38$). The rate of movement during short-range travel was substantially slower than when the crocodiles engaged in long-distance travel, when they travelled both with ($Z > 22.1$, $P < 0.01$) and against ($Z > 12.3$, $P < 0.01$) the prevailing current direction (Fig. 2d).

OUT OF WATER EVENTS

During long-distance travel the crocodiles would halt their journey once the tide turned and the current direction was flowing opposite to the directional movement of the crocodile. The transmitters emitted an acoustic signal and could only be detected by the local receiver if they were submerged, and therefore, a long absence of an acoustic signal whilst within the detection range of a receiver suggested that the crocodile had exited the river. Exiting the river during periods of unfavourable flow was demonstrated also by body temperature recordings. Before the period of absence

the body temperature of the crocodiles equalled water temperature. After being absent from the water for up to 3 h however, the body temperature could be as much as 10 °C warmer. Upon water re-entry body temperature would rapidly equilibrate to water temperature, confirming that the crocodile had been out of the water during this period. The reverse relationship between water and body temperature occurred during the night, and body temperature could be as much as 2.3 °C lower upon water re-entry, and rapidly warm. When undertaking long-distance journeys there was a significant difference in the maximum hourly body temperature between favourable and unfavourable current flow (Fig. 3a, $Z > 27.1$, $P < 0.01$), but the same pattern was not observed when crocodiles were engaged in short-distance travel ($Z > 1.2$, $P = 0.32$). During long-distance travel the maximum body temperature of the travelling crocodile was not significantly different from that of the water temperature (ANOVA, $F = 1.8$, $P = 0.9$) but was significantly warmer (ANOVA, $F = 5.4$, $P > 0.05$) than that of the water temperature when current flow was not favourable. This difference in maximum body temperature occurred because the crocodiles spent a proportion ($38.0 \pm 2.3\%$) of their time out of the water during unfavourable current flow, but not one single out of water event was recorded when current flow was favourable (Fig. 3b). During short-distance travel the croco-

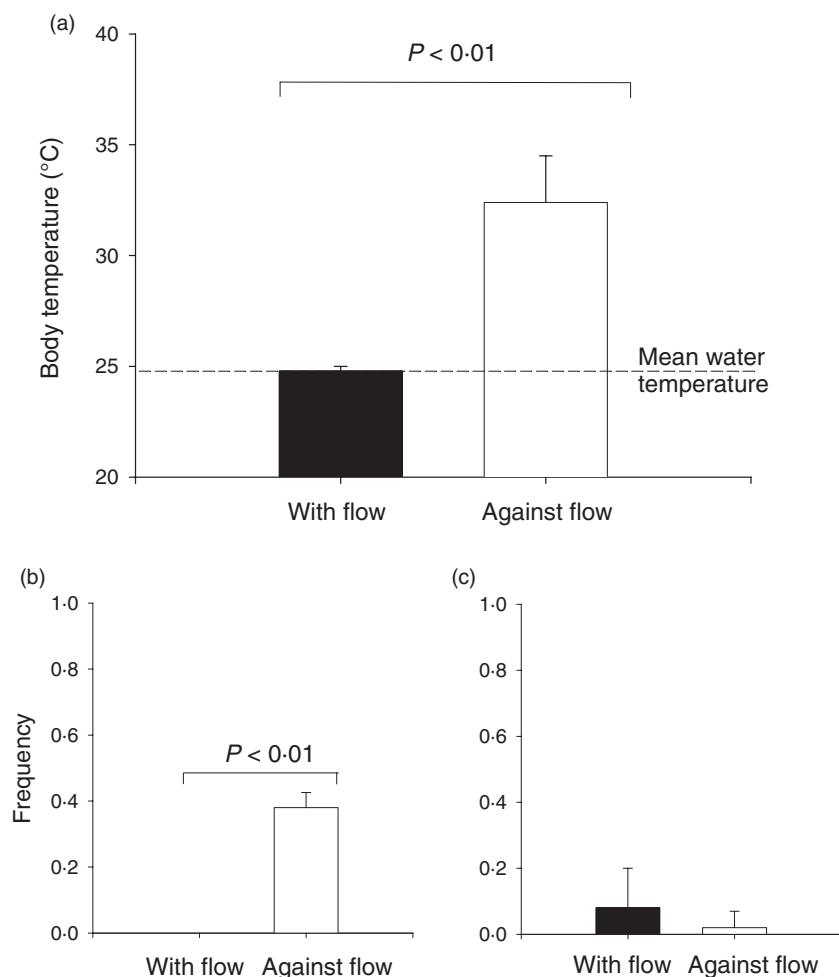


Fig. 3. The effect of current flow direction on river exiting in *Crocodylus porosus*. (a) The maximum body temperature recorded for each hour during long-distance journeys ($n = 42$, $N = 2$). (b) The proportion of time spent out of the water when engaged on journeys when the daily distance travelled was > 10 km in a constant direction. (c) The amount of time spent out of the water when engaged on journeys when the daily distance travelled was < 10 km in a constant direction. The black bars show movement when current was flowing in the same direction as the travelling crocodile, and the clear bars demonstrate movement when the current was flowing opposite to the crocodiles' direction of travel.

diles did leave the water for prolonged periods but the proportion of their time out of the water showed no significant relationship with the direction of current flow relative to their direction of travel (Fig. 3c, $Z < 1.1$, $P = 0.12$).

DIVING EVENTS

Six crocodiles which undertook long-distance travel had depth recorders incorporated into their transmitters. These crocodiles also showed periods of absence when the transmitters were not detected by the local underwater receiver, suggesting that they also exited the water for periods during unfavourable current flow. Depth data collected from the implanted transmitters showed that when current flow was favourable not one of the crocodiles exhibited a single dive, always remaining at the water surface during travel (Fig. 4a, $Z > 18.7$, $P < 0.05$), but when current was unfavourable they would stop travelling and participate in dives to depths of between 2 and 5 m. The depth profiles of these dives were flat bottomed suggesting that the crocodiles were resting on the river substratum during the dive. The mean dive duration was 18 ± 3.4 min (Mean \pm S.E., $n = 127$), but dives could last up to 1 h. During periods of unfavourable tidal flow the crocodiles spent $42\% \pm 4.7$ of their time participating in diving behaviour and laying on the river substratum (Fig. 4b). When engaged in short-distance travel crocodiles did dive during favourable tidal flow, and there was no signif-

icant difference in the amount of time that the crocodiles were submerged between favourable and unfavourable current flow (Fig. 4c, $Z > 3.8$, $P = 2.3$).

OCEAN TRAVEL

A satellite tagged *C. porosus* (3.84 m, male) left the river system and commenced ocean travel down the west Coast of Cape York Peninsula on the 17th December, 2004 (Fig. 5, Supplementary Video File S1). The timing of the coastal journey coincided with the development of a clockwise gyre that seasonally occurs within the Gulf of Carpentaria during the summer monsoon (Wolanski 1993). The average residual surface current speed in the immediate location of the crocodile during the journey was between 0.2 and 0.5 m s⁻¹ and the crocodile's average speed of movement between successive satellite fixes was 0.33 ± 0.1 m s⁻¹. There was a sharp decrease in current velocity in the vicinity of the crocodile between the 19th and 21st of December, and the crocodile moved ashore during this period, only reinitiating travel when current velocity increased in the crocodile's direction of travel. The crocodile's rate of movement slowed to > 0.14 m s⁻¹ from the 30th December 2004 to the 12th January 2005, coinciding with a localised decrease in surface current velocity (0.1 – 0.2 m s⁻¹). The crocodile moved a minimum of 590 km in 25 days, and entered the Norman River on the 12th January, 2004. It travelled to a location

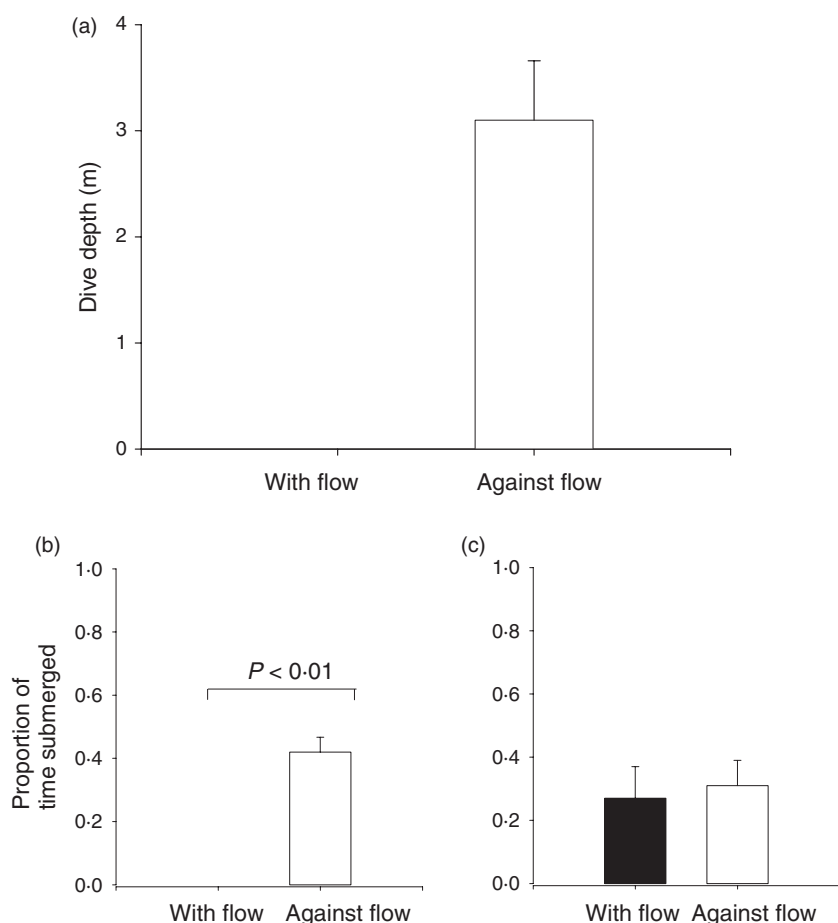


Fig. 4. The effect of current flow direction on diving in *Crocodylus porosus*. (a) The maximum depth dive attained during each hour during long-distance travel ($n = 190$, $N = 6$). (b) The amount of time spent submerged when engaged on journeys when the daily distance travelled was > 10 km in a constant direction. (c) The amount of time spent submerged when engaged on journeys when the daily distance travelled was < 10 km in a constant direction. The black bars show movement when current was flowing in the same direction as the travelling crocodile, and the clear bars demonstrate movement when the current was flowing opposite to the crocodiles' direction of travel.

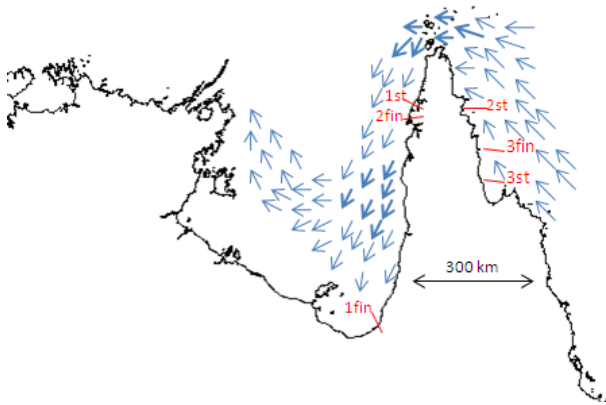


Fig. 5. Schematic diagram showing the coastal travel by three adult *Crocodylus porosus* around Cape York Peninsula, Northern Australia. Start (st) and finish (fin) locations for each journey are shown for crocodile: (1) a 3.84 m male travelled between the 18th December, 2004 to 11th January, 2005; (2) a 4.84 m male travelled between the 4th December, 2004 to 18th December, 2004; (3) a 3.1 m male travelled between the 30th September, 2003 to 5th October, 2003. Blue arrows indicate the mean velocity of the residual surface current in the local vicinity during the period of travel undertaken by each crocodile (residual surface current speed; thin arrows $> 0.1 \text{ m s}^{-1}$, thick arrows $> 0.3 \text{ m s}^{-1}$).

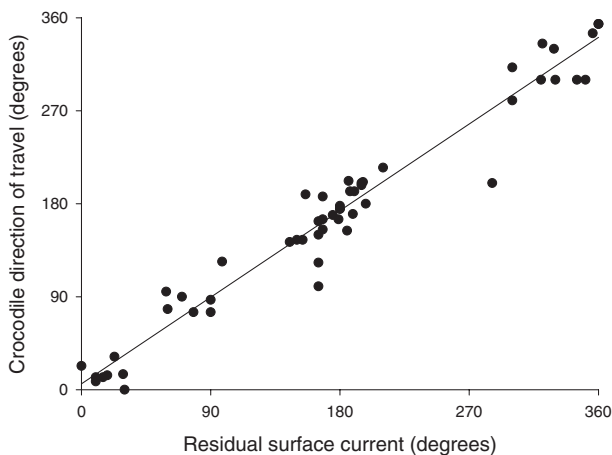


Fig. 6. The relationship between residual surface current direction and the bearing in which *Crocodylus porosus* moved between consecutive satellite fixes ($n = 56$, $N = 3$). $Y = 0.91X + 10.4$, $r^2 = 0.92$.

33 km from the river-mouth and remained there for the following 11 months, until the satellite transmitter stopped transmitting.

A second satellite tagged crocodile (a 4.84 m, male) commenced a coastal journey on the 2nd December, 2004 (Fig. 5. Supplementary Video File S2). This journey was from the east coast of Cape York Peninsula, through the Torres straits to a Wenlock river on the west coast of Cape York Peninsula. The crocodile timed its day of departure (1st December) with a strengthening in the north flowing direction of the localised coastal current system, and the crocodile moved $> 208 \text{ km}$ north in 8 days. The residual surface current upon the day of arrival at the Torres Straits was 0.5 m s^{-1} and flowing in a

west to east direction. The crocodile stopped at this position for 3 days, and only commenced moving on the 16th December. The same day the current direction switched to flow from east to west. The crocodile made a $> 130 \text{ km}$ coastal journey south down the West Coast of Cape York Peninsula in only 3 days, travelling at a rate of 0.5 m s^{-1} . The crocodile moved $> 411 \text{ km}$ in 19 days, the average speed of movement between successive satellite fixes was $0.41 \pm 0.08 \text{ m s}^{-1}$ and the residual surface current throughout the journey was between 0.3 and 0.5 m s^{-1} . On 23rd December the crocodile returned to the exact location within the river from where it was originally captured, it remained here for the next 4 months, upon which time the satellite transmitter stopped transmitting.

A third tagged crocodile (3.1 m, male) travelled north up the east coast of Cape York Peninsula (Fig. 5). The crocodile commenced its ocean voyage on the 30th September 2003, and travelled a minimum distance of 56 km in ocean water, moving $> 10 \text{ km}$ each day. Residual surface currents during the period of travel were between 0.3 and 0.5 m s^{-1} and flowing in a south to north direction. The crocodile arrived at the Nesbit River on the 5th October, 2003, and remained here for the next 6 months, upon which time the satellite transmitter stopped transmitting.

The bearing between successive satellite fixes for the three crocodiles travelling at sea (56 observations) was correlated with residual surface current velocity estimates for each of the local areas (Fig. 6). Linear (Pearsons) correlation produced an $r^2 = 0.977$ with a 95% confidence interval between 0.9619 and 0.9871, ($P < 0.01$), and therefore, a significant correlation existed between the bearing of the travelling crocodile and the residual surface current.

Discussion

The expansive geographical distribution of *C. porosus* suggests that long-distance ocean voyages are a regular occurrence between island populations. Certainly, large individuals have been sighted from vessels far out at sea (Ditmars 1957), but *C. porosus* cannot be considered a marine reptile, and primarily inhabits rivers and coastal systems. They live a low-cost energy lifestyle with limited capacity for sustained exercise (Pough 1980; Elsworth, Seebacher & Franklin 2003), and as such, their ability to purposefully traverse significant expanses of open-ocean seems extreme. This study provides an explanation as to how these remarkable feats of ocean travel may be achieved, by demonstrating that *C. porosus* adopt behavioural strategies which utilise the momentum of surface currents to transport themselves long distances.

In this study, the majority of travel exhibited by acoustically-tagged crocodiles was short-distance and occurred within a specific discrete length of river. This could be classified as movements within a home range because estuarine crocodiles are generally territorial animals with adults showing high site-fidelity (Webb & Manolis 1989). The novel findings from the study were; some crocodiles undertook considerable journeys from the home-area, travelled

considerable distances at sea, and returned to the home-area at a later date. Both male and female adult crocodiles undertook these journeys and no significant correlations were found between the timing of the journey and the seasonal or lunar cycle. The long-distance journeys did correlate with tidal cycle however, and riverine journeys were always initiated at the turn of the tide cycle, when current flow was moving in a favourable direction. Current direction would not be favourable throughout the entire duration of a journey, and during periods of opposite current flow the crocodiles would exhibit avoidance behaviours, seeking shelter out of the current by remaining for extended periods on the river substratum or by climbing out of the water onto the river bank or coastal area. There were periods (16%) during unfavourable tidal flow when the travelling crocodiles were not moving but were located at the water surface and not exhibiting diving behaviour. We suggest that during these periods the crocodiles were located on a submerged log or other vegetation enabling them to hold on and/or shelter out of the current. Spotlight surveys along the Kennedy River often located crocodiles on submerged trees or vegetation along the river bank and a grasping strategy is used by *C. porosus* to hold their position when exposed to a strong water current within an experimental swimming flume (H. A. Campbell, unpublished data).

Once the acoustic tagged crocodiles left the Kennedy River and entered the Gulf of Carpentaria it was not possible to track their movement. However, analysis of tracking data from satellite tagged *C. porosus* in the Gulf of Carpentaria showed that adult crocodiles are capable of moving hundreds of kilometres within a few weeks. The timing and velocity of coastal movements correlated with surface currents, and the crocodiles typically stopped travelling when current flow was unfavourable and only resumed the journey when surface currents were complimentary to their direction of travel. If the acoustic tagged crocodiles showed a similar movement strategy once they entered the Gulf of Carpentaria, they could potentially have travelled considerable distances before returning to the Kennedy River some weeks or months later. Future satellite tagging of adult *C. porosus* should focus on revealing the extent of these infrequent ocean voyages. Interestingly, five out of the eight crocodiles which undertook long-distance journeys had been captured in the Kennedy River in the previous year (H.A. Campbell & C.E. Franklin, unpublished data), illustrating that these crocodiles use the river as a home- area and repeatedly return after making forays out into the Gulf of Carpentaria. The exact purpose of these journeys remains speculative, but recently, considerable numbers of adult estuarine crocodiles were observed congregating to feast on an annual fish migration, perfectly coinciding their arrival with the fish run (Adam Britton, pers. comm.). The findings from this study suggest that long-distance feeding forays may not be uncommon for adult estuarine crocodiles.

The concept of *C. porosus* routinely migrating long distances by sea seems paradoxical because like all crocodilians they have a very limited capacity for sustained swimming

(Elsworth, Seebacher & Franklin 2003). Although their life-style is primarily aquatic they are adapted from terrestrial archosaurs, and their biomechanical design was primarily for land travel rather than optimal locomotory performance in water (Frey & Salisbury 2001). The water flow patterns and vortices surrounding a swimming crocodile are far less efficient than that of a fish or marine mammal (Drucker & Lauder 2000), and their critical swimming speed is substantially inferior (Elsworth, Seebacher & Franklin 2003). Nevertheless, *C. porosus* have taken to ocean travel, and this study demonstrates they have overcome physiological limitation by primarily travelling during periods when surface currents are favourable. This negates the need for active swimming, reducing daily energy expenditure and substantially increasing dispersal potential.

When traversing expanses of open-ocean *C. porosus* would be unable to drink freshwater and because they rely on a sit-and-and-wait strategy to ambush prey it seems unlikely that they would be able to feed during ocean travel. This may not be a problem however, because similar to marine turtles and pelagic sea birds *C. porosus* possess extra-renal salt secreting glands (Taplin & Grigg 1981; Franklin & Grigg 1993). These are located on the upper surface of the tongue and can maintain plasma osmolality within a narrow range (298–309 mOsm) across a wide range of salinity gradients (0–60 p.p.t.). They also possess a thick low permeable skin, which insulates them from hyperosmotic surroundings (Taplin 1984), and by obtaining all necessary water requirements from ingested food and metabolic water production (Taplin 1988; Cramp *et al.* 2008), they have the capacity to live indefinitely in full strength seawater. A 10 kg *C. porosus* can survive for up to 4 months in full strength sea-water without feeding (Taplin 1985), and a large adult (500–1000 kg) would probably be able to endure these conditions for a much longer period. By substantially reducing the energetic cost of travel through surface current utilization, combined with their marine adapted physiology and large body mass, adult *C. porosus* have the potential to undertake and survive considerable ocean voyages.

The ability of *C. porosus* to cross significant marine barriers is an important observation for the zoogeography of the eusuchian crocodiles. Contained within the geographical range of *C. porosus*, exists five freshwater inhabiting *Crocodylinae* species (*C. siamensis*, *C. palustris*, *C. novaeguineae*, *C. mindorensis*, and *C. johnstoni*). All of which possess physiological characteristics inferring they were descended from a salt-water adapted ancestor (Taplin 1988; Taplin & Grigg 1989), and whilst they can exist in salt-water environments they predominately inhabit freshwater and are rarely found in coastal or estuarine habitat (Taplin 1988). The close ancestral link between the marine adapted *Crocodylus porosus* and its freshwater cousins is exemplified by *Crocodylus siamensis*, which will readily inter-breed with *C. porosus* to produce hybrid offspring (Ratanakorn, Amget & Ottlet 1993). Members of the group *Crocodylinae* can be found on the African, Indo-Asian, Australasian and American continents, and all are derived

quite recently from a sea-going ancestor (Taplin & Grigg 1989). It is conceivable that an ocean-going crocodile, with physiological characteristics comparable to those of *C. porosus*, crossed significant marine barriers, colonised new estuarine and freshwater habitats, and secondarily, lost their ability to exist indefinitely in full strength sea-water.

According to Darwin's theory of natural selection speciation may only occur if a population is adequately separated from the parent population for a sufficient length of time' (Darwin 1859). Even relatively low levels of gene flow will homogenize the genes responsible for divergence and frequent invasions from the parent stock are widely viewed as the constraining forces of evolution (Calsbeek & Smith 2003). Although the freshwater environment appears to have provided sufficient isolation for the diversification within the *Crocodylinae* family, the same is not true for the coastal and estuarine environment. The geographical range of *C. porosus* covers over 10 000 km², and breeding populations are spread across thousands of islands, often separated by considerable ocean barriers. Because the magnitude of gene flow determines the extent by which populations diverge from one another (Barton & Hewitt 1989); the fact that no diversification of *C. porosus* has occurred in coastal and estuarine habitat whilst arising a number of times in freshwater systems, strongly suggests that frequent invasion of island populations of *C. porosus* occurs from the parental stock. Therefore, we hypothesise that sea-voyages by *C. porosus* are a frequent occurrence, and should not be viewed as occasional mishaps of navigation but as a successful dispersal strategy.

For an animal to migrate successfully it not only needs to cover the distance but also requires orientation ability to find the target. Similar to other homing species such as marine turtles (Lohmann *et al.* 2004), *C. porosus* can find their way home after being translocated hundreds of kilometres (Walsh & Whitehead 1993; Kay 2004; Read *et al.* 2007). Recent pilot studies have shown that the attachment of a magnet to the head of a crocodile during translocation will severely disrupt its homing ability (Domingues-Laso 2007), illustrating that crocodiles possess a magnetic compass sense similar to that of other true navigators (Keeton 1971; Boles & Lohmann 2003; Lohmann *et al.* 2004). The difference however between *C. porosus* and these other true navigators (marine turtles, birds, spiny lobsters) is that they have the luxury of being able to orientate themselves in the general direction of the target and consistently travel in a constant direction until they reach it (Keeton 1971; Boles & Lohmann 2003; Lohmann *et al.* 2004). This direct path is not often available for *C. porosus* which are often required to navigate around coastal headlands and through river system.

A satellite tagged *C. porosus* was translocated 129 km from the west to the east coast of Cape York Peninsula (Read *et al.* 2007). The most direct route back would have required the crocodile to make a significant overland journey, but instead the translocated crocodile undertook a journey of more than 411 km by sea (Fig. 6 & Supplementary video

file S2). This trip required the crocodile to first travel on a heading that displaced it further away from the home-area, and only once around the headland of Cape York Peninsula was it able to re-orientate itself and move on a bearing back to the home-area. This type of circuitous long-distance travel to a target location is unique amongst animals with homing ability and raises fundamental questions about the reliability of a geomagnetic compass sense for homing *C. porosus*.

This study has shown that adult estuarine crocodiles dramatically increase their travel potential by riding surface currents. This observation has profound management applications because a problem crocodile translocated to an area where residual surface currents flow in the direction of the home-area will rapidly travel back home. Moreover, changes in coastal current systems, by either natural cycle or anthropogenically driven, may result in estuarine crocodiles travelling to locations without a recent history of their presence. Because adult estuarine crocodiles pose a significant risk to humans (Caldicott *et al.* 2005), inshore current systems should be monitored in areas where humans and *C. porosus* may interact, and problem crocodiles should be translocated to areas where residual currents are not available for homeward travel.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Video file S1. Coastal movement of 3.8 M Male.

Video file S2. Coastal movement of 4.8 M Male.

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