Crocodile Control and Conservation Bill 2024

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Wildlife Warriors Submission to the Inquiry into the Crocodile Control and Conservation Bill 2024

Wildlife Warriors wishes to formally oppose the Crocodile Control and Conservation Bill, introduced by Mr Shane Knuth MP on 22nd May 2024.

“The stated objective of the Bill is to eliminate from state waterways any crocodiles that pose a threat to human life, while continuing to protect crocodiles from becoming extinct as a species.” This statement alone flies in the face of reason, contradicting itself from reality.

Any adult crocodilian has the potential to pose a risk to someone entering crocodile habitat. For this to happen, the person has ignored warning signs and lacks commonsensical knowledge of being in Northern Australia. Without exterminating the species all together, it is not possible to create completely safe waterways. In a Queensland Parliament speech (attached) on 11th May 2023, Mr Knuth said himself “It is acknowledged that we are never going to completely eliminate the threat but we can reduce the risks through culling programs to limit the number of crocodile attacks in populated areas.”

Mr Knuth once stated that “North Queenslanders want strong management that mitigates risk and gives us back our popular waterways and beaches.” The false sense of security that comes with thinking areas are safe in crocodile exclusion zones is incredibly dangerous. The general public are not ecologists, they rely on governing bodies for information. Cairns is a great example of this. The Cairns Regional Council has a website promoting swimming locations, yet there is not one mention of crocodiles being a risk. The last incident with a crocodile in Cairns was at Lake Placid, which falls within Zone B of the Crocodile Management Plan, the Active Removal Zone. This is less than fifteen kilometres from the beaches promoted by the council for swimming. This is the problem, not the crocodiles.

Wildlife Warriors and its partners, The University of Queensland and Australia Zoo, conduct the most extensive research project on crocodilians anywhere on the planet. Since 2008, we have worked studying estuarine crocodiles on the Wenlock River. Prior to this, we were studying estuarine crocodiles in Lakefield National Park. Our research is groundbreaking. We were the first to use satellite and acoustic telemetry to track crocodiles, the first to use acoustic telemetry to record body temperature and dive depths of crocodiles, the first to monitor the movements of translocated crocodiles by satellite telemetry, the first to describe the navigation and homing ability of crocodiles and the first to record crocodiles diving for more than six hours at a time, a record for air-breathing vertebrates.

One of the most incredible results from our studies (attached) has been the ability for crocodiles to travel long distances in a short time frame. In a paper co-authored by Steve Irwin, a tracked crocodile travelled almost 130km down Western Cape York Peninsula in just three days. Estuarine crocodiles are highly mobile, capable of travelling hundreds of kilometres in a matter of weeks. How does Mr Knuth propose to ensure the safety of those entering waterways in crocodile habitat when they are capable of travelling such large distances? Especially "while continuing to protect crocodiles from becoming extinct as a species?"

Let's not forget, we are dealing with a species listed as vulnerable under the Nature Conservation Act 1992 (Qld). Estuarine crocodiles (*Crocodylus porosus*) share the same level of vulnerability as other Queensland species, such as the dugong (*Dugong dugon*), glossy black cockatoo (*Calyptorhynchus lathami*), the northern population of the southern cassowary (*Casuarius casuarius johnsonii*) and northern greater glider (*Petauroides minor*). These species rely on the protection of the Queensland Government for their survival, and if a bill was proposed to cull any one of them, it would be dismissed immediately. Why should the estuarine crocodile be any different? Cassowaries pose a risk to human safety, and there has been a recorded fatality as a result of one, yet we're not discussing eliminating them from their natural habitat. Likewise, domestic dogs pose a threat to humans. The Cairns Regional Council alone investigates 800 dog attacks each year, according to their website (attached). If Mr Knuth was truly invested in public safety, perhaps working on better regulating dog ownership would be a more productive use of his time

Without wiping out the species, a species listed as vulnerable under the Nature Conservation Act 1992 (Qld), the waterways are not safe for humans. Instead, focus should be placed on continued and improved educational campaigns on how to stay safe in crocodile habitat, and signage throughout their range. In a recent interview Mr Knuth said "Any crocodile in any waterway used by humans is a direct danger to human life and should be removed immediately." Is this "continuing to protect crocodiles from becoming extinct as a species?"

Queensland should be celebrating these iconic animals. Guests from around the world have a preconceived notion of our dangerous wildlife, and want to experience it for themselves. Nature-based tourism is our future, not killing a protected species. This proposal would allow for safari hunting of estuarine crocodiles, with the Director having the power "to authorise a person to, with the consent of the owner of the land, enter the land to kill crocodiles on the land."

A study exploring the economic impact on global non-consumptive wildlife tourism (attached) shows the GDP and employment estimates through Oxford Economics.

Fig. 6. Total WT expenditure, GDP and employment estimates for Africa, Asia and Latin America

CONTINENT	GDP ($BILLION)	EMPLOYMENT (MILLION)
AFRICA	70.6	8.8
ASIA-PACIFIC	171.2	10.4
LATIN AMERICA	28.9	1.4

This is the future of tourism, not culling an animal so you can swim at the beach, not killing a vulnerable species for fun, people want to see and experience our beautiful wildlife, and Queensland operators can profit from it in turn. Queensland's population of estuarine crocodiles is approximately 25,000 individuals, just a quarter of that of the Northern Territory. Queensland doesn't have as much suitable habitat for estuarine crocodiles as the Northern Territory, so basing our practices of their management plan is ineffective. Ecotourism generates much more revenue than the crocodile consumption industry, and allowing safari or trophy hunting of the species is a huge risk to the state's reputation, one that has been built on being a place to experience wildlife. Tourism contributes over $100 billion to the Australian economy and employs more than a million people, with the natural environment the main attraction (Ecotourism Australia 2015). Ecotourism/wildlife tourism enables tourists to experience natural areas and encounter wildlife. Why risk this reputation? Trophy hunters worldwide attempt to justify their killing by making ridiculous claims to hide their conservation harms and exploitation. Trophy hunting funds corruption, under the guise of helping First Nation communities. Those that profit are hunting permit holders and government officials. Very little ends up going to those that are promised the world.

Hunter's want to shoot the biggest, most impressive crocodiles. These are the ones keeping the ecosystem in balance. When you have one large dominant male in a section of the river, he is keeping away the transient males looking to establish their territory. The reason removing the large dominant males creates a more dangerous situation for humans is that it creates a power vacuum, it leads to younger inexperienced animals moving into a territory up for grabs to fight for dominance. Removing larger crocs – those most experienced at reproduction – could also skew the population. In effect it could make populations non-viable. Again, this isn't "continuing to protect crocodiles from becoming extinct as a species."

The fact there are still calls for allowing the hunting of a native vulnerable species is baffling. The Bill proposes that the governing body would "decide the number of crocodiles that may be culled each year in any part of the State," as well as "for State leasehold land or other land that is not State land—to authorise a person to, with the consent of the owner of the land, enter the land to kill crocodiles on the land, or relocate crocodiles on the land to a crocodile sanctuary or crocodile farm or harvest crocodile eggs on the land." A three-year monitoring program (attached) conducted by the Queensland Government that finished in 2019 estimated there were between 20,000 and 30,000 estuarine crocodiles in Queensland. The Department of Environment and Science estimates the population is recovering at a rate of about 2% following their drastic drop in the 1970's as a result of hunting. This is a species in recovery, with only 1% of hatchlings surviving to adulthood.

How will the hunting be policed, when authority resources in crocodile habitat are already struggling to cover large areas of remote Queensland? In the last few years, we have found a number of killed crocodiles (attached) in the Wenlock River, as a result of illegal fishing practices and shootings. These were reported to authorities, we offered a $10,000 reward, yet there was no follow up from authorities, and no action taken to the offenders.

The Bill proposes "to authorise persons, in any part of the State, to operate a crocodile farm, or a crocodile sanctuary." On 30 July 2023, an independent review of the Federal Code of Practice on the Humane Treatment of Wild and Farmed Australian Crocodiles began. The review is long overdue, with failures to adhere to the code of practice abundantly clear in most facilities and well documented by animal welfare groups. The Australian Government's website states "with developments in humane handling and knowledge of crocodile welfare, the revised Code of Practice will reflect these developments and changes in industry processes and technology." "This review will ensure that Australia remains a global leader in the humane treatment and farming of crocodiles." We condemn the consumptive use of native wildlife. If this industry is failing to meet the current outdated code of practice, why are we discussing expanding it? Crocodile farming will soon be as taboo as farming tigers for bones, or bears for bile. The world's biggest brands, Burberry, Nike, Calvin Klein, Chanel, H&M, Macys, Puma, Tommy Hilfiger, Timberland, Vans and Victoria Secret have all banned the use of exotic animal skins, due to animal welfare concerns, and more will follow. Let's not be on the wrong side of history.

Under the Bill, the Director would have the authority to "decide the number of crocodile eggs that may be harvested each year in any part of the State." Changing environmental laws to allow crocodile farms to increase their egg production, by compromising wild crocodiles, is akin to the decision China was considering by lifting the ban on farmed rhino and tiger products. Decisions like these only further jeopardise animals in the wild and further enable the illegal trade in all crocodilian species, seven of which are Critically Endangered.

Wildlife in zoological facilities requires accurate record keeping and identification for monitoring. The introduction of a variety of DNA through the collection of thousands of new crocodiles completely eliminates the ability to keep track of the individual animal, its meat, or its skins. This is the challenge we face around the world to eliminate the illegal trade in wildlife.

A key finding in the Queensland Estuarine Crocodile Monitoring Program 2016–2019, was that "Queensland has seen the recovery of a threatened species that is a large predator, while at the same time seeing a reduction in the risk to public safety." The report goes on to state "since 1975, there have been 46 estuarine crocodile attacks on humans in Queensland, 16 of which have been fatal. The average of 0.3 fatalities per year is much lower than deaths from sharks – 1.1 deaths per year (West, 2011). Most of these attacks occurred along the coast between Townsville and the Daintree River, and as in the Northern Territory, the majority impact local, adult males (Brien et al. 2017)." The study (Brien et al. 2017) outlines that 77.1% of people attacked involved locals who regularly visited the area. 88.6% of the incidents were at the water's edge, where crocodiles are known to strike.

In a study from Charles Darwin University (attached), reported crocodile attacks were reviewed worldwide in 2015. 116 estuarine crocodile attacks were reported, Australia made up just two of these, both non-fatal. One of the attacks happened when a man approached the water's edge at a golf course. It was well known there was a crocodile inhabiting the golf course, and well signed, yet the man ignored warnings and was bitten. The second incident involved a man snorkelling in crocodile territory, at night. At some point, common sense has to prevail. Crocodiles are already paying the price for human error and population expansion. Maybe it's time for people who blatantly disobey warning signs to be fined in an effort to further minimise the risk to themselves and those that are tasked with rescuing them as a result.

Other countries with naturally occurring estuarine crocodiles see many more attacks that we do here. In some countries, attacks are very common. Indonesia, for example, sees the most estuarine crocodile attacks in the world. In the past ten years, there have been around 1,000 attacks, almost half of them fatal. Yet, they have fewer crocodiles than we do in Australia. The crocodiles are not the problem. The problem is the human population density, our behaviour and need for education. This Bill isn't about human safety, it isn't about crocodile conservation, it's about lining the pockets of those in the industry of crocodile consumption. If this bill was passed, there's no doubt there would be a push [redacted] for the Queensland Crocodile Authority to be governed by those involved with or at least connected to a crocodile farm. Wildlife Warriors has always stood for the continuing conservation of this vulnerable species and the need for a comprehensive public safety campaign as opposed to those vested interests who would like to only profit from the sale of crocodile skins and other products. We are funding our research (attached) with no hidden agenda, all of our peer-reviewed, published research is available to anyone.

Our research work is discovering new threats to these animals that could hinder their survival into the future. Threats like climate change skewing the sex ratio and ability to thermoregulate. Now is not the time to be adding extra pressure to an iconic Queensland species.

If the Bill's purpose is to "eliminate from state waterways any crocodiles that pose a threat to human life, while continuing to protect crocodiles from becoming extinct as a species," it should be dismissed on the grounds that the two goals can not be achieved together. It isn't possible to eliminate any crocodile that is a potential risk to humans, while at the same time protecting them from extinction.

Yours in Conservation,

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Estuarine crocodiles ride surface currents to facilitate long-distance travel

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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 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 ($r^2 = 0{\cdot}92$, $P < 0{\cdot}0001$).

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 km^2 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 rivers 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 down river 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 sutra; 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 collated 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 $P < 0{\cdot}01$.

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/oceancurrents/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 $P < 0{\cdot}01$.

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

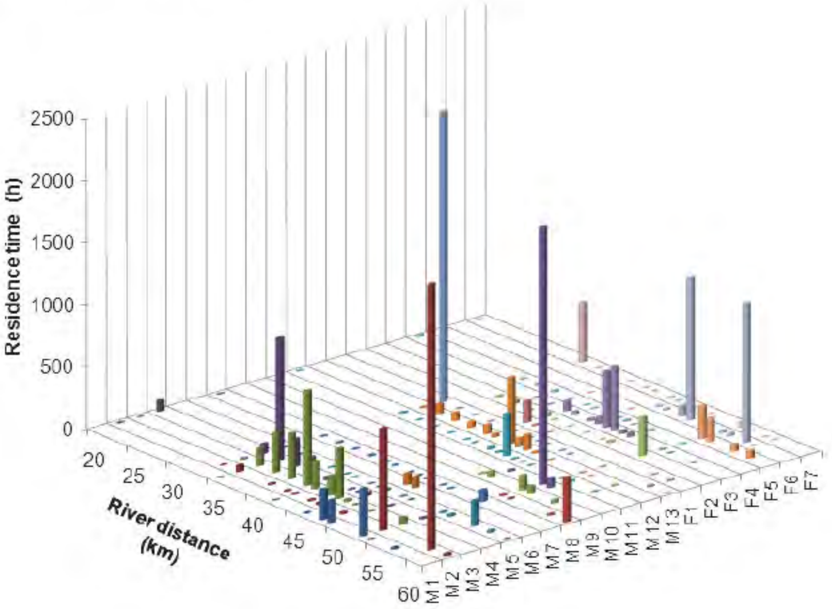

Fig. 1. The amount of time (h) that each acoustically tagged *Crocodylus porosus* (*n* 20) spent at discrete locations along the Kennedy River. River distance is expressed km from the River mouth. Crocodile ID is on the *z* axis (M, male; F, female), Crocodiles M2, M3, M5, M7, M11, F4 & F7 all undertook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

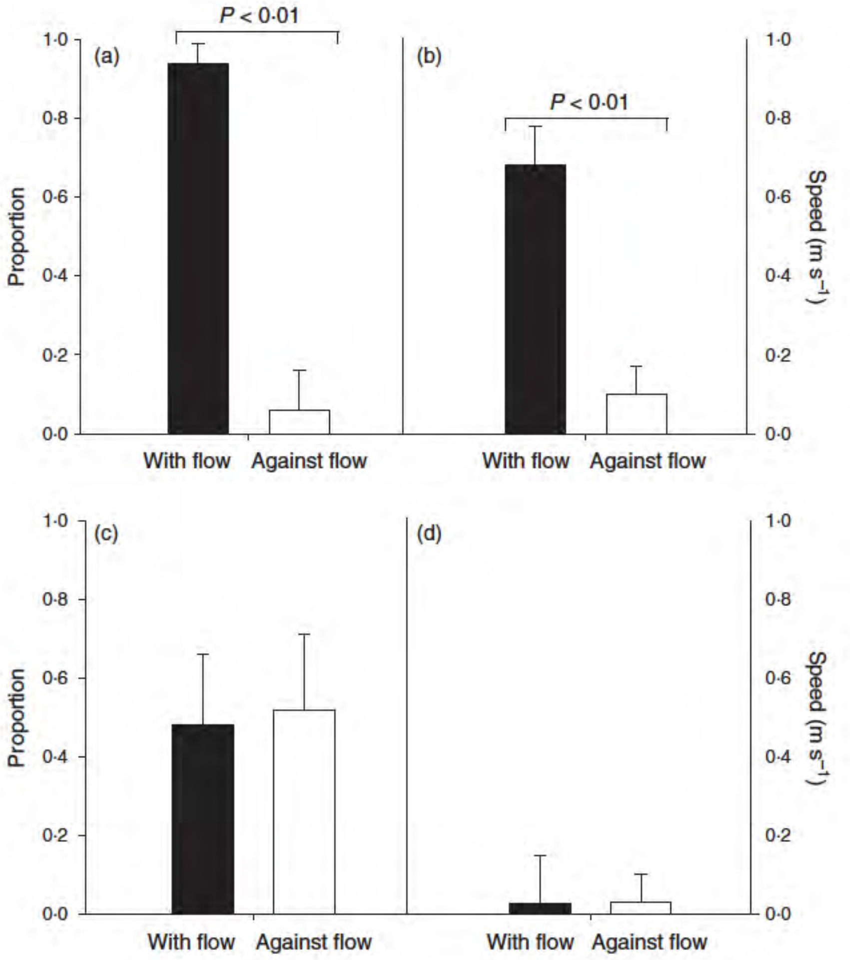

Fig. 2. The effects of current directional flow on movement during long and short distance travel in *Crocodylus porosus* (*n* 8). The black bars show movement when the current was flowing in the same direction as the travelling crocodile and the clear bars demonstrate movement when the current was flowing 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, $Z > 18{\cdot}9$, $P < 0{\cdot}01$). Although a large size difference existed between tagged individuals (total body length 2·6 4·9 m) there was no significance difference ($Z > 0{\cdot}8$, P 0·87) in the rate by which the crocodiles travelled along the river. The mean rate of movement downstream was 0·68 ± 0·10 m s^{-1} and the rate of movement upstream was 0·58 ± 0 05 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 ($Z > 18{\cdot}2$, $P < 0\ 01$).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, $Z > 18{\cdot}5$, $P < 0\ 01$). In contrast, short distance movement did not exhibit a strong association with current direction (Fig. 2c, d.f. 440, $Z > 0{\cdot}9$, 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 ($Z > 22{\cdot}1$, $P < 0{\cdot}01$) and against ($Z > 12{\cdot}3$, $P < 0{\cdot}01$) 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 equilibrated 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, $Z > 27{\cdot}1$, $P < 0{\cdot}01$), but the same pattern was not observed when crocodiles were engaged in short distance travel ($Z > 1{\cdot}2$, 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, $P > 0{\cdot}05$) 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 ± 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

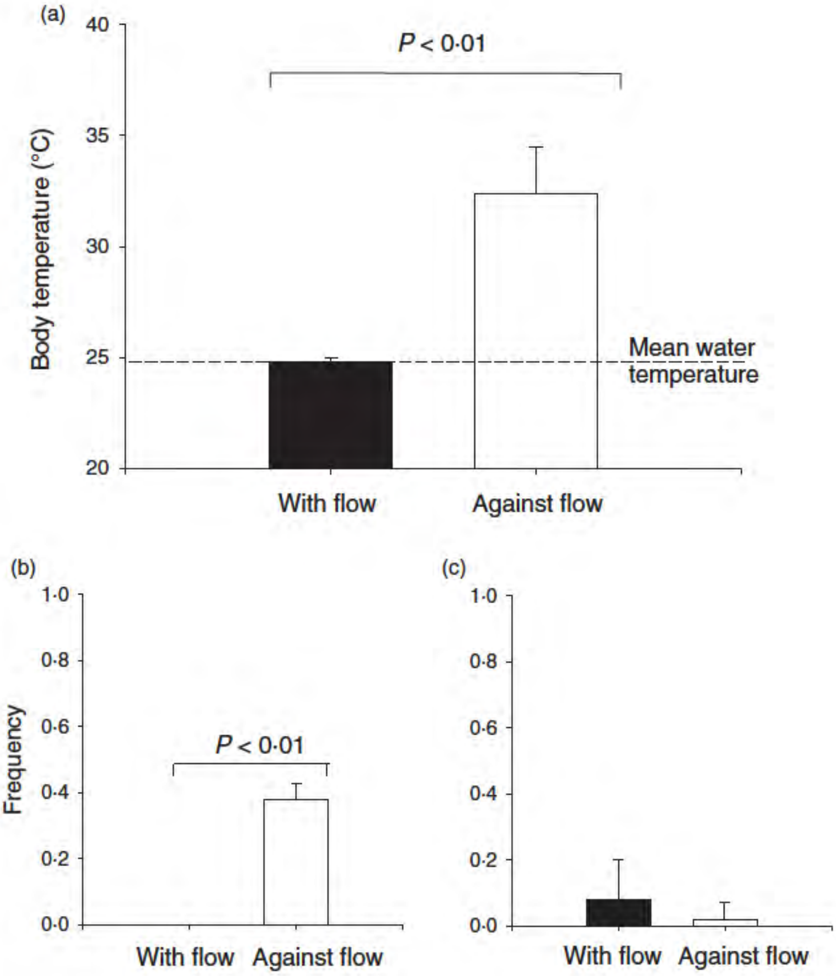

Fig. 3. The effect of current flow direction on river exiting in *Crocodylus porosus*. (a) The maximum body temperature recorded for each hour during long distance journeys (n 42, N 2). (b) The proportion of time spent out of the water when engaged on journeys when the daily distance travelled was > 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, $Z < 1{\cdot}1$, 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, $Z > 18{\cdot}7$, $P < 0{\cdot}05$), 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 ± S.E., n 127), but dives could last up to 1 h. During periods of unfavourable tidal flow the crocodiles spent 42% ± 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 significant difference in the amount of time that the crocodiles were submerged between favourable and unfavourable current flow (Fig. 4c, $Z > 3{\cdot}8$, 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 $>0{\cdot}14$ 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

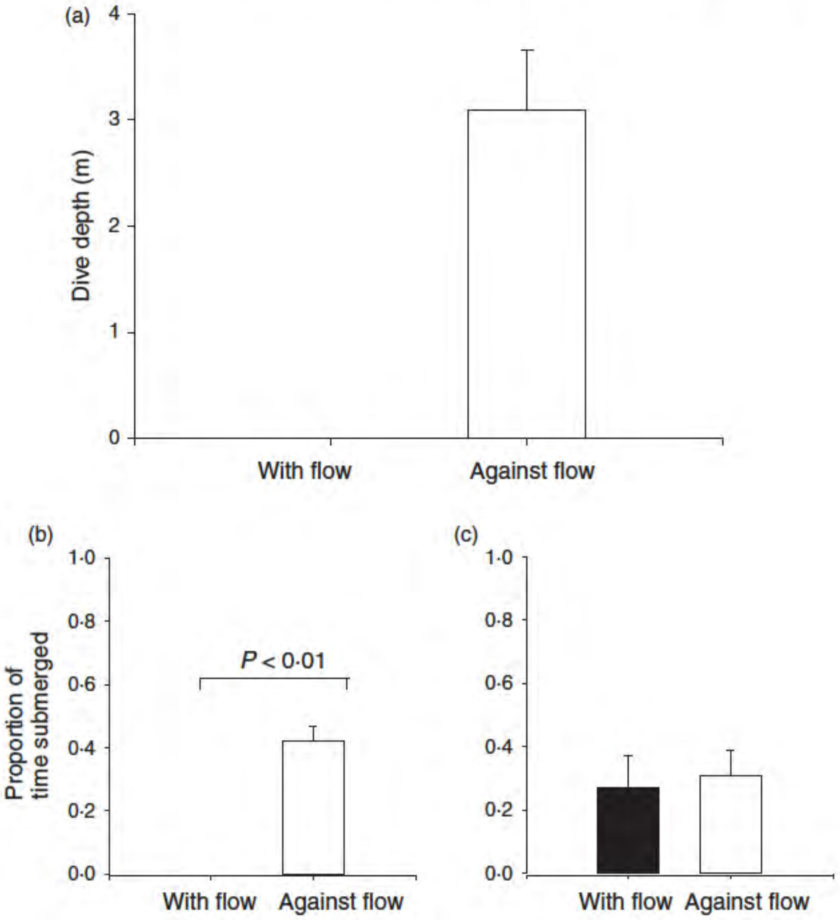

Fig. 4. The effect of current flow direction on diving in *Crocodylus porosus*. (a) The maximum depth dive attained during each hour during long distance travel (n 190, N 6). (b) The amount of time spent submerged when engaged on journeys when the daily distance travelled was >10 km in a constant direction. (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.

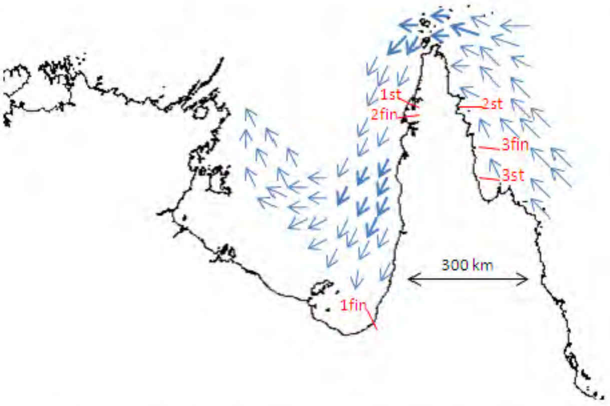

Fig. 5. Schematic diagram showing the coastal travel by three adult *Crocodylus porosus* around Cape York Peninsula, Northern Australia. Start (st) and finish (fin) locations for each journey are shown for crocodile: (1) a 3·84 m male travelled between the 18th December, 2004 to 11th January, 2005; (2) 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 m s^{-1}, thick arrows >0·3 m s^{-1}).

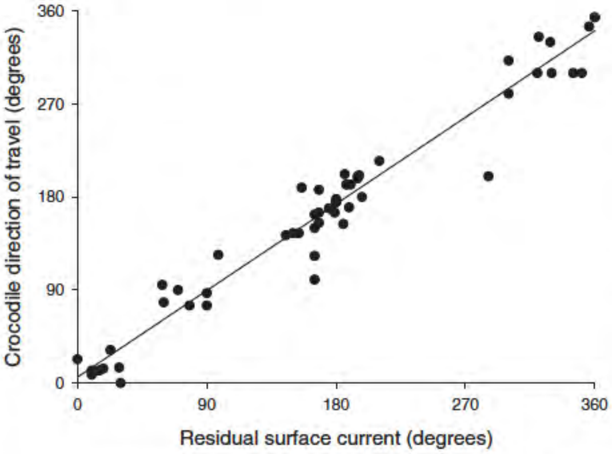

Fig. 6. The relationship between residual surface current direction and the bearing in which *Crocodylus porosus* moved between consecutive satellite fixes (n 56, N 3,). Y $0{\cdot}91X + 10{\cdot}4$, r^2 0·92.

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 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 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 km in 19 days, the average speed of movement between successive satellite fixes was 0·41 ± 0·08 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 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. novaeguneae, 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 km^2, 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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Home Range Utilisation and Long-Range Movement of Estuarine Crocodiles during the Breeding and Nesting Season

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Abstract

The estuarine crocodile (*Crocodylus porosus*) is the apex-predator in waterways and coastlines throughout south-east Asia and Australasia. *C. porosus* pose a potential risk to humans, and management strategies are implemented to control their movement and distribution. Here we used GPS-based telemetry to accurately record geographical location of adult *C. porosus* during the breeding and nesting season. The purpose of the study was to assess how *C. porosus* movement and distribution may be influenced by localised social conditions. During breeding, the females (2.92±0.013 metres total length (TL), mean ± S.E., n = 4) occupied an area<1 km length of river, but to nest they travelled up to 54 km away from the breeding area. All tagged male *C. porosus* sustained high rates of movement (6.49±0.9 km d^{-1}; n = 8) during the breeding and nesting period. The orientation of the daily movements differed between individuals revealing two discontinuous behavioural strategies. Five tagged male *C. porosus* (4.17±0.14 m TL) exhibited a 'site-fidelic' strategy and moved within well-defined zones around the female home range areas. In contrast, three males (3.81±0.08 m TL) exhibited 'nomadic' behaviour where they travelled continually throughout hundreds of kilometres of waterway. We argue that the 'site-fidelic' males patrolled territories around the female home ranges to maximise reproductive success, whilst the 'nomadic' males were subordinate animals that were forced to range over a far greater area in search of unguarded females. We conclude that *C. porosus* are highly mobile animals existing within a complex social system, and mate/con-specific interactions are likely to have a profound effect upon population density and distribution, and an individual's travel potential. We recommend that impacts on socio-spatial behaviour are considered prior to the implementation of management interventions.

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Introduction

Animals generally confine their movements within discrete areas. The size, placement and shape of the activity space has been termed the home range, and reflects the animals' behavioural repertoire as it searches to procure food, shelter, and mates [1]. For many species social conditions influence the size of the home range, and consequently, the abundance and distribution of the population. Understanding home range dynamics is essential for the pragmatic management of any species [2], but is particularly important in managing top predators because of their influence upon lower trophic levels [3,4,5].

The estuarine crocodile (*Crocodylus porosus*) is the apex predator in its environment and will feed upon a variety of prey items [6]. The species has a wide distribution across northern Australia, occurring in coastal areas, estuaries, rivers, inland swamps, billabongs, and off shore islands [7,8,9]. Unlike a vast majority of the world's apex predators, the Australian *C. porosus* population has undergone significant growth over the last 30 years. Once in risk of imminent extinction the current Australian population is estimated to be greater than 75 000 non hatchling individuals [10,11,12,13]. Although the population density varies considerably between river systems [14], such a large growth in population is likely to be altering the dynamics of the wider community and ecosystem [5]. This will occur not only by the consumption of lower trophic animals but also through the alteration of prey species' behavioural ecology [3].

Crocodylus porosus are generally considered to be highly territorial animals, with dominant males excluding con specifics from their home range [15]. More recently however, telemetry studies have recorded large adult male *C. porosus* living in close proximity to each other, thereby refuting previous claims of *C. porosus* as an exclusively territorial species [8,16]. Understanding which of these social conditions is most apparent is of profound importance towards management because the former would result in social conditions altering population density, dispersal, and distribution whilst the latter would not.

Previous estimates of home range upon *C. porosus* have relied upon either visual sightings or the manual collection of location data via VHF radio telemetry [8,16]. We suggest that the home range estimates of these studies may have been biased by serial autocorrelation because temporal irregularities occurred in the period between location fixing [17]. Furthermore, these studies and others upon crocodilians have defined the home range using mid stream linear distance or the minimum convex polygon method [18,19]; whilst these techniques provide a measure of the full extent of the area visited by an individual they ignore patterns of selection within the home range. This is important if we are to assess the difference between an individual's daily usage of an area compared to an area that is merely passed through or only frequented occasionally. In order to make this assessment, kernel utilisation distributions (KUDs) are convenient analytical tools, because they calculate density based upon the entire sample set of relocations during the period of interest rather than the emphasis being on the most outward location points [20]. It was the aim of this study to use KUDs to assess the relationship between daily movements and area utilisation distribution in male and female *C. porosus*. We selected to monitor the crocodiles during the breeding and nesting season (September February) as the effects of social conditions upon movement and space use were expected to be most apparent during these periods.

To apply kernel utilisation distribution plots it is important to collect accurate location data at a sufficiently high frequency and regularity [21]. To achieve this, we utilised high precision global positioning system (GPS) based telemetry data loggers, which had an inbuilt capacity to parse the collected location data through the ARGOS satellite system. In the light of previous telemetry studies upon *C. porosus* [8,16], we hypothesised that there would be profound differences in space use between males and females and the home ranges of individuals would overlap within and between the sexes. Furthermore, due to the high temporal resolution and spatial accuracy of the GPS based location data, we suspected that new insights into crocodile movement, interaction, and space use would also be revealed.

Materials and Methods

Study site and animals

Trapping was conducted on the Wenlock River, Cape York Peninsula, Australia during August 2010 (Fig. 1). A field camp was run from the Steve Irwin Wildlife Reserve (142.18°N, 12.38°E). The trapping occurred from the freshwater tidal reaches of the river down to the macro tidal brackish water, between 20 and 60 km from the river mouth. The bank vegetation in the lower reaches of the trapping zone was mangrove palm (*Nypa fruticans*) changing to *Melaleuca* dominated forests. It has been suggested that out of all the river systems along the western side of Cape York Peninsula the Wenlock system provides the most suitable nesting habitat for estuarine crocodiles [22].

Adult *Crocodylus porosus* (males 3.91±0.14 m total length, mean±S.E, n 8; females 2.93±0.13 m total length, n 4) were captured between the non tidal freshwater reaches of the Wenlock River through to the macro tidal brackish (Fig. 1). The traps were floated on the water surface or placed at the water edge along the river bank. Each trap was baited with wild pig (*Sus scrofa*) and the trap door was sprung by the crocodile when pressure was applied to the bait, via a trigger mechanism [23]. Once captured, crocodiles were removed from the trap and manually restrained. Total length (TL) and snout vent length (SVL) measurements were taken and a local anaesthetic (5 ml of Lignocaine, Troy laboratories, Smithfield, Australia) was injected under the nuchal rosette. Once the anaesthesia had taken effect, a single hole was drilled in each of the four raised osteoderms of the nuchal rosette [24]. Stainless steel multi strand, plastic coated wire (80 kg breaking strain) was inserted through the drilled holes and laced into attachment points on the GPS based satellite transmitter (in 2009 5×GPS units Sirtrack, Hamilton, New Zealand; in 2010, 13×TGM 410, Telonics, Arizona, U.S.A.). The GPS units were secured onto the dorsal surface of the crocodile with aluminium crimps threaded onto the stainless steel wire (Fig. 2). The process of removing the crocodile from the trap to eventual release took approximately 60 min. The crocodiles were released at the point of capture. To avoid any bias in crocodile behaviour occurring from the baited traps or increased boat traffic during the trapping period, only GPS based location data obtained after 01 September were used in the final analysis.

Data analysis

The devices utilised the global positioning system of satellites to determine geographical location twice daily (0800 h and 1800 h). The location data were stored on board the unit and parsed to the ARGOS satellite system between 1000 h 1600 h every other day. For each of the GPS based location fixes, the accompanying satellite dilution of precision (SDOP) value was used to define the positional resolution and precision. Stationary logging tests (7 d) prior to the study were used to pre determine the average degree of error for each GPS unit. All units performed equally and an SDOP of≤3 had a mean accuracy of error 12.1±1.1 m. All location fixes with an SDOP≤3 were excluded from the final analysis.

To assess home range size, we adopted the fixed kernel (FK) method [21]. Kernel density estimators are known to be sensitive to their choice of the smoothing parameter (h) [25]. The least squares cross validation (LSCV) method has been suggested as the most accurate way of estimating the appropriate smoothing parameter [25], it was not however suitable for the present study because it resulted in the delineation of numerous small disjunct contours, excluding connecting stretches of river. A second commonly used smoothing estimator, the reference bandwidth method [26], resulted in large areas beyond the outermost locations being included in the utilisation distributions. To ensure a contiguous home range boundary extending throughout the length of the river and accurately represent the outermost locations, we selected a smoothing parameter of h 750 m. For each individual, the 95% and 50% volume contour of the KUD (hereafter the KUD 95% and KUD 50%, respectively) were determined using the 'adehabitatHR' package [27] implemented in the statistical software R [28]. To examine temporal variation in home range use volume contours were constructed for six time periods (01 September 30 September, 01 September 31 October, 01 September 30 November, 01 September 31 December, 01 September 31 January and 01 September 28 February). Crocodile movement was constrained within the river channel, and therefore, the area produced by the FK method was considered over representative of the actual area utilised by *C. porosus*. Stretches of river intersecting the volume contours were consequently extracted to ensure that habitat inaccessible to *C. porosus* were not included in the final home range estimates. A high resolution spatial polygon of the Wenlock and Ducie River catchment was constructed using satellite imagery data (Fig. 1) and converted to a 50×50 m raster object using ARCGIS 10 (ESRI, Redlands, California, U.S.A). Areas of river contained within the KUD 95% and KUD 50%, and the corresponding centroid within the KUD 50%, were obtained using functions contained within the 'sp' [29], 'rgdal' [30] and 'rgeos' [31] R packages. This river intersection method reduced the KUD 95% by 90.7±4.1% and the KUD 50% by 71.4±3.2%.

To explore the finer scale movements in tagged *C. porosus*, two measures of directional movement were investigated. The first measure, the distance moved from the KUD 50% centroid during the period 01 September 30 September, would reveal exploratory

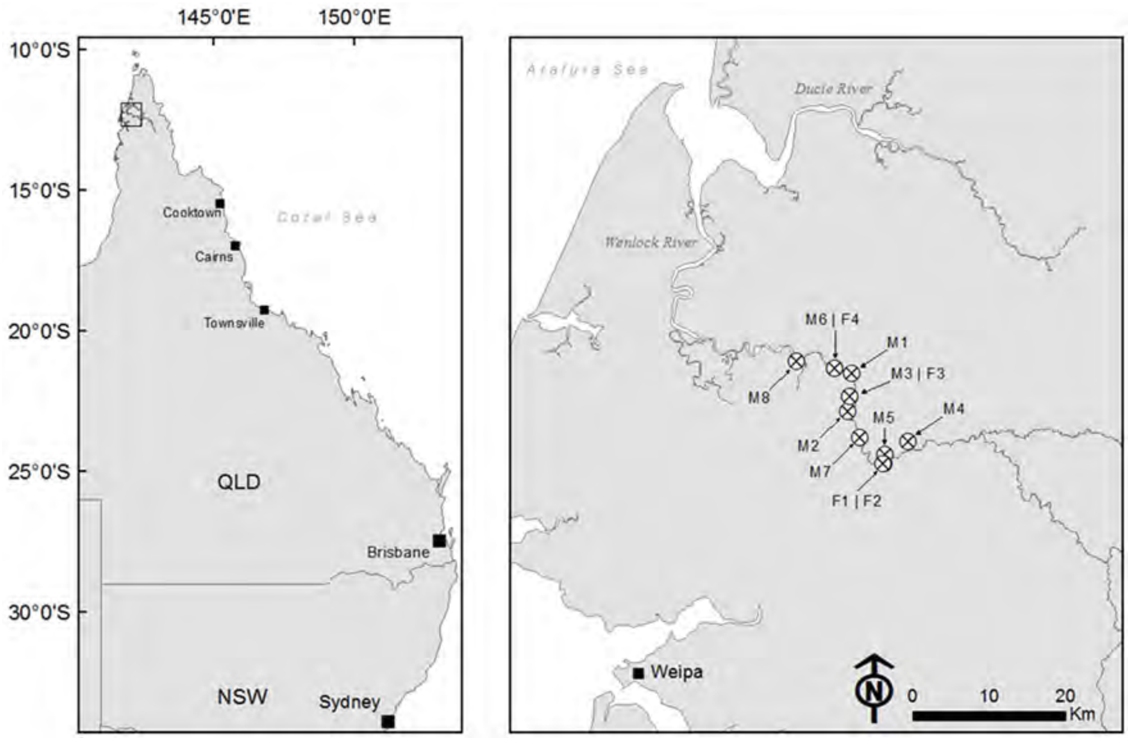

Figure 1. The Wenlock and Ducie River, Cape York, QLD, Australia. The capture locations of each *Crocodylus porosus* tagged for the study are displayed.
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movements from the centre of the home range. The second measure, the minimum distance between two locations in series, would reveal periods of activity. As crocodile movements were limited by the trajectory of the river, the minimum distance moved between two locations was calculated along the trajectory of the river using the 'raster' [32] and 'gdistance' packages [33] in R.

A general linear mixed model (GLMM) was used to assess the influence of body size and sex on movement patterns in *C. porosus*. Daily rate of movement (ROM) was included as the response variable, with days from 01 September (date) and body mass (extrapolated from SVL using the conversion factors in [34]) as covariates, sex as a factor, and crocodile ID as random effect. A second model assessed the relationship between the daily distance each individual was located from the centroid of its KUD 50%, with date and body mass as covariates, sex as a factor, and crocodile ID as random effect. Due to the correlation between body mass and sex the interaction between these variables was included in our model. Analysis was undertaken in Statistica 10 (Statsoft Inc, Tulsa, USA) and $P<0.05$ was considered significant.

Figure 2. ***Crocodylus porosus*** **with GPS based satellite transmitter attached to the nuchal rosette.**
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Results

The majority of the crocodiles tagged in this study remained within the Wenlock River for the duration of the study, but one male travelled to the adjacent Ducie River system, and some males and females moved into seasonal creeks located far upriver. Location data were collected twice daily for eight male and four female *C. porosus* from the 01 September 2010 until the 28 February 2011 (Table 1). 7.1±0.4% of location fixes did not have a sufficiently low SDOP for inclusions in the analysis and were therefore removed from the analysis.

Male Movements

The application of kernel density estimators to the location data and calculation of the cumulative home range illustrated that the movement patterns of the eight males could be grouped into two discrete categories. The 'nomadic' males ($n = 3$) were defined by the fact they did not demonstrate a stable KUD 95% during the 6 month study (Fig. 3a), whilst 'site fidelic' males ($n = 5$) displayed a KUD 95% which remained stable throughout the study (Fig. 4a).

The 'nomadic' males ($n = 3$) travelled extensively throughout the Wenlock and Ducie River catchments (Fig. 3a). They did not confine their movements to a discrete area on the area, and therefore the KUD 50% comprised only a fraction (13.6±4.9%,) of their total KUD 95% (Table 1). Because there was no defined home range, the location fixes rather than the KUDs were plotted on the maps to illustrate space use (Fig. 3a). The 'nomadic' males rate of movement averaged 384.3±29.1 m h^{-1} during darkness and 233.4±56.3 m h^{-1} during daylight hours (Table 1). During the six months of tracking the 'nomadic' males moved many

Table 1. Summary statistics for four female and eight male *Crocodylus porosus* tracked by GPS-based telemetry between 01 September 2010 and 28 February 2011.

Croc ID	Total Body Length (m)	Day ROM (m/h)	Night ROM (m/h)	Total distance moved (km)	KUD 95% (km^2)	KUD 50% (km^2)	Max distance from centroid
M1	3.2	301	352	824	34.2*	6.6*	73.2
M2	3.7	153	428	1054	42.1*	6.4*	69.2
M3	3.9	245	373	1269	72.5*	4.7*	165.4
M4	4.3	290	589	1179	9.0	4.2	19.2
M5	3.9	67	118	173	7.3	3.5	12.2
M6	3.7	84	248	197	8.7	3.6	27.9
M7	4.1	166	447	964	11.2	5.1	9.6
M8	4.5	200	270	324	7.1	4.2	8.07
F1	3.0	123	56	258	12.8	3.9	54.3
F2	2.9	17	39	127	7.2	2.2	54.8
F3	3.2	34	92	165	4.9	0.8	33.1
F4	2.6	27	23	154	1.1	0.5	22.5

*indicates that the monthly kernel utilisation distribution (KUD) had not stabilised by the end of the study.

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hundreds of kilometres and on average travelled 102.6±40.8 km from the KUD 50% centroid (Fig. 3b). The mean total length of the 'nomadic' males was 3.6±0.2 m (mean ± S.E.).

As the name implies the 'site fidelic' males (n 5) exhibited a stable KUD 50% in which they confined their movements during the 6 months of study (Fig. 4a). The KUD 95% and KUD 50% were comparable across the group (Table 1), and the KUD 50% comprised a large component of the total KUD 95% (48.1±2.8%). There was overlap in the KUD 50% between males, but this was never greater than 47.1% (35.1±6.1% mean±S.E., n 8). The 'site fidelic' males moved a minimum river distance of 334.4±83.7 m h ^{1} during darkness, decreasing to 161.4±41.2 m h ^{1} during daylight hours (Table 1). Although the average hourly rate of movement for the 'site fidelic' males was less than exhibited by the 'nomadic' males, there was no significant difference in the daily distance travelled between the two groups throughout the study (Table 2). The 'site fidelic' males moved back and forward within their home range and therefore the daily distance they were located away from the KUD 50% centroid closely matched the daily rate of movement (Fig. 4b). The maximum river distance the 'site fidelic' males were located away from the KUD 50% centroid averaged 15.4±3.7 km for the group (Table 1). The mean total length of the site fidelic males was 4.1±0.18 m.

Female movements

The four tagged female *C. porosus* were of a similar size range and were smaller than the tagged males (Table 1). All females occupied the main trunk of the river and exhibited a defined KUD 95% that was stable between 01 September and 01 December (Fig. 5a). The KUD 50% of two females overlapped at 32.1 and 34.4% area, whilst the other two females held discrete KUD 50% in close proximity. The daily rate of movement for females was much lower than recorded for the males (night 52.5±13.4 m h ^{1}; daylight 50.3±22.2 m h ^{1}), and they did not exhibit the male preference for nocturnal activity (Table 1).

During December and January, each female showed an approximate 30% expansion of their KUD 95%. This increase in the KUD 95% and KUD 50% was due to a sharp increase in daily activity and a lengthening of the distance the female was located away from the KUD 50% centroid (Fig. 5b). F1 travelled upriver whilst F2, F3 and F4 travelled downriver, and within a 24 h period all females were located a considerable distance from the KUD 50% centroid. It seemed logical due to the timing that these long range movements exhibited by the females were towards nesting areas. F2, F3 and F4 remained at the new location for less than 48 h before travelling back to the KUD 50% centroid within a 24 h period. They remained within their original KUD 50% for 1 2 weeks before undertaking the same journey back to the nesting location. Once at the nesting location for the second time, they remained there until the end of the study (28 February). F1 did not show this repetitive movement and undertook a single long distance movement in January, remaining at the new location until the end of the study.

GLMM

The general linear mixed effects model showed that body mass had no significant effect upon the daily rate of movement (ROM) or the river distance an individual was located away from its KUD 50% centroid (Table 2). Sex did have a significant effect upon ROM but not distance from the KUD 50% centroid and date had a significant effect upon both ROM and distance from the KUD 50% centroid. Crocodile ID exerted a significant effect within the model upon both ROM and distance from the KUD 50% centroid, but classifying males into either 'nomadic' or 'site fidelic' groups accounted for the significant effect of crocodile ID ($F_{1,9}$ 67.4, $P<0.01$).

Discussion

Male movements

We recorded two distinct behavioural tactics exhibited by tagged male *C. porosus* throughout the six month study. The daily rate of movement was not significantly different between groups exhibiting either behavioural tactic, but the temporal directionality of movement defined each group. Males exhibiting a 'nomadic' tactic ranged throughout the Wenlock and Ducie River catchments; their movement along the river were typically unidirectional upon consecutive days and confined only by river geography. In contrast, males exhibiting a 'site fidelic' tactic

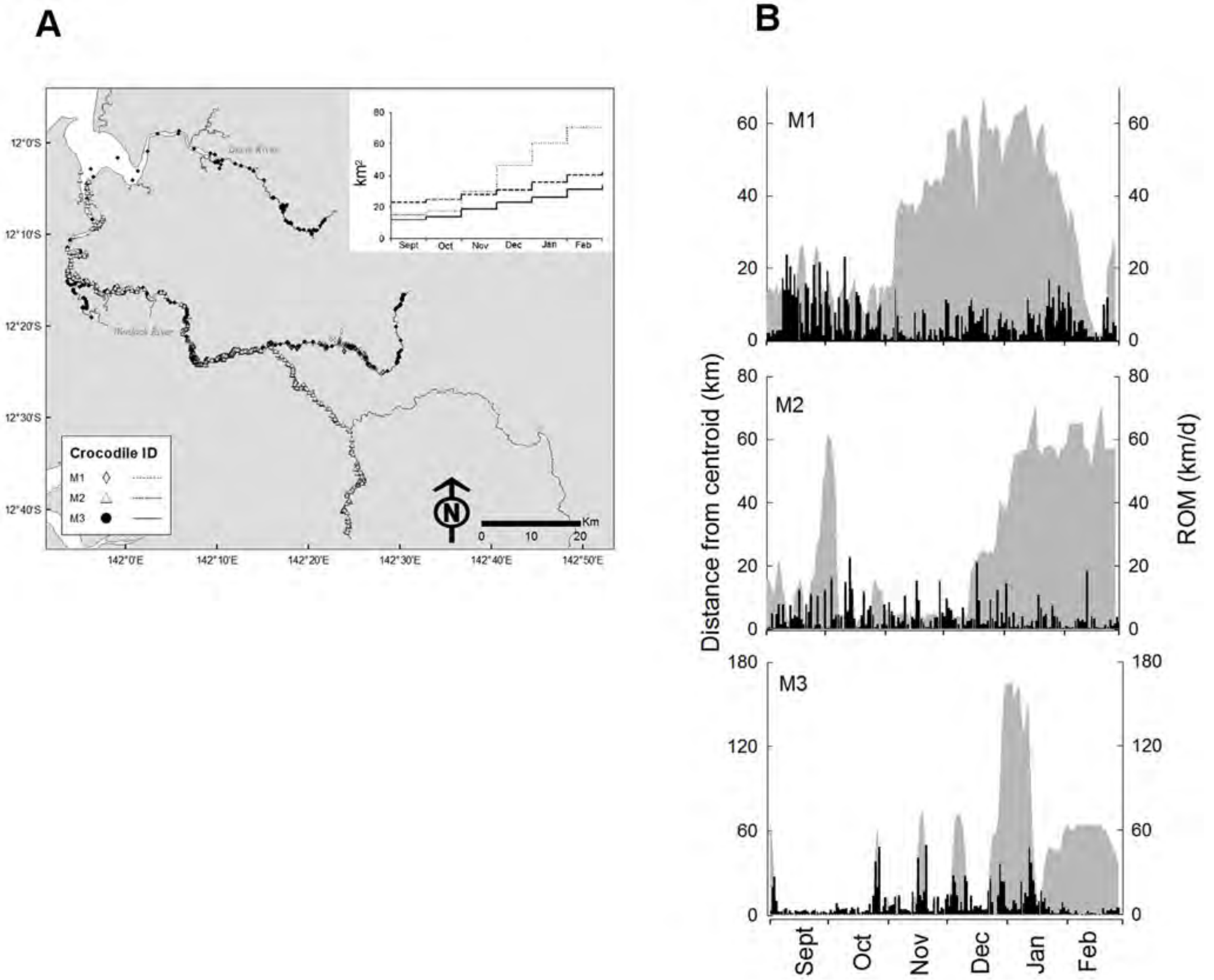

Figure 3. Movement patterns of 'nomadic' male Crocodylus porosus. (a) GPS location fixes obtained twice daily between 01 September and 28 February (n = 3). Inset line graph shows the monthly cumulative KUD 95% for each individual. (b) The relationship between daily rate of movement (ROM) and daily distance from the KUD 50% centroid (grey = primary y axis; black = secondary y axis).
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confined their movements within a discrete stretch of river. Each individual male maintained its selected behavioural tactic throughout the breeding and nesting season.

The patterns of movement recorded by GPS based location fixing and defined by KUD home range analysis strongly reflected territorial patrolling behaviour and mate defence [35,36]. Tagged con specifics were located inside the home range of the 'site fidelic' males, but the rate of movement of these individuals would have resulted in them passing through the home range quickly, and the lack of total exclusion may simply be a function of the large home range area and the high mobility of the con specifics. It is likely that the 'nomadic' males passed through the territories of many other untagged 'site fidelic' males during this period.

The present study was undertaken during the breeding and nesting season and all tagged males would have been of reproductive age. Body size is a good surrogate of social status in *C. porosus* [37], and although behavioural strategy was not significantly segregated by size in this study, we argue that it is the most likely determinate between a 'nomadic' or a 'site fidelic' lifestyle. Certainly, the dichotomy of movement patterns were strongly reflective of the 'fighting' or 'sneaking' alternative reproductive tactics often displayed within polygamous mating systems [38,39]. That is, dominant males maximise their reproductive success by defending mating rights with co habiting females, whilst subordinate males maximise their chance by 'sneaking' copulations with unguarded females. Further support for this theory in *C. porosus* populations comes from the genetic analysis of eggs collected from nests in the wild, which showed multiple paternity is widespread with some clutches having more than two sires [40].

A surprising observation that contradicts much of the literature [6,15] was the sustained high daily rates of movement exhibited by all the tagged *C. porosus*. Even the site fidelic males travelled hundreds of kilometres during the study, albeit within a discrete area. Translocated male *C. porosus* have been previously reported to have travelled over hundreds of kilometres in a quest to return home [16,41,42]. These were however, considered extreme rates of movement, undertaken by the individual only because of the manipulated conditions and a strong homing instinct. On the contrary, high frequency GPS based location sampling revealed

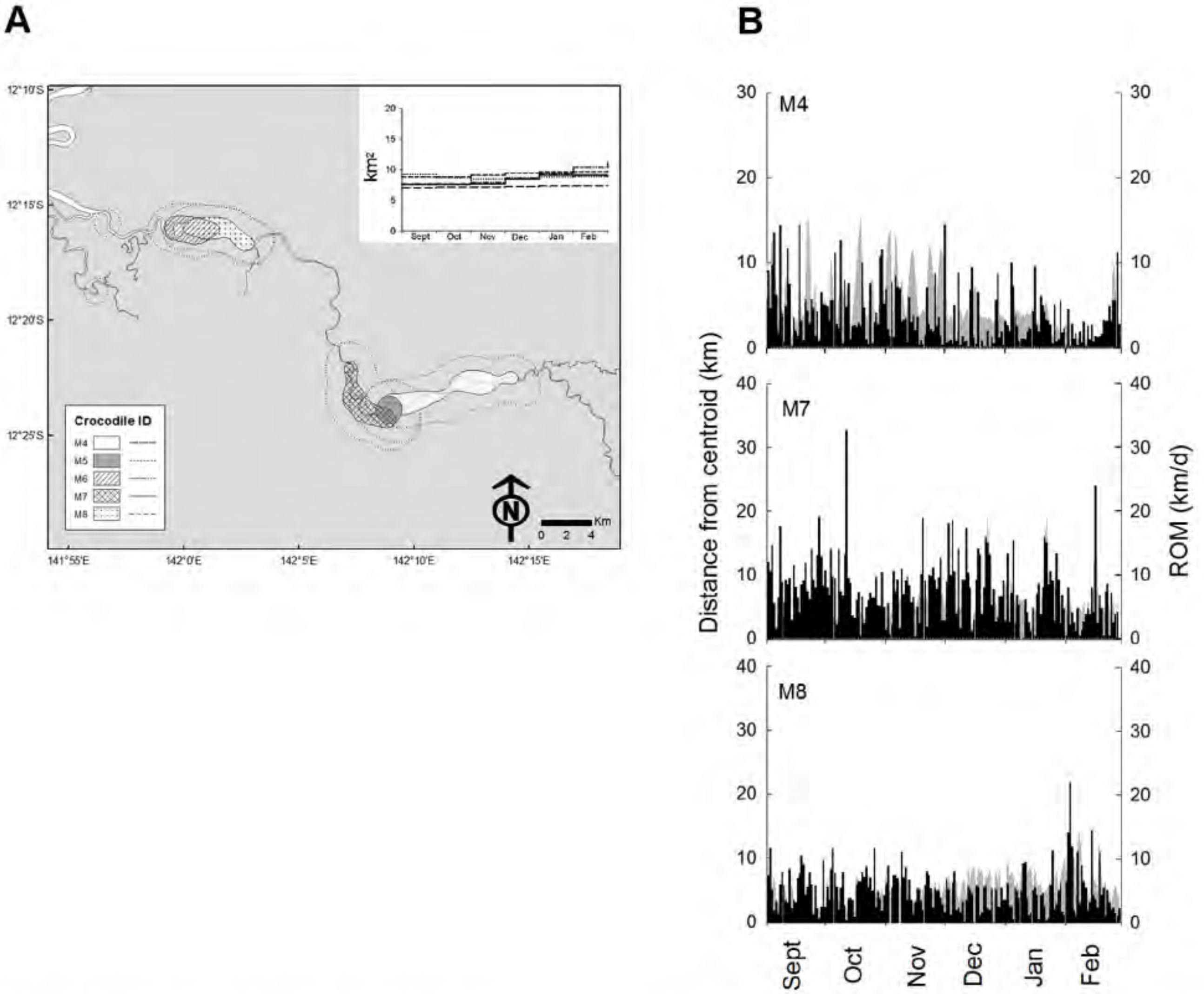

Figure 4. Movement patterns of 'site fidelic' male Crocodylus porosus. (a) KUD 50% and KUD 95% (dotted boundary) calculated from GPS location fixes recorded between 01 September and 28 February (n = 5). Inset graph shows the monthly cumulative KUD 95% for each individual. (b) The relationship between daily rate of movement (ROM) and daily distance from the KUD 50% centroid (grey = primary y axis; black = secondary y axis).
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that adult male *C. porosus* are extremely active animals routinely moving many kilometres per day. Presumably, it is because dominant males move back and forth within the confines of a territory that lower rates of location sampling or anecdotal observations have given the impression of far lower potential for movement in *C. porosus*.

Table 2. The results from two general linear mixed-effects models to examine the covariates and factors influencing daily rate of movement (ROM) and site-fidelity for *Crocodylus porosus* (male = 8; female = 4).

		Daily ROM		Daily distance from KUD 50% centroid	
	DF	F	P	F	P
Sex	1,9	19.67	0.001	0.99	0.76
Body mass	1,9	0.29	0.6	1.3	0.27
Date	1,2158	4.8	0.02	629	0.0001

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Female movements

In northern Australia, *C. porosus* nest from November through until March [43]. The time between copulation and the laying of eggs in captive *C. porosus* is between 4 to 6 weeks [6], and therefore, courtship and mating may occur anywhere between the end of September and early December. During this period our tagged female *C. porosus* confined their movements within a few kilometres of the main trunk of the river. It has been suggested previously that female *C. porosus* remain close to the nesting location throughout the year [43]. This was not the case in the present study however, and all our tagged females travelled considerable distances (up to 54 km) to a location where we presume they nested (based upon movements that were representative of attentive nest guarding). Such large movement between the breeding and nesting site has

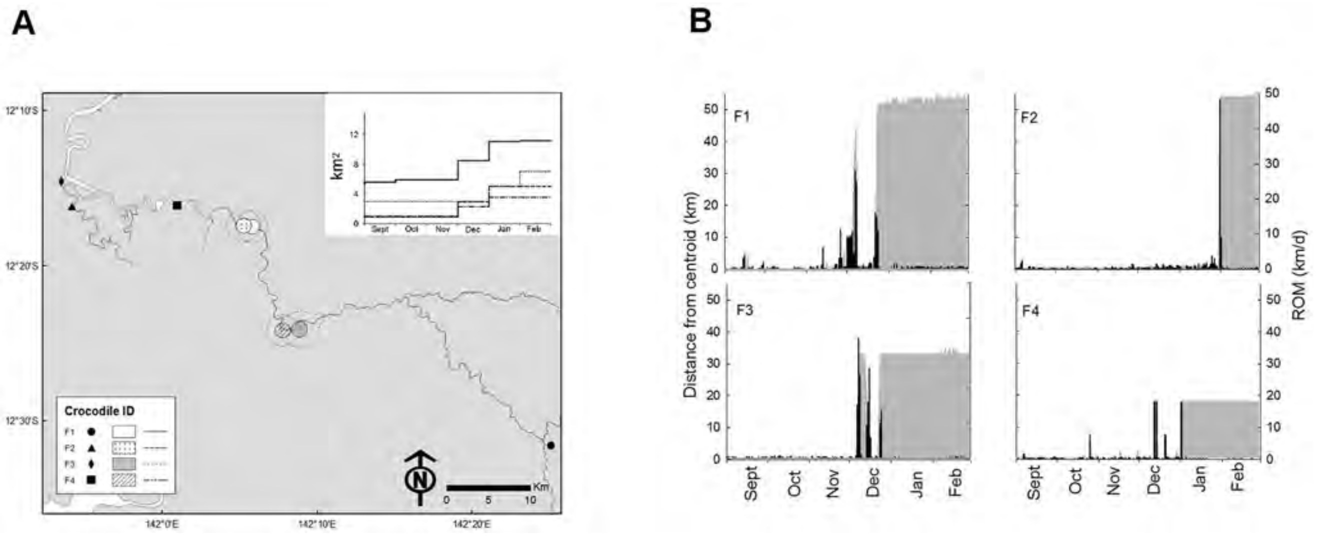

Figure 5. Movement patterns of female Crocodylus porosus. (a) The KUD 50% and KUD 95% (dotted boundary) calculated from GPS location fixes recorded between 01 September and 28 February (n = 4). Inset graph shows the monthly cumulative KUD 95% for each individual. (b) The relationship between daily rate of movement (ROM) and daily distance from the KUD 50% centroid (grey = primary y axis; black = secondary y axis).
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not been reported previously for female *C. porosus*, and may be reflective of the local environment.

The females that were captured and tagged in this study inhabited the tidal freshwater reaches of the river. In this area, the river is relatively narrow and bordered by steep sandy banks sparsely covered with *Melaleuca* trees. The river would be fast flowing through this section in the wet season, and this location does not contain good nesting habitat for *C. porosus*. Prior to nesting, three out of the four tagged females travelled downstream to a much wider, saline brackish, section of the river. In this stretch, the river is bordered by thick stands of mangrove, *Nypa* palms and salt marsh; vegetation and habitat that is much more suited for *C. porosus* nesting [44]. Moreover, this section of the river contains a disproportionally high density of hatchling *C. porosus* compared to other stretches of the river [10]. This suggests that female migration into this area may be a common behavioural strategy within the local population. One of our tagged females did however; migrate over 40 km upstream from the breeding area to the nesting location. This area did not appear to be ideal *C. porosus* nesting habitat [44], but there was a large permanent freshwater swamp in close proximity.

It seems reasonable to assume that the tagged female *C. porosus* travelled long distances to a nesting location because of better nest building materials, access to freshwater, and a reduced likelihood of the nest being flooded during the wet season [44]. What is less clear is why the females did not breed in the locality of the nesting areas and save themselves from these energetically expensive journeys. A possible reason is that the breeding area had better resources than at the nesting areas. Over a four year period we have laid numerous traps throughout a 60 km stretch of the Wenlock River but only caught females of breeding size within a few discrete locations (Campbell, personal observation). The GPS location data revealed that during the breeding period the females exhibit high site fidelity to these areas. We argue that these breeding areas are located within productive sections of the river, and the females select these areas in order to build up fat stores for egg gestation and nesting. If this is true then it suggests that *C. porosus* have a social system based upon resource based mate choice. That is, the females select areas containing the best resources and the males defend territories around these areas to maximise their mating opportunities [45,46]. Further investigation is required to confirm this social structure, which would have profound influence upon population density and distribution.

A novel observation of this study was that three out of the four tagged females travelled to the locality of the nest site a few weeks prior to the actual nesting movement. These journeys would have required considerable energetic expenditure, and therefore are likely to have offered some advantage to the offspring. We can only speculate on what this may have been, and the motivation for this repeated movement so close to nesting remains an avenue of future investigation.

Effects upon the ecosystem

The movements of the 'nomadic' and the 'site fidelic' males would have resulted in very different feeding opportunities and likely required disparate foraging strategies. The 'nomadic' *C. porosus* would need to select a variety of prey items from freshwater and saline brackish ecosystems, whilst 'site fidelic' *C. porosus* would need to take prey whenever it was available within the limits of their home range. Consequently, *C. porosus* are likely to vary in their degree of individual specialisation across spatial scales. Stable isotopic studies upon the tissues of American alligators (*Alligator mississippiensis*) in the Florida Everglades revealed a population composed of both generalist and specialist feeders [46]. There was a strong correlation between ingested prey items and broad scale movements, and we argue that alternative behavioural tactics driven by social status may have underpinned the observed diet selection by individuals.

When highly mobile predators move rapidly between habitats and feed on a variety of prey species, they create habitat linkages which transport nutrients and energy between systems [5]. A predator that rapidly moves between habitats and switches prey will stabilise the ecosystem by increasing pressure upon one channel of energy whilst freeing up a depleting energy channel from strong predatory pressure [3]. In contrast, a sessile predator may take food whenever available, resulting in negligible transport of energy or nutrients. The dichotomy of movement strategies observed in this study for adult *C. porosus* would result in very different top down regulation upon trophic interactions and the coupling of ecosystems and habitats. Consequently, understanding the relationship between *C. porosus* density, spatial movement, and home range dynamics are important in defining the wider community and ecosystem effects of a growing *C. porosus* population.

Implications for management

Since the legislated protection of *C. porosus* there has been a general increase in population abundance across northern Australia. Within some rivers, crocodile density has remained stable for the last 10 to 20 years whilst total crocodile biomass has continued to increase, whereas other rivers are increasing in crocodile density but with no matching increase in total biomass [14]. The social dynamics of the *C. porosus* in this study may aid to explain some of these observed trends. For example, the theory of female resource based mate choice [47,48] in *C. porosus* would serve to stabilise population density in areas of good crocodile habitat, and because displacement is unlikely to be achieved by a smaller rival, total crocodile biomass of the area would increase over time. Conversely, rivers or areas with fewer resources would not be selected by females, and dominant males would not hold territories around these areas. Therefore, the population in these poorer quality habitats is primarily composed of smaller subordinate crocodiles, with density but not biomass increasing over time.

Estuarine crocodiles pose a potential risk to the public and a management intervention implemented across northern Australia is to remove crocodiles from around urban centres and areas of high human visitation [48]. A high majority(>75%) of the *C. porosus* captured in permanently set traps are males between 2 and 3 m total length (Yusuke Fukuda, Scott Sullivan, personal communication), and the high rates of movement exhibited by the subordinate males in this study explains this capture bias. Although implemented less frequently, the removal of dominant male *C. porosus* is also considered as a viable management intervention to reduce crocodile density in particular areas. We recommend that the impact of this management intervention is thoroughly evaluated because, as has been shown for other vertebrate species, dominant male removal can cause social perturbations and can increase movement and immigration from neighbouring areas [49,50,51]. Only by thorough evaluation of each management intervention, taking into account any consequences of social perturbation, can the desired outcome be achieved in the management of *C. porosus*.

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Author Contributions

Conceived and designed the experiments: HAC CEF. Performed the experiments: HAC TRI CEF. Analyzed the data: HAC RGD. Wrote the paper: HAC RGD.

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Speech By

Shane Knuth

MEMBER FOR HILL

Record of Proceedings, 11 May 2023

PRIVATE MEMBERS' STATEMENTS

Crocodile Management

Mr KNUTH (Hill—KAP) (3.12 pm): For years the KAP has warned the state government about the threat that crocodiles pose to human life and to the tourist industry in North Queensland. We have already tabled two bills in parliament and we will be tabling our Crocodile Control and Conservation Bill 2023 in the coming months—that is, three bills.

Crocodile numbers are exploding as more and more crocodiles move into populated waterways and beaches. We know that North Queenslanders cannot trust governing from Brisbane on the issues that need to be fixed locally. Our bill aims to locally manage the crocodile population in Queensland while continuing to preserve and protect crocodiles in the wild.

The bill will establish the Queensland Crocodile Authority, which will be based in Cairns and not Brisbane where there are no crocs at all. The authority will make all decisions and deliver all programs on crocodile management issues, with the advisory committee established to represent Indigenous communities, tourism businesses, Surf Life Saving Queensland and all other relevant stakeholders. It is important that the program is flexible to cater for cultural sensitivities in some Indigenous communities that see the crocodile as a totem. The Queensland Crocodile Authority will also oversee funding, licensing and the development of crocodile and egg harvesting, farming and other related economic activities and opportunities for Indigenous communities.

Another key part of the bill is a zero tolerance policy on crocodiles in populated waterways and beaches. For instance, every year the Northern Territory culls between 250 and 300 crocodiles in the Darwin Harbour. That has not adversely affected populations in other parts of the Northern Territory. In North Queensland we should also establish concentrated annual culling programs to target populated areas where we do not want crocodiles.

The government has to decide what value they place on human lives in North Queensland and it has to manage the dangerous consequences of humans and crocodiles living alongside each other. It is acknowledged that we are never going to completely eliminate the threat but we can reduce the risks through culling programs to limit the number of crocodile attacks in populated areas. North Queenslanders want strong management that mitigates risk and gives us back our popular waterways and beaches. The fact that you can cull cats, dogs, horses, pigs and kangaroos but not man-eating crocodiles is complete madness. I feel sorry for the tourism industry, which is trying to promote pristine beaches, islands and waterways only for tourists to be greeted by croc signs upon arrival. It is time we put human lives, the tourist industry in North Queensland and our quality of life first.

(Time expired)

WORLD TRAVEL & TOURISM COUNCIL

THE ECONOMIC IMPACT OF GLOBAL WILDLIFE TOURISM

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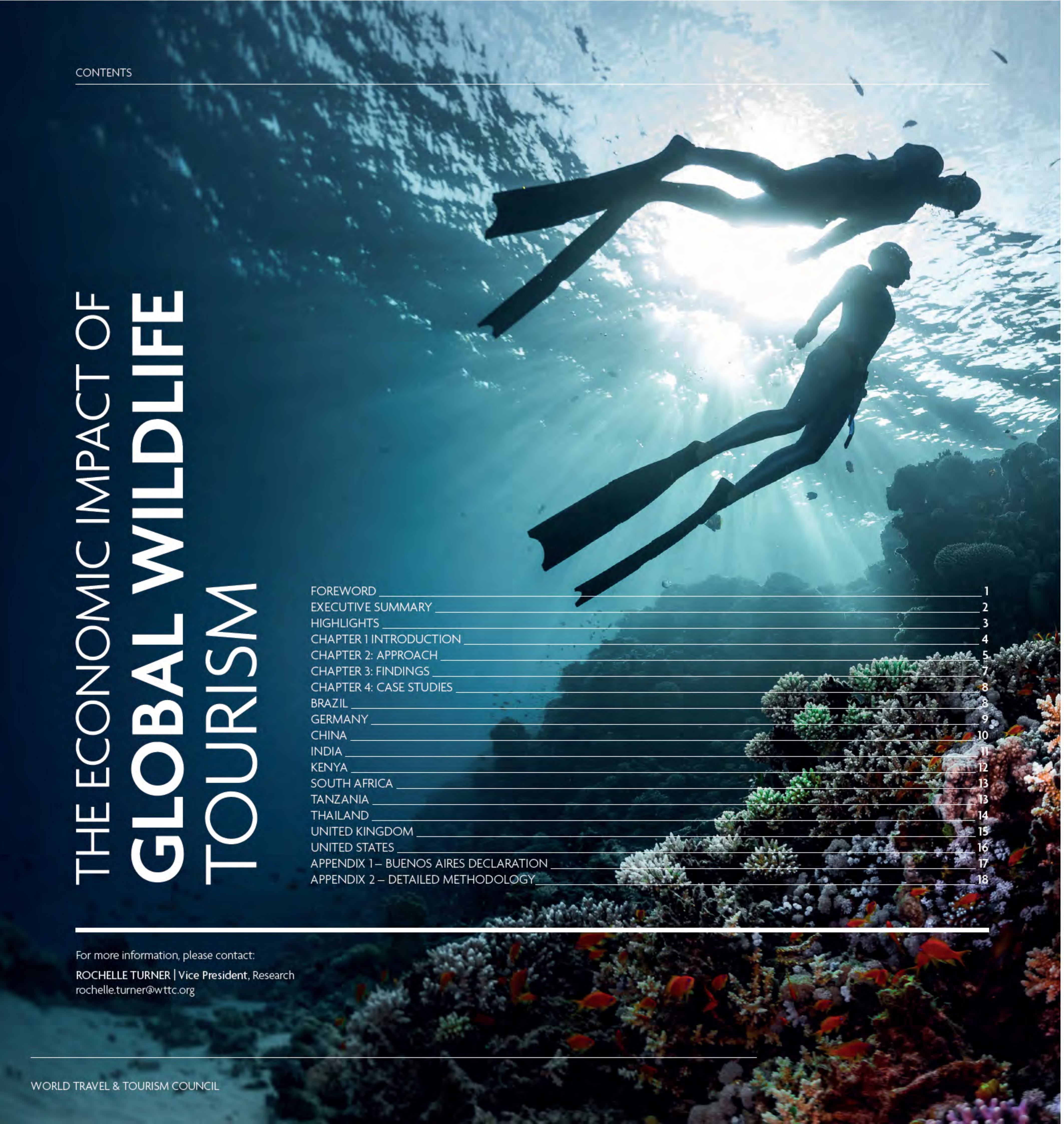

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FOREWORD

Travel & Tourism can play a tremendous role in combatting the global scourge that is the illegal trade in wildlife. Through this research on the economic contribution of wildlife tourism, we hope to draw further attention to the enormous economic opportunities associated to Travel & Tourism and thereby further substantiate the rationale for greater wildlife protection.

I witnessed first-hand how tourism can prevent wildlife from being poached and traded illegally. In Mexico, by protecting the wintering hibernation areas of the Monarch Butterfly in dedicated biosphere reserves, thousands of tourists each year are able to enjoy the most spectacular migration of millions of butterflies. The people in the villages and towns surrounding these reserves benefit enormously from the protection of the wildlife. People who visit the region to view these beautiful creatures create important jobs for residents in conservation, tour-guiding, accommodation and scientific discovery while providing broader economic value to support the prosperity of the families and wider communities in the area.

This research quantifies the importance of wildlife tourism to build greater awareness of its value and showcase the need for protection among policymakers and government budget holders. While the Travel & Tourism sector accounts for 10.4% of global GDP, wildlife tourism represents 3.9% of this figure, or $343.6 billion; a figure equivalent to the entire GDP of South Africa or Hong Kong. Of equal significance is the fact that around the world, 21.8 million jobs or 6.8% of total jobs sustained by global Travel & Tourism in 2018 can be attributed to wildlife.

I am proud that WTTC is working with its Members to eradicate illegal trade in wildlife, devising a zero-tolerance policy and raising awareness of the issue among one billion consumers. Over 110 of WTTC Members and the wider Travel & Tourism community came together in 2018 to sign the Buenos Aires Declaration to collectively work towards this goal. Our work, supported by our collaboration with WWF, has already reached over 100 million tourists.

With wildlife tourism representing over five times the value of the illegal wildlife trade, it is essential that we continue with our advocacy efforts to drive understanding of the nature of the Travel & Tourism sector along with improved governance of the world's flora and fauna.

Gloria G.

Gloria Guevara Manzo
President & CEO
World Travel & Tourism Council

EXECUTIVE SUMMARY

Over the years, threats to wildlife around the word, ranging from habitat destruction, climate change and the impacts of poaching have increased significantly. Preventing the illegal trade in wildlife is an immense challenge.

The World Travel & Tourism Council (WTTC) has been promoting industry action to support global efforts to tackle the illegal trade in wildlife. In April 2018 WTTC launched the Buenos Aires Declaration on Illegal Wildlife Trade to bring sector initiatives together under one umbrella[1]. The declaration now has over 110 signatories and was showcased during the High Level IWT Conference in London in October 2018. WTTC's ambition is to raise awareness of the issue with one billion consumers and through a partnership with WWF, devise a zero-tolerance policy and toolkit.

Tourism has a unique role to play by providing economic opportunities for communities and an economic rationale for the protection of endangered species and protecting wildlife habitats. In the Travel & Tourism sector which contributes 10.4% of global GDP and supports one in ten jobs (319 million), quantifying the value of wildlife tourism is an important first step in providing the economic case. Having the data to show how preserving and protecting wildlife through tourism can act as a positive counterbalance to environmentally destructive yet economically profitable practices, is a step towards helping communities and authorities realise the benefits that nature can bring.

Wildlife tourism (WT) – here defined as viewing and experiencing animals in their natural habitat – is increasingly recognised as an important part of the wider Travel & Tourism sector.

This report provides an estimation of the global economic contribution of WT and suggest that it:

- Directly contributed $120.1 billion[2] in GDP to the global economy in 2018 or 4.4% of the estimated direct global Travel & Tourism GDP of $2,751 billion in 2018[3]. Significantly, this represents over five times the value of the illegal wildlife trade.
- Once additional multiplier effects across the global economy are allowed for, the total economic contribution of wildlife tourism comes to $343.6 billion. Equivalent to the entire economy GDP of South Africa or Hong Kong.
- WT therefore sustained 21.8 million jobs, equal to 6.8% of total jobs sustained by global Travel & Tourism in 2018. The 21.8 million jobs supported by wildlife tourism is the equivalent of the entire population of Sri Lanka.
- Across Africa, wildlife tourism represents over one-third of Travel & Tourism revenue.

Apart from improved governance, the increasing use of social media to assess visitation and understand visitor preferences for wildlife tourism and other forms of recreational activities hold promise for future efforts to understand the nature of the sector.

These figures should be caveated by the fact that they are "order of magnitude" estimates based on a variety of sources. With the further development of WT, improved management and efforts to better record visitation numbers and spend, more refined figures could be developed in future. Apart from improved governance, the increasing use of social media to assess visitation and understand visitor preferences for WT and other forms of recreational activities also hold promise for future efforts to understand the nature of the sector.

The impact of WT at the "local" level is also investigated in more detail through a series of country case studies of the key WT markets of UK, Germany, United States, Brazil, South Africa, Tanzania, Kenya, India, Thailand and China.

Figures in this report are presented in Figure 1, expressed in 2018 dollars with foreign currencies converted at PPP exchange rates, unless otherwise indicated.

Fig. 1. Direct and total economic contribution of WT, 2018

CONTINENT	DIRECT				TOTAL	
	EXPENDITURE ($BILLION)	GDP ($BILLION)	SHARE OF T&T	EMPLOYMENT (MILLION)	GDP ($BILLION)	EMPLOYMENT (MILLION)
NORTH AMERICA	25.4	13.5	2%	0.2	37.6	0.5
EUROPE	28.5	13.3	1.6%	0.2	35.4	0.6
AFRICA	48.8	29.3	36.3%	3.6	70.6	8.8
ASIA-PACIFIC	118.2	53.3	5.8%	4.5	171.2	10.4
LATIN AMERICA	19.9	10.7	8.6%	0.5	28.9	1.4
TOTAL	241.0	120.1		9.1	343.6	21.8
SHARE OF TOTAL GLOBAL T&T (%)	4.2%	4.4%		7.4%	3.9%	6.8%

Source: Oxford Economics, Figures may not sum to totals due to rounding

HIGHLIGHTS

The World Travel & Tourism Council (WTTC) has been promoting industry action to support global efforts to tackle the illegal trade in wildlife. To date, over 110 WTTC Members and leaders from the wider global Travel & Tourism sector have signed the Buenos Aires Declaration, on illegal wildlife trade (IWT). Our ambition is to raise awareness of the issue with one billion consumers and through a partnership with WWF, devise a zero-tolerance policy and toolkit.

Quantifying the value of wildlife tourism (tourism that involves watching and experiencing with wildlife in its own natural habitat) as an important niche within global Travel & Tourism is a crucial step towards providing the data that helps provide the economic value of protecting wildlife habitats.

In 2018, wildlife tourism directly contributed $120 billion to economies. Adding in the financial benefits through the supply chain, the total contribution of this niche provided $343.6 billion or 3.9% of global Travel & Tourism GDP[4] in 2018.

The direct contribution of wildlife tourism is worth over five times that of the illegal wildlife trade. The positive action that can be taken through this kind of tourism to empower local communities to pursue sustainable livelihood opportunities, to provide poacher compensation and education workshops and to spread monetary benefits from local or national parks are key ways that support Target 15.7 under UN Sustainable Development Goal 15 to combat poaching and trafficking of protected species.

Wildlife tourism supports 21.8 million jobs either directly or indirectly across the world; 6.8% of total Travel & Tourism jobs. The 21.8 million jobs supported by wildlife tourism is the equivalent of the entire population of Sri Lanka.

The regional shares of wildlife tourism within the wider Travel & Tourism sector differ quite widely - ranging from a hugely significant 36.3% in Africa to 8.6% in Latin America and 5.8% in Asia-Pacific to a low of 2% in North America and just 1.6% in Europe.

Case studies show that Protected Areas, where most wildlife tourism takes place, have developed rapidly over the past few decades in response to burgeoning population growth and a need to protect biodiversity and forest cover. The financial benefits brought from wildlife tourism are also likely to greatly exceed the approximate $10 billion[5] in annual costs of managing these Areas.

Apart from improved governance, the increasing use of social media to assess visitation and understand visitor preferences for wildlife tourism and other forms of recreational activities hold promise for future efforts to understand the nature of the sector.

01

INTRODUCTION

Each year, the illegal wildlife trade (IWT) is worth at least USD 23 billion[6]. IWT is the fourth largest category of illegal global trade and is responsible for threatening a broad range of endangered species[7]. Protecting wildlife is therefore an immense challenge.

The global Travel & Tourism sector is an important part of the world economy accounting for 10.4% of global GDP and supporting one in ten jobs on the planet (319 million)[8]. Quantifying the value of wildlife tourism as an important niche within global Travel & Tourism is a crucial step towards providing the data that helps prove the economic value of protecting wildlife habitats; acting as a positive counterbalance to environmentally destructive yet economically profitable practices.

Wildlife tourism (WT) – here defined as viewing and experiencing animals in their natural habitat – is increasingly recognised as an important part of the overall Travel & Tourism sector. The importance of WT is all the greater given the threats that have emerged to wildlife around the world, ranging from habitat destruction, climate change and the impacts of poaching. However, while the importance of this form of tourism is often recognised, statistics on WT are often dated, incomplete or conflated with other forms of tourism.

Accordingly, this report undertakes that task, using both top down (aggregated) and bottom up (disaggregated) data sources to determine global estimates for the economic contribution of WT. These estimates include direct expenditure, GDP and employment effects of WT at the continental and global levels.

In addition, estimates of the total impact of WT on GDP and employment on these geographies and at a global level have been developed, allowing for the "multiplier effects" of spending by WT suppliers, WT and supply chain workers, investment and government spending.

Country case studies of the key WT markets of the UK, Germany, United States, Brazil, South Africa, Tanzania, Kenya, India, Thailand and China are also examined in this report.

Fortunately, there are several cases of effective programs and 'local level' initiatives to prevent illegal wildlife trade to draw on. For instance, Kenya's National Wildlife Strategy 2030 provides evidence-based support for tackling poaching[9], while a collection of Conservancies (such as Olderkesi Wildlife Conservancy) have implemented land management and monitoring strategies to prevent poachers[10]. GPS-supported, community-based forest crime prevention approaches are being developing in the Amazon in Brazil, with prospects for many African countries[11].

APPROACH

02

The economic estimation of WT has been of interest to many in the tourism and academic fields in recent years, however good data in the area are scarce.

While writers such as Fillion et. al. (1994) have provided much-cited estimates in the past, these estimates are dated, and their current relevance is unclear[12]. Another key issue is definitional. Some studies refer to "ecotourism", "nature" (or "nature-based" tourism) "adventure tourism", "special interest" tourism, "rural tourism" and to WT interchangeably or with little attempt to separate these activities. Still others include zoos and fenced wildlife parks in such tourism.

This study sees a distinction between the following types of tourism:

- Wildlife Tourism - in essence, this study defines WT as tourism in which wildlife watching experiences and/or interactions are an important motivator. It therefore excludes settings such as zoos (or zoo-like parks), circuses or theme parks involving animal performances. The definition also excludes consumptive wildlife tourism such as hunting and fishing. In other words, it is restricted to what is sometimes known as "non-consumptive" WT involving watching and experiencing with wildlife in its own natural habitat.
- Adventure tourism – is viewed as involving some form of activity such as rafting, canyoning, caving etc.
- Ecotourism - is considered to be tourism involving experiences with flora, fauna, landscapes and potentially cultures in a natural setting (and so is slightly broader than wildlife tourism).
- Nature-based tourism - encompasses both ecotourism and WT – for example it could include rural activities such as farm stays.

The figure below illustrates how this study views WT in comparison to the other related forms of tourism. Needless to say, not all studies adhere to these definitional distinctions, while others introduce further or different sub-categories.

Fig. 2. Wildlife tourism and associated tourism

A further complication (which of course occurs with many forms of tourism) is that an individual tourist may have many reasons for undertaking a trip. A trip to Africa for example may include a wildlife watching safari but also involve purchasing handicrafts, tasting local food or exploring local cultures.

Nonetheless, assessing the economic impact of WT is of great importance to many countries and stakeholders. This is particularly the case in an environment when wildlife faces many threats, ranging from habitat destruction and climate change to poaching.

The discussion below provides details of the approach taken in this study to the assessment of WT and the definition of Protected Areas (PAs) which are closely associated with such tourism, as explained below. A more detailed discussion of the methodology is provided in the Appendix 2.

METHODOLOGY

A way forward to developing an estimation of WT may be found in the work of Balmford et. al. (2015)[13]. This extensive study sought to provide estimates of global visitation and spend in defined Protected Areas (PAs). In essence, PAs, as defined by the International Union for the Conservation of Nature (IUCN), are defined geographical spaces, recognised, dedicated and managed to achieve nature conservation[14]. PAs typically encompass national parks and other designated wilderness spaces. More formally, PA's are grouped into several governance types, as indicated in the box below[15].

A key initial issue in undertaking the work was to distinguish between WT in North America and Europe and the other continents (Latin America, Asia and Asia-Pacific). For this reason, a dual bottom-up/top down analysis was undertaken for this study, namely:

- North America and Europe - "Bottom up" data sources from the US, Canada, the UK and Germany were used to determine visitation and spend figures.
- Africa, Asia-Pacific and Latin America- In the case of these continents, the approach was essentially "top down", using the PA visitation estimates of Balmford et al. as a base. However, significant modifications were made for tourism growth, a WT "filter", inflation and the use of supplementary estimates in some cases.

This approach yielded estimates for the various continents. Results for the bottom up and top down analysis were then combined to produce a global direct spending total. Data from the Oxford Economics Global Travel Service Databank was used to convert these spend estimates to GDP and employment figures.

Direct tourism spending also has indirect effects (e.g. spending by WT suppliers, WT and supply chain workers and investment and government spending). The spill-over (or multiplier) effects of the direct tourism spending estimated above, were derived using information from Oxford Economics Global Travel Service Databank. This allowed tor the development of total economic contribution (GDP and employment) figures for WT at the continental and global scale.

PROTECTED AREAS

Much of global WT takes place in Protected Areas (PAs). PAs are defined by the IUCN as falling into the following categories:

- Ia Strict Nature Reserve - strictly protected areas set aside to protect biodiversity and also possibly geological/geomorphic features, where human visitation, use and impacts are strictly controlled.
- Ib Wilderness Area - Usually large unmodified or slightly modified areas, retaining their natural character and influence without permanent or significant human habitation.
- II National Park - protected areas which are large natural or near natural areas which also allow for visitation.
- III Natural Monument or Feature: - protected areas set aside to protect a specific natural monument, such as a landform, sea mount, submarine cavern or geological feature.
- IV Habitat/Species Management Area – these protected areas aim to protect particular species or habitats and management reflects this priority.
- V Protected Landscape/ Seascape - protected areas where the interaction of people and nature over time has produced an area of distinct character with significant, ecological, biological, cultural and scenic value.
- VI Protected area with sustainable use of natural resources - protected areas conserve ecosystems and habitats together with associated cultural values and traditional natural resource management systems.

In practice, this and many other WT or similar studies exclude PAs falling into Category Ia and Ib as these are generally off-limits to human visitation.

03

FINDINGS

The research analysis suggests that WT made up $120bn or some 4.4% of the estimated direct global Travel & Tourism GDP of $2,751 billion in 2018[16][17], and directly supported 9.1 million jobs. When including the indirect and induced benefits of WT, the figures rise to $343.6bn, or 3.9% of the global share of Travel & Tourism GDP and 6.8% of all jobs in Travel & Tourism (21.8 million).

The regional direct shares of Travel & Tourism that WT represent differ quite widely across the world ranging from a low of 1.6% in Europe and 2% in North America, to 5.8% in Asia-Pacific, 8.6% in Latin America, and a hugely significant 36.3% in Africa.

The global direct GDP figure seems consistent with past UNWTO estimates that "nature tourism" captures 7% of the global tourism expenditure (bearing in mind that WT is likely to be smaller than broader definitions of nature tourism)[18]. While not a spend (or WT) estimate per se, another interesting comparison is the work of Levin et al.. who find that 11% of global geo-tagged Flickr photographs are taken within PAs, noting that such photos are a reliable surrogate for visitation[19].

Balmford et al. have suggested that spending on PA development and maintenance runs at approximately $10 billion globally[20]. This suggests that the global returns to WT are likely to greatly exceed the financial costs of PA management[21].

These figures should be caveated by the fact that they are "order of magnitude" estimations based on a variety of sources. With the further development of both WT, improved PA management and efforts to better record visitation numbers and spend, more refined figures could be developed in future. Apart from improved governance, the increasing use of social media to assess visitation and understand visitor preferences for WT and other forms of recreational activities also hold promise for future efforts to understand the nature of the sector.

These WT estimates are necessarily broad and intended to give a "big picture" viewpoint on the state of WT across the global tourism industry a whole. It is also useful to consider the development of WT in key individual markets, as these will have their own pattern of development. Accordingly, the country Case Studies explored below (and the details provided in the Appendix) provide further details on sources and/or aspects of WT in key WT markets across the world.

Fig. 2. Direct and total economic contribution of WT, 2018

CONTINENT	DIRECT			TOTAL	
	EXPENDITURE ($BILLION)	GDP ($BILLION)	EMPLOYMENT (MILLION)	GDP ($BILLION)	EMPLOYMENT (MILLION)
NORTH AMERICA	25.4	13.5	0.2	37.6	0.5
EUROPE	28.5	13.3	0.2	35.4	0.6
AFRICA	48.8	29.3	3.6	70.6	8.8
ASIA-PACIFIC	118.2	53.3	4.5	171.2	10.4
LATIN AMERICA	19.9	10.7	0.5	28.9	1.4
TOTAL	241.0	120.1	9.1	343.6	21.8
SHARE OF TOTAL GLOBAL T&T (%)	4.2%	4.4%	7.4%	3.9%	6.8%

Source: Oxford Economics, Figures may not sum to totals due to rounding

04

CASE STUDIES

The quantitative analysis above provides some indication of the magnitude of global WT. However, it is also useful to take a more in-depth look at ten countries that are some of the key WT markets across the world. This section examines WT in Brazil, China, Germany, India, Kenya, South Africa, Tanzania, Thailand, United Kingdom and the United States which collectively account for 61% of global total Travel & Tourism spending. The information gathered for these case studies also assisted in forming broader estimates of the magnitude of WT to varying degrees. Accordingly, the case studies for the United States, UK and Germany focus on more quantitative aspects of estimation, while the remainder provide more of a broad overview of WT in the respective countries

BRAZIL

Brazil's size, position and growing international prominence (despite recent political and economic turmoil) has made it an increasingly important market for WT. While the fact that the majority of the Amazon rainforest lies within the country makes it an obvious WT destination, another key draw lies to the south of the Amazon, where the wetlands of the Pantanal in Mato Grosso do Sul provide a key habitat for the jaguar, along with deer, otters, eagles, tapirs and giant anteaters.

Though one of the most famous ecosystems in the world and of key interest to wildlife tourists (with authors such as Newhouse quantifying that it is one of WT's global "hotspots) WT in the Amazon basin itself is still relatively limited, with past estimates indicating that tourism accounts for only 1% percent of regional GDP[22]. Though considered megadiverse in terms of its fauna and flora, WT has been relatively slow to develop in comparison to other regions[23].

Nonetheless, there are indications that WT (and related forms of tourism) have been growing substantially in Brazil in recent years. Brazilian government data indicates that federal PA visitation increased from 3.6 million in 2008 to 10.7 million in 2017[24].

Past Brazilian government work has also examined the phenomenon of "ecotourism" and by extension WT, indicates that 65% of domestic Brazilian visits to PAs are motivated by contemplacao ou contato com a natureaza ("contemplation or contact with nature")[25]. 2007 survey work indicated that some 3.4% of domestic Brazilian travellers reported ecotourism as their main motivation for travel while a 2009 survey recorded 1% of Brazilians stating that their main motivation for domestic travel was observation of flora and fauna[26]. Likewise, other studies have indicated that 22% of Brazilian adventure and ecotourists were motivated by wildlife watching[27].

Other work by the Brazilian Ministry of Tourism recorded that nature tourism, ecotourism and adventure tourism were (collectively) cited by 22.2% of international tourists as the main motivator to visit Brazil in 2008, up from 12.8% in 2004, though this appeared to have fallen back to 16.3% by 2017[28].

Estimates based on extensive work by Souza to investigate tourism in Brazilian federal PAs indicate that domestic tourists spent some $43 per day (in 2016 dollars) in these PAs and typically spent some 2.5 days per visit. However, these figures exclude the costs for domestic transportation to and from PAs (which could be considerable given their remote nature in many cases)[29]. These figures also exclude costs incurred by foreign visitors. As is the case in African WT these could be considerable, as foreign tourists often spend large amounts on wildlife/adventure "experiences". Work done by Tortato et. al (2017) indicates that the cost of lodge accommodation/tour packages in the Pantanal amounts to $412 per day[30]. Foreign tourists are likely to make up a large proportion of these lodge patrons.

Jaguar tourism on the Pantanal itself provides an interesting case study of approaches to address the tensions which may arise between WT and local rural industries in Brazil and elsewhere. Tortato et al. for example find that the value of local WT greatly exceeds local cattle losses due to jaguar predation and suggest that a voluntary tourist fund be set up, diverting some tourism benefits to rancher compensation.

GERMANY

WT in Germany has a long history, often intermingled with national traditions of recreational hiking and wanderlust. The country also enjoys internationally renowned locations of natural beauty including the Schwarzwald (Black Forest) and Harz Mountains.

These traditions are reflected in data on the propensity of Germans (and foreign visitors) to undertake trips to the country's Nationalparks (National Parks), UNESCO Biosphärenreservate, (UNESCO Biosphere Reserves) and Naturparks (Nature Parks). According to Naturtourismus in Deutschland 2016 (2016) survey work by the Bundesamt für Naturschutz (BfN) for the period between 2007 and 2015 indicated an average of 53.09 million National Park visitor days per year while a separate study extending this methodology to Biosphere Reserves indicates an average of 65.3 million visitor days per year[31]. These figures total 118.6 million visitor days per year (including both foreign and domestic visitors).

In addition, some 65% of "nature tourists" were found to be motivated by to Tier- und Pflanzenwelt erleben ("experience the flora and fauna").[32]

Naturtourismus in Deutschland 2016 also allows for the estimation of visitor spending in National Parks and Biosphere Reserves, indicating a total spend of €5.7 billion or an average of €48.3 per visitor day in 2016 terms. Note however that no data could be collected in respect of Nature Parks, so these visitation figures will be lower bound nature tourism estimates.

Nonetheless, if combined with the "flora and fauna" motivation factor above (65%) and converted to dollars, this suggests that German WT accounts for 77 million visitor days and $5.3 billion in in-country spending per annum (in 2018 terms) before adjustment for inbound tourism costs.

Combined with data on the total number of German visitor days, both foreign and domestic, (4.1 billion in 2016) this in turn allows for an estimation of the proportion of wildlife tourism in relation to all visitor days (1.9%).[33]

This estimate excludes Nature Parks but includes both flora and fauna motivated tourism. These two effects may cancel each other out to some extent. However, it should be noted that, relative to total visits, the figure may still be at the lower bound, given that total visits include a large number of day trips for various purposes (e.g. shopping). Nonetheless, these estimates are remarkably similar to those obtained for UK WT using different sources, with both suggesting that WT accounts for around 2% of total visits or visitor days in each country.


Black Forest, Germany

CHINA

With their unique natural landscapes and rich flora and fauna, Chinese nature reserves are the most popular areas in China for WT activities[34]. China has 120 PAs, including 16% of its terrestrial land and 5% of its marine areas.[35] These PAs include National Forest Parks, National Key Scenic Resorts, National Natural Reserves, National Geoparks, National Wetland Parks, National Mining Parks, and National Water Reserve Parks. China's national parks have developed rapidly over the past few decades in response to a burgeoning population with an increased disposable income, vacation time, and personal transportation. The country's nature reserves include World Heritage Site status locations: Yellow Mountain (Huangshan), Shennongjia and Jiuzhaigou; which are protected by stringent conservation management regimes.

The Yunnan Province, bordering the Tibetan Himalayan ranges, is home to the greatest number of plant species in China, has 55% of China's vertebrates and roughly 200 endangered and/or rare species including: the Asian elephant, Asian leopard, Yunnan golden monkey, gibbons, wild ox, hornbills and other birds. Yunnan has networks of over 20 reserves, with seven of these classified as Level A nature reserves under the Chinese conservation system in terms of national importance, due to their outstanding natural features and biodiversity[36].

Historically, it has been difficult for China to attract large numbers of international wildlife tourists in the current context due to limited infrastructure in rural areas (where prime ecotourism destinations are located), visa restrictions, and in some cases, the poor condition of the necessary human and organisational resources[37]. Since the first National Forest Park was established in China in 1982 (Zhangjiajie National Forest Park) various types of parks have been established, and their numbers have increased rapidly. Today, there are 1,865 areas classified as National Parks based on the IUCN Guidelines for Protected Area Management Categories[38].

WT and, by extension, ecotourism in China is as much about cultural heritage, as it is about conservation, and indeed culture and nature are not seen as distinct concepts[39]. Wen and Xue (2008) acknowledge the differences in ecological values between Eastern and Western cultures. Western concepts of ecotourism view it as an experience, occurring in the present moment within the natural environment[40]. The Chinese view such tourism as an experience of the unification between nature and humanity and the opportunity to connect one's present with the past. This view is influenced by the evolving notions of Confucianism, Buddhism and Taoism.

WT and ecotourism in Chinese nature reserves enjoy an elevated status because of their role in funding conservation efforts and scientific research, protecting ecosystems, benefiting rural communities, promoting development in rural regions, and enhancing ecological and cultural awareness by educating the visitors. Liu, Wang, Qian, Qin, and Jiang (2009) analysed the data collected from a survey of the status of management in Chinese nature reserves, finding that 75% of nature reserves had ecotourism operations, 23% did ecotourism development planning or tried to operate small-scale ecotourism, and only 2% of nature reserves did not implement any ecotourism[41].

Although the intention of National Park systems in China is to raise environmental quality, and to protect biodiversity and social livelihoods, their success has varied. Future success will be measured by their capacity to reduce poverty, to promote long-term rehabilitation of wildlife habitats, and to simultaneously protect Chinese culture and biodiversity. The lack of attention to environmental elements means that parks often fall short of meeting the criteria of sustainability, as defined by the UN General Assembly and conservation bodies[42]. Unsurprisingly, the vast majority of PAs are governed by national-level ministries or agencies. The Government of China, having realised the importance of sustaining and protecting its environment and natural resources, has accepted the basic concept that tourism, and particularly ecotourism, can help preserve the integrity of natural systems while providing economic opportunities[43]. This is an important first step and a positive sign for the near future, since - if this intent is indeed genuine - China's authoritarian regime has a track-record of swiftly rolling-out environmental restoration initiatives (as seen in the unprecedented rise of its renewable energy development).

INDIA

From the mountains of the Himalayas to the seacoasts of Kanyakumari and from the Thar deserts of Rajasthan to the humid forests of the northeast; India is one of the 12-mega bio-diverse countries of the world and has a rich cultural heritage. The country has roughly 7% of the mammals, 12.6% birds, 62% reptiles, 4.4% amphibians, 11.7% fishes and 6% plants of the world[44]. In many PAs, tourist surveys report that a primary purpose is to view tigers[45].

Renowned biodiversity features including the Western Ghats and Eastern Himalayas. Great variation in climatic condition has given appearance to variety of forest types including tropical and sub-tropical forests in these regions, temperate and alpine forests in central and western Himalayan and desert forests in the arid and semi-arid regions. According to Forest Survey of India (2017), about 7,08,273 km, constituting 21.5% of its geographical area is under forest cover in the country[46]. In total, India has 672 PAs, covering 6% of its terrestrial area[47].

As a part of the updating and cross-checking of Balmford et al.'s work, conducted for this study, data was collected for 20 of India's PAs, with considerable dispersion across the country. A sample of annual visitors per day for select PAs included: Kanha with 101,533 visitors, Mudumalai with 124,322, Satpura with 162,785, and Periyar with 490,866 visitors.

The northern part of India is famous for its hills, plains, rivers, and monuments, including the Himalayas, the Ganges. The Indian Ocean, Arabian Sea and the Bay of Bengal offer a very large coastline. The Sundarbans is the largest single block of tidal halophytic mangrove forest in the world. It has an area of -10,000 km2 of which 40% is in India and is a UNESCO World Heritage site. The Sundarban National Park is a national park, tiger reserve, and a biosphere reserve located in the Sundarbans delta in the Indian state of West Bengal[48].

In India, tourism is one of the largest net foreign exchange earners and the largest service industry, with a direct GDP contribution of 3.6% according to WTTC data. In terms of legislative support, the national ecotourism policy and guidelines aim to preserve, retain and enrich natural resources and to ensure regulated growth of ecotourism with its positive impacts on environmental protection and community development. Most PAs are governed by sub-national ministries or agencies.

WT and ecotourism have rapidly grown in India as people become more conscious of the environmental hazards and the importance of the existence of diverse flora and fauna. Despite this, there remains vast potential for higher growth in the future, coupled with the need to focus on nature conservation and extending economic benefits to the local communities.

Huangshan Moutains, China

Thar Desert of Rajathan, India

KENYA

Kenya has a rich abundance of wildlife that thrives in habitats stretching from the Indian Ocean to forested ecosystems, vast savannah woodlands, mountain peaks, and to the bottom of the Great Rift Valley. The country has 411 PAs, covering 12% of its terrestrial area and 1% of its marine area. A large share of the governance types for these areas are unreported, followed by 19% federal governance[49]. A widespread PA system is in place with over 10% of its land area currently gazetted as national parks, national reserves or forest reserves: the system to date is comprised of 23 national parks, 28 national reserves, 4 marine national parks, 5 marine national reserves and 4 national sanctuaries[50]. Based on social media data of geotagged ecotourist photos, Willemen et al. (2015) find that Kenyan Reserves, Samburu National Reserve and Mukogodo Forest Reserve, are among the top wildlife tourist attractions in Africa[51].

WT has grown in Kenya over the past several decades, with early initiatives influenced by policy changes that saw the creation of national parks and reserves and banning hunting. Taking a historical perspective, in the 1980s, the WT industry boomed, relatively speaking, with increased lodge capacity and size to cater for increasing visitor numbers. Since then, however, funding for WT related infrastructure has significantly reduced[52]. Past estimates indicate that WT accounted for about 70% of tourism earnings and more than 10% of total formal sector employment in the country[53]. Despite the growth of both private reserves and beach tourism, the heart of Kenya's WT and ecotourism industry remains its national parks and reserves and their surrounding buffer zones.

Kenya has led some of Africa's earliest experiments in community-based conservation using park and tourism revenues and began the first efforts to systematically adopt a set of principles and practices in its national park system. The private sector has also been key to the development of WT and ecotourism in Kenya. Today, roughly 75% of ecotourism ventures are public-private partnerships[54]. Yet in regulatory terms, the Wildlife Conservation and Management Act still recognises the state as the sole regulator of matters related to wildlife, a position perceived as restrictive and insensitive to the realities of wildlife conservation, particularly the potential role of local people. In order to address this gap, the Kenya Wildlife Service (KWS) was created through subsidiary legislation that allows private people to participate in wildlife conservation and WT subject to compliance with legislative requirements[55].

As its human and livestock population grows, the sustainable development and management of its nationally-vital wildlife resources and of its robust safari tourism sector remains a major concern[56]. The country is experiencing an accelerated decline of its wildlife population[57].

Masai Mara National Reserve, Kenya

SOUTH AFRICA

South Africa has 1,544 protected areas, covering 8% of its terrestrial land and 12% of its marine area. The majority of protected areas are governed by individual landowners, which is atypical compared with the other national case studies that are primarily government run[58]. Kruger National Park in South Africa is in a league of its own because of its diversity of animals as well as advanced environmental management techniques and policies. It is one of the largest parks in Africa covering ~20,000 km2. It is well-managed and maintains large and relatively stable animal populations. Grünewald et al. (2016) find that most park visitors are locals, with 79% being South African[59].

Visitors spend large proportions of their viewing time on predators such as lions, leopards and cheetahs. Addo Elephant National Park in the Eastern Cape province is the only park where the Big Seven can be viewed, including: the African elephant, Cape buffalo, African lion, African leopard, African rhino as well as whales and Great White sharks. Across the country's PAs, Lindsey at al. (2009) find that mega-herbivores and large carnivores are most popular, particularly among first-time and overseas visitors. Despite this, African visitors and experienced wildlife viewers tend to be more interested in bird and plant diversity, scenery, and rarer, less easily-observed and/or less high-profile mammals[60].

As a part of the updating and cross-checking of Balmford et al.'s work conducted for this study, visitor statistics were collected for 19 South African protected areas. Kruger National Park was top-ranking in terms of visitation with approximately 1.5 million visitors annually as at 2007. Cape Peninsula National Park also saw an average of 1,462,649 visitors per year from 2002 to 2006[61]. Meanwhile, iSimangaliso Wetland Park was the first site in South Africa to be awarded World Heritage status. It contains most of South Africa's remaining swamp forests and is Africa's largest estuarine system.

A wide range of past studies have focused on South Africa as a primary case study for WT trends. Conducting surveys of South African wildlife tourists, Boshoff et al. (2007) found that 23% of respondents visited South Africa's national parks 'frequently', compared with 13% to its provincial parks and reserves and 4.5% to its private reserves[62]. Social media studies, such as Willemen et al. (2015), show that Addo Elephant National Park in South Africa is among the African PAs with the highest potential to attract wildlife tourists based on attractive species occurrence[63]. Overall, the sustainability implications of South Africa's WT growth appear to be positive. For instance, the proliferation of private WT destinations (e.g. private game reserves) has contributed to the large-scale conversion of previous agricultural land to conservation land use[64].

TANZANIA

Tanzania is endowed with a rich storehouse of nature-based tourist attractions. Tourism is focused primarily around its renowned attractions in the great plains of the Serengeti, the wildlife spectacle of the Ngorongoro Crater, Mount Kilimanjaro as well as the island of Zanzibar with its lush tropical beaches[65]. The Serengeti National Park is one of the best places to see the Serengeti wildebeest migration, while Africa's highest mountain - Mount Kilimanjaro lies in Tanzania's Kilimanjaro National Park[66]. The most popular PAs in Tanzania include the Ngorongoro Crater with roughly 40% of visitors to PAs in Tanzania, followed by Serengeti National Park at 25%, Tarangire with 11.2%, and Arusha with roughly 10.8%[67].

Tanzania has a great variety of PAs with immense biodiversity, including national parks, game reserves, marine parks and forest reserves. As at 2017, this includes 16 national parks, 28 game reserves, 44 game-controlled areas and 38 wildlife management areas. These areas range from marine habitats to grassland and mountain terrains. Indeed, approximately one third of Tanzanian territory is protected[68]. Protected wildlife areas in Tanzania span 246,260 km², covering 26.6% of the country's total land area[69]. According to the World Bank (2018), Tanzania has roughly 1.9 million ecotourism visitors per year[70]. Tanzania's 840 PAs cover an uncommonly large proportion of its terrestrial area at 38%, with 3% marine area coverage. Almost all PAs are governed by federal ministries or agencies[71].

Overall, tourism in Tanzania continues to grow. Roughly 46% of international tourists experience a wildlife activity, compared to 26% with a beach holiday component and 11% undertaking hunting and fishing[72]. Entrance fees to PAs, are much greater for tourists than locals. For instance, from 2015 to 2017 game reserve entrance costs averaged US$41 for international tourist adults versus US$3.35 for Tanzanian citizen adults[73]. While a cost to foreigners, this is good news for tourism revenues. WTTC estimates indicate that the tourism sector contributed 11.7% to Tanzania's GDP, with 2.3 million people supported in the sector's employment. Currently, Tanzania's national parks are working towards International Standards Organisation (ISO) certification for service excellence in tourism[74].


Andaman Sea, Thailand

THAILAND

Thailand's PAs are highly dispersed across the country, covering a range of habitats from upper and lower montane rain forests or cloud forest in the north and parts of the northeast to dry dipterocarp forests, and from seashore and mangrove to islands or archipelago in the Gulf of Thailand and Andaman Sea. Khao Yai National Park, an ASEAN heritage site for example, is dominant in its different ecosystem types and home to many species of wildlife and plant to be considered under endangered, rare or endemic status[75].

Spectacular mountain views of Doi Suthep, Doi Pui National Park in northern Thailand and Dong Phayayan Khao-Yai Forest are examples of long-standing, popular destinations. Due to these abundant natural and cultural resources and an already-booming wider tourism market, the WT and broader ecotourism potential of Thailand is high in terms of attracting both Thai and foreign tourists. Thailand's investment in tourism infrastructure to support and enhance its reputation as a premier tourism destination benefit its fledgling WT and ecotourism industries.

Increasing trends in WT activity in Thailand have been further spurred on by environmental challenges. Indeed, between 1961 and 1991, Thailand lost some 50% of its remaining forest cover due to anthropocentric factors. As such, a main aim of the Thai government in the past decade has been to protect the remaining natural forests by establishing a PA system. Comprised mainly of national parks and wildlife sanctuaries, PAs now cover roughly 15% of the country[76]. Thailand's PA system was originally established in 1962 with Khao Yai designated as its first national park. The National Ecotourism Development Policy of 1998 supports pilot projects of village-based ecotourism to support sustainable livelihoods.

Today, Thailand's PAs are distributed widely across the country and are comprised of roughly 14% national parks, 7% wildlife sanctuaries and another 1% non-hunting areas and forest parks; all as a proportion of total land area[77]. Thailand has 238 PAs in total, covering 19% of the country's terrestrial area and 2% of marine areas. This includes 120 national parks (3 that are ASEAN Heritage), 24 marine national parks, 58 wildlife sanctuaries and 13 non-hunting areas[78]. The vast majority of protected areas are governed by federal ministries or agencies.

Both WT and broader ecotourism in Thailand has become focused on promoting tourism at the community or village level, with wider objectives of reducing rural poverty, and sustaining resources use in conservation areas[79]. The Thai Government sees such community-based tourism as raising the income of rural people, whilst conserving their culture and the environment[80]. Thailand offers a wide range of treks to experience hill tribe villages, elephants, rafting and kayaking, among others. Roughly 70% of Thai domestic tourists and 30% of foreign tourists engage in ecology-related activities during their travel[81]. Yet despite Thailand's growing WT and ecotourism activity, standards remain low with many small operators being weak in promotion and marketing.

UNITED KINGDOM

WT in the UK has a long and rich tradition, with key attractions including the Peak and Lakes Districts, Dartmoor National Park and the Scottish Highlands. Birdwatching – including fewer common species such as eagles and puffins - is ever popular, along with an interest in observing deer, red squirrels, badgers and mountain hares.

WT is of particular interest to the Scottish economy, where past estimates suggest that it accounted for 1.12 million annual trips and £276 million in gross expenditure in 2009. WT accounted for 5.2% of all domestic tourism trips to Scotland in that year[82].

Excellent WT data also exist for Great Britain sourced through past surveys of domestic overnight (The GB Tourist) and day tourism (The GB Day Tourist)[83]. These both record the numbers of trips involving "wildlife watching/ birds watching" as well as the days spent, and spending involved in such trips.

While the best disaggregated data appear to date from 2015, these allow for a good estimation of the relative extent of British WT (about 3% of overnight domestic trips and 1.9% of tourism day trips).

A further valuable source is VisitBritain's Valuing Activities: Final Report[84]. This allows for the apportionment of total expenditure of trips involving WT to specific WT activities (15% in the case of domestic overnight holiday trips and 42% in the case of domestic tourism day visits). Accordingly, these figures were used to determine the actual spend on WT.

The resulting figures for Great Britain were then uplifted to account for Northern Ireland (and so develop a UK figure).

An indication of the extent to which overseas visitation to England is motivated due to WT can be found in work by VisitEngland where 7% of overseas leisure travellers indicated they had undertaken such activities during their last trip to England[85]. Foreign WT spend figures were derived by apportioning average overseas traveller spend to WT (derived from Oxford Economics Global Travel Service Databank) using the domestic UK overnight holiday figures noted above (15%). All foreign and domestic WT figures were then adjusted to 2018 values. These figures suggest that 2.1% of UK foreign and domestic trips involve WT to some degree, with domestic spend per person per trip of $70.27 and total in-country spend of $2.4 billion (before adjustment for an inbound travel component).


Peak District, England

UNITED STATES

The United States has a longstanding tradition of enjoying life in 'the great outdoors" with Americans enjoying access to a rich diversity of landscapes and environments spread over a large landmass.

Combined with a large domestic population and strong foreign visitation this makes the country one of the key international markets for WT.

Visitation data reflect these facts. Data for US National Parks record 330.9 million visits in 2017, compared to 275.6 million in 2007[86]. Of course, as indicated, not all of these visits are necessarily related to WT nor is all WT conducted in National Parks. However, with the help of the National Survey of Fishing, Hunting and Wildlife Associated Recreation[87], conducted every 5 years (the latest data being for 2016), the US has excellent WT data.

These data provide a set of accounts for both "stay at home" wildlife watchers and those who venture away from home (i.e. make trips of over 1 mile). It is the latter group that are of most interest for this report. These data indicated that such American domestic wildlife tourists made 258 million trips, accounting for 386 million visitor days, with direct travel spending of at least $11.6 billion on wildlife tourism trips away from home in 2016. Details on auxiliary equipment, day packs, special clothing and other wildlife watching equipment costs provided in the same report were added to this to arrive at a total WT spend of some $16 billion in 2016 dollars[88].

Given 2.3 billion domestic person trips in 2016, these figures suggest that 11.3% of US domestic trips may relate to WT. However, this is likely to be an overestimate, given differences between these two data sources[89].

The National Survey data also indicate that the great majority (79%) of American domestic WT away from home takes place in public lands, with smaller proportions (10%) taking place only in private lands.

While less detail is available on details on international visitation, 2016 survey work indicates that 4% of international leisure visitors indicated that "Environmental/Eco. Excursions" was a motivator for their trip[90].

While ecotourism may not be synonymous with WT, the relatively modest figures involved means this can serve as a useful proxy for foreign WT to the United States. Combining these figures indicates that the value of United States WT was some $21.3 billion in 2016. This figure was adjusted to 2018 terms to arrive at a domestic WT spend figure of $22.1 billion for this report. This figure was then adjusted to allow for inbound transportation costs.

01

APPENDIX

BUENOS AIRES DECLARATION

In 2018 at the WTTC Global Summit in Buenos Aires, over 40 WTTC Member CEOs made a commitment to helping to eradicate the scourge of wildlife trafficking in the world.

To date, over 110 WTTC Members and leaders from the wider global Travel & Tourism sector have signed a declaration on illegal wildlife trade (IWT). WTTC and the signatories will work together towards a common goal of changing behaviour of 1 billion travellers as it relates to illegal wildlife trade.

Signatories to date include:

- Abercrombie & Kent
- Adventure Travel Trade Association (ATTA)
- AECO - Association of Arctic Expedition Cruise Operators
- African Parks
- African Travel & Tourism Association (Atta)
- Airbnb
- AITO - Association of Independent Tour Operators
- All for Nature B.V
- Amadeus
- American Express
- American Express Global Business Travel
- American International Group, Inc.
- ANVR - Dutch Association of Travel Agents and Tour Operators
- Associação Onçafari
- Beautiful Destinations
- Beijing Tourism Group
- Best Day Travel Group
- Botswana Tourism Organisation
- Brazilian Luxury Travel Association
- Caiman Ecological Refuge
- Cayuga Collection of Sustainable Luxury Hotels and Lodges
- City Sightseeing
- Cox & Kings
- Cristalino Lodge
- Ctrip
- Dallas Fort Worth International Airport
- Destinations International
- DMK Lawyers
- Dufry
- Dusit International
- Emaar Hospitality Group
- Emirates Group
- Etihad
- eTurbo News
- Europamundo Vacaciones
- Eurotur
- EXO Travel
- Expedia
- Global Exchange Group
- Global Rescue LLC
- Global Sustainable Tourism Council (GSTC)
- Google Inc.
- Grupo Posa
- Grupo Puntacana
- Grupo Security
- Hilton
- HNA
- Hogg Robinson Group
- Hostelling International USA
- Hyatt Hotels Corporation
- IC Bellagio
- International National Trusts Organisation
- Intrepid Group
- JLL
- Journey Mexico
- JTB
- Just a Drop
- Ladevi
- Mandarin Oriental
- Marival Group
- Marriott
- Minor Hotels
- Mystic Invest
- National Geographic Partners
- NYC & Company
- Ol Pejeta Conservancy
- OTI Holding
- Panorama Group
- PATA
- Pride Media
- Rajah Travel Corporation
- Ras Al Khaimah Tourism Development Authority
- RENCTAS
- Riverwind Foundation
- Royal Caribbean Cruises Ltd.
- SEE Turtles
- Silversea Cruises
- SOS Pantanal Institute
- South American Tours
- Swain Destinations
- Tale2tail
- Tauck Inc
- The Long Run
- The Nature Conservancy
- The Travel Corporation
- Thomas Cook
- Thompson Okanagan Tourism Region
- TOFTigers Initiative
- Tony Charters and Associates
- Tourism Industry Aotearoa
- TourismCares
- Travel + Leisure
- Travel Weekly US
- Travesías Media
- TripAdvisor
- TTG Asia
- TUI Group
- Turismo de Sevilla
- UNWTO
- V&A Waterfront
- Value Retail Plc
- Via Venture - Discover Guatemala
- Virtuoso
- Visit California
- Volcanoes Safaris
- WAZA
- WESGRO
- Wildlife Tourism Australia
- WWF
- WYSE Travel Confederation
- Yunnan Mekong Group

02

APPENDIX

DETAILED METHODOLOGY

Definitional issues

In estimating the scale of global WT, a first step is to have a working definition of such tourism. As noted, definitions of WT vary (and data does not always precisely match varying definitions). There is also the confounding factor of pinning down the importance of different attributes (including wildlife) in assessing visitor motivation.

However, in essence, this study defines WT as tourism in which wildlife watching experiences and/or interactions are an important motivator. It therefore excludes settings such as zoos (or zoo-like parks), circuses or theme parks involving animal performances. The definition also excludes consumptive wildlife tourism such as hunting and fishing. In other words, it is restricted to what is sometimes known as "non-consumptive" WT involving watching and experiencing with wildlife in its own natural habitat.

Past work

A way forward to developing an estimation of wildlife tourism may be found in the work of Balmford et al. (2015)[91]. This extensive study sought to provide estimates of global visitation and spend in defined Protected Areas (PAs). In essence, PAs, as defined by the International Union for the Conservation of Nature (IUCN), are defined geographical spaces, recognised, dedicated and managed to achieve nature conservation[92]. PAs typically encompass national parks and other designated wilderness spaces. More formally, PA's are grouped into several governance types, as indicated in the "Protected Areas" box in chapter 2 of this report[93].

Balmford et al. estimated PA-related visitation and visitor spend estimates at the continental (Asia/Australasia, Africa, Europe, North America, Latin America) and global levels. The analysis was extrapolated from 2,663 records of visits to 556 PAs downloaded from the Global Database of Protected Areas (GDPA). However, Category 1, Antarctic and marine sites were excluded from the analysis.

Given the nature of PAs and their close association with complex ecosystems, wildlife, and accordingly WT (especially in Africa, Asia and Latin America) this work provides valuable insights into the order of magnitude of such visitation and expenditure.

Caveats

While the work presented in Balmford et al. is useful as a road map to estimating the magnitude of global WT, there are several caveats associated with using it as an aid to determine the global magnitude of WT. These are listed in brief below:

- PA tourism vs wildlife tourism – Balmford et al.'s work refers to PAs. Not all PA tourism is necessarily related to WT, although WT is likely to be a key component or motivator of such travel in many cases.

- PA visitation in North America and Europe vs other continents - In the case of North America and Europe, the use of PA visitation as a guide to WT may be quite misleading due to the broad scope of such areas and their accessibility for a variety of recreational purposes.[94] Conversely PAs in South America, Asia and Africa would generally appear to be in less accessible areas requiring more deliberate purpose to enter[95]. This distinction has been supported by more recent work, focussed specifically on WT which suggests that PAs in North America and Europe are significantly less likely to be selected as WT destinations then those in Africa, Asia and Latin America[96]. While this means that Balmford et al.'s work is a very useful indicator of WT outside of North America and Europe, independent work is required to assess WT's magnitude in those two continents.

- Time period – The time period referred to relates to the average of PA visitation during the period 1998-2007 but global tourism has developed considerably since that time.

- Direct vs total values – Balmford et al.'s work refers only to the direct value of tourism spending without estimating GDP, indirect (multiplier) or employment effects.

- Other sources - There may be more up-to date or useful data on PA and/or wildlife or related tourism in non-English language publications. This could shed further light on the nature of such tourism. However, a further challenge in using such sources is that these may be difficult to access and/or use varying definitions as indicated above.

With the caveats above in mind, this study has proceeded along the following lines in estimating the value of WT.

GEOGRAPHIC AREA EXPENDITURE ESTIMATES

North America and Europe vs other continents

As indicated, a key initial issue in undertaking the work was to distinguish between WT in North America and Europe and the other continents (Latin America, Asia and Asia-Pacific). For this reason a dual bottom-up/top down analysis was undertaken for this study, namely:

- North America and Europe - "Bottom up" data sources from the US, Canada, the UK and Germany were used to determine visitation and spend figures.
- Africa, Asia-Pacific and Latin America- In the case of these continents, the approach was essentially "top down", using the PA visitation estimates of Balmford et al. as a base. However, significant modifications were made for tourism growth, a WT "filter", inflation and the use of supplementary estimates in some cases.

This approach yielded estimates for the various continents. Results for the bottom up and top down analysis were then combined to produce a global spend total[97].

Arches National Park, Utah

North America and Europe

Excellent data for the United States, directly reporting WT visitation and tourism spend can be found in the US Fish and Wildlife Service's, National Survey of Fishing, Hunting and Wildlife Associated Recreation[98]. The data of interest relate to "away from home" wildlife watchers- i.e. both day and overnight trips away from the immediate vicinity of the home residence (over 1 mile). These data allow for the separation of WT from other forms of PA or natural area visitation.

Data on foreign visitation to the US associated with WT can also be inferred from US National Travel & Tourism data which lists the proportion of visitors (4% of leisure travellers in 2016) who indicated that "Environmental/Eco. Excursions" was a motivator for their trip[99].

Canadian domestic travel data on WT can also be determined from past work on domestic travel motivations (which imply that around 5% of Canadian domestic leisure trips involve WT) and recent travel survey data[100]. Detailed data from British Colombia (BC) on the proportion of foreign (US) visitation motivated by WT were used to determine the proportion of foreign visitation to Canada driven by WT[101].

Estimates were updated to 2018 values through the use of relevant US and Canadian CPI data. The combined data sets suggested a visitation of 276 million trips per year with an in-country spend per trip of $89 for North America.

European WT visitation and spend estimates were based on data from both the UK and Germany.

Good data on UK domestic WT can be found in past UK overnight domestic and tourism day visit data (i.e. non-regular day trips away from a home locality and lasting 3 hours or more) as reported in Visit Britain's The GB Tourist and The GB Day Visitor. This data records trip and spend figures for trips involving "wildlife watching/bird watching". The most recent disaggregations relating to such data appear to relate to 2015[102].

Additional UK work allowed for the allocation of specific WT spend from general expenditure in domestic overnight and day trips involving WT[103]. Other studies report the proportion of foreign leisure visitors engaging in UK WT[104]. Foreign visitor spend on UK trips involving WT was then derived by combining this proportion with foreign spend per overnight trip (from the Oxford Economics Global Travel Service Databank). The resulting amount was then allocated to WT specific activities according to the domestic overnight visitor spending allocation used for domestic UK tourists above.

In the case of Germany, detailed German nature tourism recreational data are reported in the German language publication Naturtourismus in Deutschland 2016. Data on the number of visitor days and spend per day in German National Parks and UNESCO Biosphere Reserves are reported in this publication. In addition, this study also provides survey data on the proportion of "nature tourists" who are specifically motivated to undertake such tourism due to Tier- und Pflanzenwelt erleben ("experience the flora and fauna"). Some 65% of nature tourists indicated that they were motivated by such an interest in experiencing flora and fauna and this can be seen as roughly analogous to the proportion of such tourists who could be seen as wildlife tourists[105].

Multiplying the visitor days and visitor spend by the proportion of flora and fauna visitors provides an estimate for WT in Germany. This includes both foreign and domestic tourists, as no distinction is made between the two in the estimation of National Parks and Biosphere Reserve visitor numbers.

A cross-check of both the UK and German results indicated that the proportion of WT relative to total UK and German foreign and domestic tourism is remarkably similar, being roughly 2% in both cases[106].

The results of the UK and German work were then combined and extrapolated to a Europe-wide figure for 2018, adjusting for inflation and differences in purchasing power[107].

Finally, spend data for both North America and Europe were then converted to WT GDP and employment estimates for both continents. This was done by deriving tourism GDP/expenditure and tourism employment/expenditure ratios for North America and Europe from Oxford Economics Global Travel Service Databank. Allowance was also made for inbound travel costs in the case of foreign tourists, again using data in the Oxford Economics Global Travel Service Databank.

This process produced the spend figures indicated in the figure below. All expenditure and GDP figures are in 2018 dollars.

Swantis, Schwende District, Switzerland

Fig. 3. Direct expenditure, GDP and employment estimates for North America and Europe, 2018

CONTINENT	EXPENDITURE ($BILLION)	GDP ($BILLION)	EMPLOYMENT (MILLION)
NORTH AMERICA	25.4	13.5	0.2
EUROPE	28.5	13.3	0.2

Source: Oxford Economics

All tourism also has "multiplier" effects – as direct tourism expenditure causes further rounds of spending through spending impacts on supply chains and tourism and supply chain worker purchases, along with additional impacts on investment and government spending.

The combination of direct and multiplier effects allows for the estimation of total tourism impacts.

Oxford Economics Global Travel Service Databank also allows for the estimation of such multiplier effects for North America and Europe (as well as the other continents). This data was used to derive total GDP and employment impacts for WT for both of these geographies.

Total WT contribution figures for North America and Europe are presented in the figure below.

Whale Watching, Glacier Bay landscape, Alaska

Fig. 4. Total WT GDP and employment estimates for North America and Europe, 2018

CONTINENT	GDP ($BILLION)	EMPLOYMENT (MILLION)
NORTH AMERICA	37.6	0.5
EUROPE	35.4	0.6

Source: Oxford Economics

Other continents (Africa, Asia-Pacific, Latin America)

The approach for Africa, Asia/Australasia and Latin America was based on Balmford et al.'s dataset for PAs. However, this was extensively modified to allow for the following factors:

- A wildlife "filter" to distinguish between PA visitation and dedicated WT.
- Tourism growth factor to allow for the growth since the end of the dataset examined by Balmford et al. (i.e. since 2007).
- A review of the author's PA visit spend per day figures including allowance for more conservative Latin American figures and inflation.

Los Glaciares National Park, Argentina

Wildlife filter

In terms of the first of these factors, as indicated it can be difficult to distinguish WT from other forms of general or closely related tourism (e.g. nature tourism) both for definitional reasons and due to the mix of motivations people have in undertaking a trip. The North American and European work was based on data sources which allowed for the direct estimation of WT. While WT is strongly associated with PA visitation, there may be other and/or intermingled reasons for such PA visits.

Accordingly, a variety of sources were consulted to determine what proportion of PA tourism might be associated with WT:

- German data, cited above, indicates that some 65% of those undertaking "nature tourism" are motivated by a desire to experience flora and fauna[108].
- Data from Indian tiger reserve visitors indicates that only 34% would visit these PAs if tigers were not present (or conversely 66% can be said to be primarily motivated to visit by the presence of wildlife – i.e. tigers)[109].
- Brazilian data suggests that 65% of domestic Brazilian visits to PAs are motivated by contemplacao ou contato com a natureaza ("contemplation or contact with nature")[110].
- Analysis of Instagram and Flickr images taken at Kruger National Park suggests that roughly between 38% (Instagram) and 77% (Flickr) of images relate to "biodiversity (i.e. wildlife) , with other themes being landscapes, human activity, posing, food and accommodation. Excluding "derivative" attributes such as food, accommodation and posing (which are essentially a by-product of the visit rather than likely to be a key motivator) further analysis of these data suggests a weighted average of 61% of images include wildlife (though some will include other attractors in this context such as landscapes)[111].

Taken together, these data are remarkably consistent and suggest that the proportion of PA visitors for whom WT is a strong motivation may be in the 60-65% range. Erring on conservative side, a wildlife filter of 60% of PA visits being motivated by wildlife viewing/experiences has been set for this report.

Tourism growth factor

As indicated, another issue with Balmford et al.'s overall approach is that its data relate to an average of PA visitation from 1998-2007. While this database is of great value for its uniquely global extent, global tourism has developed significantly in recent years particularly given the economic rise of emerging markets. Accordingly, there is a need to allow for tourism growth.

Although claims have been made over the years that WT has or is growing much faster than overall tourism, these claims may be dated, made for specific countries or at specific times and may not necessarily be true for geographical regions across the board.

Ideally a growth estimation could be made using an update of Balmford et al.'s original database. However, as the authors themselves noted, many of these data are "scattered and noisy".[112] In addition, their sources rely on a mix of secondary data as well as primary ones (e.g. personal communications) not all of which are replicable.

Two main approaches were therefore explored in developing growth rates to extrapolate visitation data from 2007 to 2018, namely:

- Method 1 - Growth was estimated using the change in international and domestic visitor nights in Asia-Pacific, Africa and South America recorded by Oxford Economics Global Travel Service Databank between 2007 and 2018[113].
- Method 2 – The data set in Balmford et al. was updated to the fullest extent possible by re-examining the author's sources, providing new historical estimates for the time period originally identified by the authors as well as updates for the period 2007-2018.

Both Methods were then applied to develop separate PA spend figures (allowing for a wildlife filter as described above and adjustments for visitor day spend and inflation described below). A comparison was then made between them. The difference between Method 1 and Method 2 was found to be in the order of 10% in term of overall expenditure estimates, with Method 2 producing the higher estimated spend. Method 1 was preferred due to its more conservative stance and its basis in a more consistent dataset at a continental scale. However, the relatively modest difference between the two Methods is notable. Notwithstanding this, it is acknowledged that individual National Parks and/or PA growth rates may have been high in recent years. For example a parallel review of selected English and foreign language publications for this study indicated:

- Visitation to Thai National Parks increased from 11.8 million in 2014 to 19.6 million in 2018 (66% growth)[114].
- The number of tourists visiting Indian Wildlife Reserves grew from 1.7 million in 2004-05 to 4.6 million in 2014-15 (171% growth)[115].
- Visitors to South African National Parks rose from 4.7 million in 2007-08 to 6.7 million in 2016-17 (43% growth)[116].

These high implied growth rates may in part be reflective of growing wealth and accompanying interest in WT in emerging markets.

However as noted, such data tend to be scattered and noisy covering varying contexts and years. Some data exist for PAs, others for sub-components such as National Parks or other attractants of wildlife tourism. There may be many other instances where visitation has been less marked and/or where National Park visitation growth has not been fully represented in PA visit growth. Accordingly, as indicated, a more broad-based (and potentially conservative) approach has been adopted, using continent-wide tourism overnight growth rates as indicated above.


Amboseli National Park, Kenya

Spend per day and inflation

In addition to these general adjustments, attention was also paid to the median spend per day data reported by Balmford et al. for the various geographies. The authors indicate that their visitor day expenditure data is related to the proportion of foreign visitors to PAs, with a relatively low proportion of foreign tourists in Asia/Australia (13%), higher in Latin America (20%) and highest in Africa (61%). Accordingly, their originally estimated daily visitor spend (in 2014 dollars) for these three continents is lowest in Asia/Australasia ($85 per day), higher in Latin America ($311 per day) and highest in Africa ($698 per day), with the high(er) access costs in these markets and the presence of high spending dedicated foreign visitors (e.g. overnight safari visitors) obviously acting to push day spend up.

UNWTO data also offer some support for Balmford et al.'s day spend figures for Africa and those for Asia to appear reasonable[117]. However, survey data for domestic Brazilian visitation to three selected PAs suggest relatively modest daily spend figures (roughly $43 per day in 2016)[118]. These data are limited to three PAs, exclude the costs of domestic transport to access the PAs (which could be substantial) and as in other parts of the world the starkly differing nature of the foreign visitor WT experience means that foreign tourist spending per day is likely to be considerably higher (e.g. $412 per night for lodge package tourists in the Pantanal)[119]. Nonetheless, De Cruz et al. also report similar figures to Souza and given the above-mentioned preponderance of domestic visitation to Latin American PAs, Balmford et al.'s spend figures for the region may be on the high side[120]. For this report, an alternative daily spend figure of $131 has been adopted. This figure is based on the weighted average spend per domestic and international visitor night for South America in 2018, sourced from the Oxford Economics Global Travel Service Databank.

This provides a figure for Latin American spend in 2018 terms. As Asian and African spends per day were assessed by Balmford et al. in 2014 dollars, allowance was made for inflation (5%) to adjust these figures to 2018 terms.

Adjusting the Balmford et al. data to allow for a wildlife filter, tourism growth and more conservative Latin American data archive produces the spend figures indicated in the figure below. As is the case with the North American and European figures described above, these figures were converted to direct and total GDP and employment figures using conversion ratios and multipliers derived from Oxford Economics Global Travel Service Databank. Allowance was also made for inbound travel costs in the case of foreign tourists, again using data in the Oxford Economics Global Travel Service Databank.

Fig. 5. Direct WT expenditure, GDP and employment estimates for Africa, Asia and Latin America

CONTINENT	EXPENDITURE ($BILLION)	GDP ($BILLION)	EMPLOYMENT (MILLION)
AFRICA	48.8	29.3	3.6
ASIA-PACIFIC	118.2	53.3	4.5
LATIN AMERICA	19.9	10.7	0.5

Source: Oxford Economics

Fig. 6. Total WT expenditure, GDP and employment estimates for Africa, Asia and Latin America

CONTINENT	GDP ($BILLION)	EMPLOYMENT (MILLION)
AFRICA	70.6	8.8
ASIA-PACIFIC	171.2	10.4
LATIN AMERICA	28.9	1.4

Source: Oxford Economics

NOTE ON DATA CONSISTENCY

It should be noted that data in this report have been drawn from a variety of sources. For example, as indicated in the discussion above, the direct expenditure estimates in this report have been derived from a variety of sources including inflation adjusted data in dollars (from Balmford et al's findings for Africa and Asia), the Oxford Economics Travel Service Database data (for Latin American spends) and primary data estimates (for Europe and North America). While care has been taken to harmonise estimates where possible, allowing for factors such as inflation and purchasing power in the case of foreign currencies, this should be noted in considering these results and comparisons to global and regional Travel & Tourism work and appropriate caution applied. However, this challenge is common in WT analysis and indeed was noted in Balmford et al.'s own work. That said, as indicated, reasonableness tests were applied to the estimates undertaken above and the estimates undertaken suggested consistency between primary data sources. For example, despite being derived from widely different sources, estimated North American in-country trip spends ($89 per trip) are of the same order of magnitude as estimates for the UK ($70 per trip) with German data suggesting $69 per day.

ENDNOTES

1 See appendix for signatories of the Buenos Aires Declaration

2 All figures 2018 US dollars unless otherwise indicated

3 World Travel & Tourism Council (2019) Travel & Tourism Economic Impact 2019 World. The WT estimates include both domestic spending and an allowance for estimated WT-related international inbound transport expenditure. While care has been taken to harmonise estimates where possible, it should be noted that as the WT data in this report are derived from a variety of sources some care must be taken in comparing to World Travel & Tourism Council (WTTC) Travel & Tourism estimates.

4 Due to lack of consistency with regard to collection of visitation figures and spending in wildlife areas, these figures can only provide an order of magnitude. Further development of both wildlife tourism and improved management of protected areas could allow for better accounting of value in future

5 Balmford et. al. op. cit.

6 https://www.weforum.org/agenda/2016/09/fighting-illegal-wildlife-and-forest-trade/

7 IATA (2018) Illegal Trade in Wildlife: Factsheet, Available: https://www.iata.org/pressroom/facts_figures/fact_sheets/Documents/fact-sheet-wildlife.pdf

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11 Oxford Martin Programme on the Illegal Wildlife Trade (2019) GPS-supported, Community-Based Forest Crime Prevention in the Brazilian Amazon, Available: http://www.illegalwildlifetrade.net/2018/11/22/gps-supported-community-based-forest-crime-prevention-in-the-brazilian-amazon/

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13 Balmford A, Green JMH, Anderson M, Beresford J, Huang C, Naidoo R, et al. (2015) "Walk on the Wild Side: Estimating the Global Magnitude of Visits to Protected Areas". PLoS Biol 13(2): e1002074. doi:10 1371/journal.pbio.100207

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15 See IUCN "Protected Area Categories" https://www.iucn.org/theme/protected-areas/about/protected-area-categories accessed 12 February 2019

16 World Travel & Tourism Council (2019), op. cit. The WT estimates include both domestic spending and an allowance for estimated WT-related international inbound transport expenditure. While care has been taken to harmonise estimates where possible, it should be noted that as the WT tourism data in this report are derived from a variety of sources some care must be taken in comparing to WTTC Travel & Tourism estimates.

17 All financial figures have been expressed in 2018 dollars, with any conversions from foreign currency in primary sources made using PPP exchange rates.

18 Agrawal, K., and Baranwal, H., "Environmental Sustainability of Ecotourism" in The International Journal's Research Journal of Economics & Business Studies, Vol. 1, No. 9 June-July 2012

19 Levin, N, Kark, S., Crandall, D. (2015) "Where have all the people gone? Enhancing global conservation using night lights and social media" Ecological Applications 25(8) 2015. One would of course expect to be WT to be smaller than PA tourism as indicated by this paper. If the 60% WT filter used for Asia, Africa and Latin America is applied to the 11% figure suggested by the authors then this produces a figure of 6.6%. Of course, while many Flickr images are taken during tourist trips many others may simply be taken during the course of everyday life.

20 Balmford et al. op. cit.

21 This comparison is offered as a broad indicator of the gulf between the benefits offered by WT and the costs of PA management only. Technically speaking, a more refined approach would allow for the combination of producer and consumer surplus against PA costs to develop a more formal WT cost-benefit analysis on an economic welfare basis. This study does not undertake a welfare economics approach and does not include such measures, though Gross Operating Surplus (GOS) Producer Surplus benefits alone are over five times PA management costs. Consumer Surplus benefits would be on top of this. It is also acknowledged that some WT takes place outside of PAs per se, the great majority of global WT takes place within such locations.

22 Newhouse, H. (2017) op. cit.; D'Cruze N, Machado FC, Matthews N, Balaskas M, Carder G, Richardson V, Vieto R (2017) "A review of wildlife ecotourism in Manaus, Brazil" Nature Conservation 22

23 Tortato et. al. (2017) op. cit.

24 Souza, T. V. S. B.; Simões, H. B.; (2018).Contribuições do Turismo em Unidades de Conservação Federais para a Economia Brasileira - Efeitos dos Gastos dos Visitantes em 2017

25 Brasil Ministério do Turismo (2010) Ecoturismo: orientações básicas, 2. ed. Note this was made clearly distinct from other activities such as repouso ou fuga da rutina (rest or escape from routine) which accounted for a further 23% , sport (4%), ecological learning (3%), studies and research (2%) or reporting and documentaries (2%) or other professional work (1%)

26 Ibid

27 Brasil Ministério do Turismo (2010) Perfil do turista de aventura e do ecoturista no Brasil

28 Brasil Ministério do Turismo (2010) op. cit; Brasil Ministério do Turismo (2018) Estudo da DemandaTurística Internacional Fichas Sínteses 2013-2017

29 Souza op. cit. (2016)

30 Tortato et. al. (2017) op. cit. Note this figure excludes restaurant meals, side trips, crafts purchases or other local services.

31 BTE Tourismus und Regionalberatung (2016) Naturtourismus in Deutschland 2016 Berlin; Bundesamt für Naturschutz (BfN) (Hrsg.) (2016) "Regionalwirtschaftliche Effekte durch Naturtourismus in deutschen Nationalparken" in BfN Skripten Nr. 431. Bonn; Merlin, C. & Kraus, F. (2016) "Wirtschaftliche Effekte des Tourismus in Biosphärenre servaten Deutschlands" in Natur und Landschaft (January 2016; 91. Jahrgang).

32 BTE Tourismus und Regionalberatung (2016) Naturtourismus in Deutschland 2016 Berlin The visitation and spend estimates exclude German Naturparks (Nature Parks) which may mean that these figures are an underestimate of total WT. However, note that the motivation figure includes both fauna and flora, so to the extent that some visitors are motivated primarily by flora, this might counterbalance this.

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94 While the authors noted that largely cultural PAs had been excluded from their study (e.g. the US National Historic sites, Memorials and Battlefields). 85% of Balmford et al.'s recorded global PA visits occurred in North America and Europe. It should be noted that despite the exclusions indicated, the most visited PA in their study was the Golden Gate National Recreation Area in urban San Francisco, which received 13.7 million visits per year. By contrast the Serengeti National Park in Tanzania recorded 148,000 visits per annum. See University of Cambridge "Worlds protected natural areas receive eight billion visits a year" https://www.cam.ac.uk/research/news/worlds-protected-natural-areas-receive-eight-billion-visits-a-year accessed 12 February 2019.
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97 In addition, an allowance was made for the inbound travel (or portion of inbound travel) associated with international WT was made using trip expenditure information sourced from the Oxford Economics Global Travel Service databank.
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99 US National Travel and Tourism Office, 2016 U.S. Travel and Tourism Statistics (Inbound):, Sector Profess Leisure (Vacation-net) Travel Profile: Arrivals to the US http://tinet.ita.doc.gov/outreachpages/download_data_table/2016%20Excel%20PDF%20LEISURE%20(vacation-net)%20final.pdf accessed 16 February 2019. It is acknowledged that this may be a high end indicator, given that these categories may not be precisely analogous to WT, however the relatively small number of international trips relative to US domestic ones and the small proportions involved means that any overestimation is likely to be small.
100 More specifically, combining data in Ontario Ministry of Tourism (2007) Travel Activities and Motivations of Canadian Residents and from Statistics Canada (2017) Travel Survey of the Residents of Canada, and allowing for some activity overlap in WT activities, implies that roughly 5% of overnight domestic overnight leisure trips (or 4.7% of all domestic overnight trips) involved WT. Data from Statistics Canada (2017) were used to extrapolate this to domestic day trips (defined as trips of 40km or more, one way).
101 Based on Tourism British Colombia (2009) Wildlife Viewing Product Overview. This reported that 5.5% of Canadian domestic leisure tourists and 13.9% of US leisure tourists were motivated to visit due to WT activities. The Canadian figure was similar to the 5% WT proportion of domestic leisure trips estimated above, which acts as a cross check to these figures. Accordingly the 13.9% figure was used to estimate the proportion of international tourists drawn to Canada due to WT. As for US international WT tourism data, these may be an upper end estimate, given the particular attractions of BC but the relatively small size of the international sector means this is unlikely to be a major factor.
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103 Visit Britain (2015) Valuing Activities: Final Report
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106 Or more specifically 2.1% of trips in the case of the UK and 1.9% of visitor days in the case of Germany.
107 Conversions to dollars were made at OECD PPP rates sourced from https://data.oecd.org/conversion/purchasing-power-parities-ppp.htm and adjusted for inflation to produce 2018 values. The combined UK and German spend was then weighted by differences in population and GDP per capita (sourced from the Oxford Economics Global Economics Databank) to derive values for Europe.
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117 UNWTO (2018) op. cit. suggests an average tour price of $US 433 per person per day plus $55 per person per day for out of pocket expenses (or $488 per person in total). These figures are still lower than Balmford et al.s suggested ones but the scope of the UNWTO study may not be as extensive. In addition, the report notes that the "luxury" end of the market had prices of up to $2,500 per day though it should be noted that Balmford et al.'s use of median values would damp down the effect of these extremes.
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Crocodile social environments dictated by male philopatry

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Original Article

Crocodile social environments dictated by male philopatry

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Examining the social behaviors of solitary species can be challenging due to the rarity in which interactions occur and the large and often inaccessible areas which these animals inhabit. As shared space-use is a prerequisite for the expression of social behaviors, we can gain insights into the social environments of solitary species by examining the degree of spatial overlap between individuals. Over a 10-year period, we examined how spatial overlap amongst 105 estuarine crocodiles *Crocodylus porosus* was influenced by season, sex, and movement tactic. We discovered that crocodiles displayed highly consistent spatial overlaps with conspecifics between months and across years. Furthermore, male crocodiles that exhibited a greater degree of site fidelity displayed more stable social environments, while females and males that were less site-attached had more dynamic social environments with spatial overlaps between conspecifics peaking during the mating season. Our results demonstrate how long-term tracking of multiple individuals within the same population can be used to quantify the spatial structure and social environment of cryptic and solitary species.

Key words: **acoustic telemetry, *Crocodylus porosus*, estuarine crocodile, home range, sociality.**

INTRODUCTION

Sociality in animals has typically been defined as the tendency for individuals to form and live within groups of conspecifics (Alexander 1974; Avilés and Harwood 2012). This definition reflects an early focus in animal behavior research towards understanding the evolution of complex social behaviors (e.g., cooperation, altruism, and reciprocity) among group-living species such as primates (Sussman et al. 2005; Silk 2009). However, all species regardless of their level of gregariousness must navigate an environment which includes conspecifics. In this "social environment", individuals must choose which conspecifics to interact with (and which to avoid) to maximize access to resources (Dammhahn and Kappeler 2009; Fichtel et al. 2018) and reproduce (Heap and Byrne 2013), while minimizing inherent risks such as predation (Carter et al. 2009), infanticide (Pusey and Packer 1994), disease transmission (Weber et al. 2013; Mejía-Salazar et al. 2017), and inbreeding (Gardner et al. 2013). As such, the social environment forms the foundations on which the social behaviors and complexity (i.e., social organization, social structure, mating, and care systems) of a species develop and evolve (Kappeler 2019). Field-based observations across a range of taxa have revealed the presence of social behaviors in species typically considered to be solitary. These behaviors include: 1) fitness benefits from familiarity with neighbors (Siracusa et al. 2021); 2) long term associations and group membership (Shine et al. 2005; Godfrey et al. 2014); 3) cryptic communities (Mourier et al. 2012); 4) kin-based associations (Clark et al. 2012; Schuttler et al. 2014); and 5) direct reciprocity (Elbroch et al. 2017). Together, these observations support the argument that species do not need to be group-living to be considered "social", and likewise solitary species should not necessarily be defined as "asocial" (Elbroch et al. 2017).

For many solitary species, examining how individuals of the same species interact in the wild can be challenging due to the rarity in which interactions occur (Elbroch and Quigley 2016) and the large and often inaccessible areas over which animals move and interact. Advances in animal tracking technology are providing new and relatively unbiased insights into animal movements, space-use, and spatial overlap that are increasingly being used to quantify the social behavior of wild animal populations (Jacoby et al. 2016; Mejía-Salazar et al. 2017). Here, an individual's movement decisions and how it overlaps in space with conspecifics forms the basis of their social environment (Bonnell et al. 2017; Strickland and Frère 2017). The composition, density, and stability of this social

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environment can directly influence the social decisions made by individuals (e.g., whether to interact with or avoid conspecifics), which further shapes the social structure of the population (Kurvers et al. 2014; Koski and Burkart 2015; Strickland et al. 2018). Consistency in spatial overlaps between conspecifics over extended periods (e.g., repeatability in dyadic spatial overlap) and a high degree of site fidelity are also known to be prerequisites for the development of social structure (Wolf et al. 2007). Indeed, as the proportion of home-range overlap between conspecifics increases, so does the observed association and interaction rates, with this pattern seen across a wide range of taxa (Frère et al. 2010; Mourier et al. 2012; Wakefield 2013; Best et al. 2014). Recent advances in tracking technology have increased our capacity to monitor space use amongst large cohorts of individuals simultaneously and across multiple years, resulting in an emerging body of literature integrating the spatial and social behaviors of populations (Strandburg-Peshkin et al. 2015; Spiegel et al. 2018; Peignier et al. 2019). From these studies, we are increasingly seeing the importance of understanding how the spatial structuring of populations varies through time (e.g., between seasons or across years), and according to individual phenotypes, to gain insights into animal sociality in a natural setting that are often not possible when relying solely on visual-based approaches (He et al. 2019; Albery et al. 2021).

The estuarine crocodile *Crocodylus porosus*, is the largest and most widely distributed extant crocodylian; found from the east coast of India, throughout Southeast Asia to northern Australia (Webb and Manolis 1989). Estuarine crocodiles are typically described as solitary, with individuals living within dominance hierarchies whereby dominant males exclude other males from their home ranges and control access to females, nesting areas, food, and living space (Messel et al. 1981; Messel and Vorlicek 1986; Lang 1987). Estuarine crocodiles are also regarded as the most agonistic and least social crocodylian (Lang 1987), with interactions between conspecifics potentially leading to severe injuries (i.e., loss of limbs, tail, and lacerations) and death (Webb and Manolis 1989). However, telemetry studies tracking multiple co-habiting individuals have revealed substantial spatial overlap between males in both lacustrine and riverine systems (Kay 2004; Brien et al. 2008; Campbell et al. 2013), and the formation of aggregations around feeding opportunities (Gallagher et al. 2018). Tracking studies have also revealed that individual crocodiles within the same population are not homogenous in the way they use space, with some individuals adopting a more nomadic strategy while others are more site-attached (Campbell et al. 2013; Dwyer et al. 2015; Hanson et al. 2015; Baker et al. 2019). Time of year can also influence crocodile behavior, with males becoming less tolerant of male conspecifics (Grigg and Kirshner 2015) and females migrating to their nesting sites during the breeding and nesting periods (October–March) (Baker et al. 2019). Little however is known about how differences in movement behavior and time of year affects crocodile social environments, and how stable spatial overlaps are between tagged individuals across multiple consecutive years.

In this study, we explored the degree of spatial structuring within a wild population of estuarine crocodiles over a 10-year period. To monitor the movements of individual crocodiles continuously over consecutive years, we used implanted acoustic transmitters and a network of fixed acoustic receivers. This allowed us to track 105 individuals (63 males, 42 females) of various age classes as they moved throughout 180 km of river and estuarine habitat. We then used the monthly home range overlap between tagged conspecifics to quantify the social environments of this population and to investigate how the spatial structure of this wild population was mediated by animal sex, movement strategy, and proximity to the crocodile mating season. We hypothesized that estuarine crocodiles would display temporally stable social environments, with males that were more site philopatric having greater stability and consistency in their home range overlap over time than those individuals that were less site-attached.

METHODS

Crocodile capture and tracking

Between 2008 and 2018, crocodile traps were deployed yearly along a 47 km stretch of the Wenlock River, Cape York, Australia (Figure 1). Traps were positioned within macro-tidal brackish and non-tidal freshwater environments, with traps either floated on the water surface or placed at the high tide mark on the riverbank. Traps were set between August and September each year, baited with pieces of either wild pig *Sus scrofa* or domestic cattle *Bos taurus* and sprung by a trigger mechanism. Small crocodiles (<2 m total body length (TL)) were captured by hand using spotlighting and a lasso. Once restrained, the animal's sex and TL were recorded.

A combination of coded implanted acoustic transmitters and an array of fixed hydrophone receivers were used to remotely monitor individual crocodile movements following the methods described in Franklin et al. (2009). In brief, a local anesthetic (Lignocaine, Troy Laboratories, NSW, Australia) was injected behind the left forelimb and a vertical incision (~4 cm) was made. A pocket was created between the dermis and muscle via blunt dissection and a coded acoustic transmitter (V16T-6x, VEMCO Amirix Systems, NS, Canada) inserted. The pulse transmission rate of transmitters was set to transmit randomly between 90 and 120 s. The projected battery life of 7–10 years permitted the recording of movements from individuals across multiple years. After surgery was completed, crocodiles were released into the river at their point of capture. To detect for the presence of tagged crocodiles, an array of hydrophone receivers (VR2-W, VEMCO) were placed throughout the Wenlock and Ducie River systems (Figure 1a). Each receiver was connected to a concrete anchor placed on average 4.70 ± 4.37 km apart (mean ± SD; 0.38–19.6 km) and situated 2–20 m from the riverbank and approximately 1 m below the surface. As the detection radius of each receiver was approximately 400 m and as the width of the study river was rarely >400 m wide, it would be rare for a crocodile to pass by a receiver without being detected. All procedures were carried out with approval from The University of Queensland Animal Ethics Committee (SIB/302/08/ARC, SBS/204/11/ARC/AUST ZOO (NF), SBS/215/14/AUST ZOO/ARC) and under Queensland Environment Protection Agency Permits (WISP00993703, WISP05268508, WISP13189313).

Classifying crocodile movement patterns

To determine how individual movement decisions influenced a crocodile's social environment, we grouped tagged animals into three distinct categories based on their movement behavior. In brief, eight movement metrics were generated from raw detection data that collectively described crocodile movements and space use. These metrics were the monthly presence/absence from the acoustic receiver array, number of days detected per month, number of short-term centers of activity per day, monthly core (50%) and extent (95%) home range area, mean home range overlap from previous month, mean distance travelled per day, and

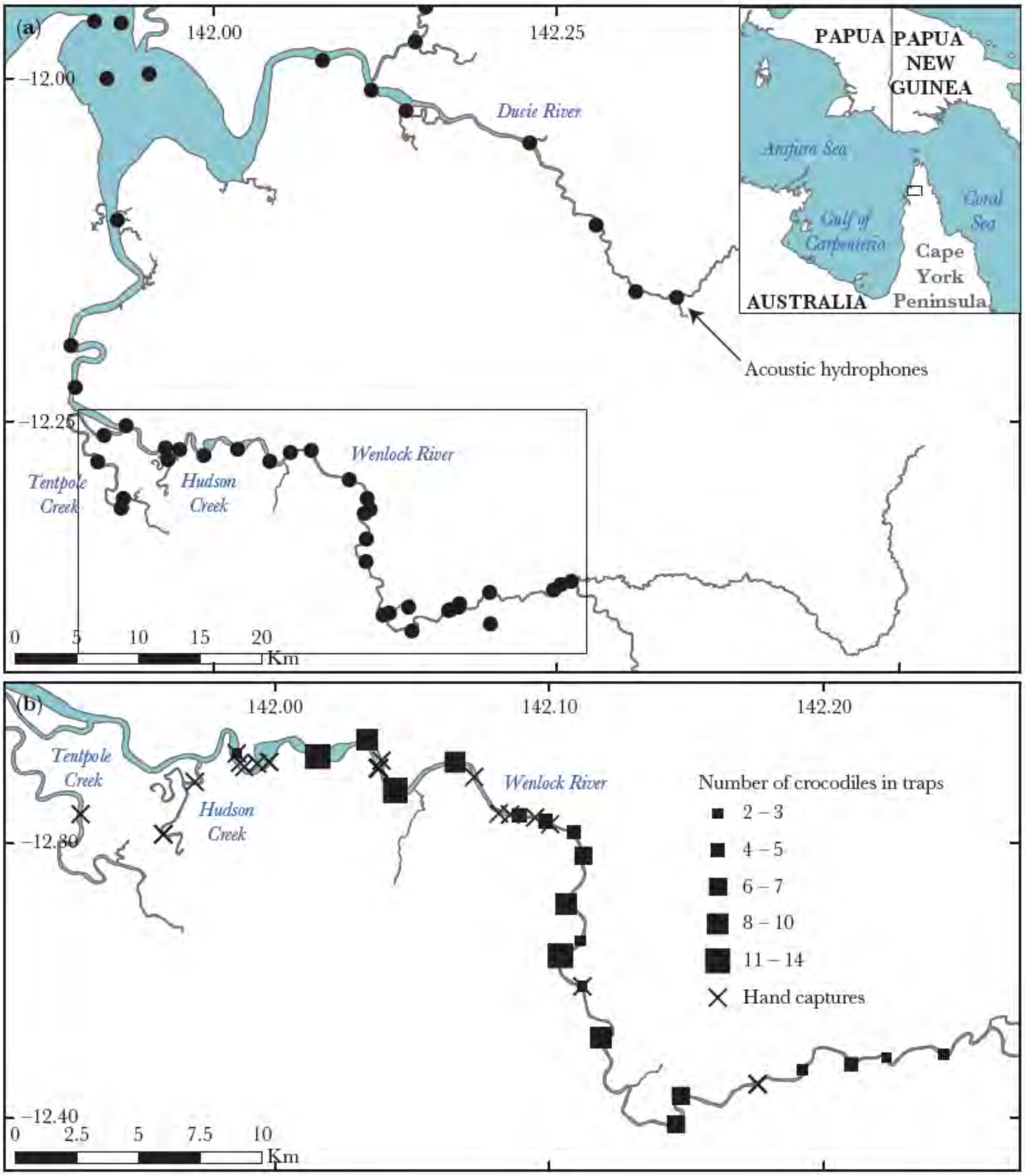

Figure 1

(a) The hydrophone receiver array deployed throughout the Wenlock and Ducie Rivers, Queensland, Australia. (b) The location of estuarine crocodiles *Crocodylus porosus* captured in traps (■) or by hand (X) in the Wenlock River. Size of the square indicates the number of individuals captured at traps (excluding recaptures) that possessed the minimum detections per month required for inclusion within the study.

mean monthly distance from home range centroid (Supplementary Material 1). A principal components analysis was performed using the eight-movement metrics. Ward's agglomerative hierarchical cluster analysis and K-means clustering were then performed on the first two principal components of the eight-movement metrics, with male crocodiles found to cluster into either a high site fidelity "resident" tactic or low site fidelity "nomadic" movement tactic. Female crocodiles were placed within their own movement tactic, as while individuals typically display high site fidelity (Campbell et al. 2013), female crocodiles have been observed migrating up to 60 km to suitable nesting locations during the nesting period (October–March) (Baker et al. 2019). While we acknowledge the potential for individual variation in the movements of females (as evidenced by ontogenetic shifts in nesting behavior; Baker et al. 2019), females were placed within their own movement tactic to facilitate between sex comparisons.

Generating home ranges

To determine the spatial structure of the crocodile population in this study, we first calculated the monthly home range of each individual following the framework outlined by Udyawer et al. (2018). In summary, raw tag detections were converted into short-term centers of activity (COA) using the *VTrack* (Campbell et al. 2012) package in the R statistical environment (R Core Team 2019). COAs account for the potential biases in space use estimates when using an array of fixed detection points by determining the weighted average position of an individual within a user-defined temporal bin (Simpfendorfer et al. 2002). As the movements of crocodiles were restricted to aquatic areas within the boundaries of the river system, COA estimates were assigned to the corresponding closest point on the river using the *sf* (Pebesma 2018) R package. A temporal bin of 6 h was selected to prevent clustering of locations around receivers, while also avoiding the masking of movements between hydrophone receivers (Udyawer et al. 2018). As the majority of our study site is tidal in nature, 6 h also represents the approximate time period for a single tidal cycle (Lyon et al. 2017). Next, we estimated the monthly home range size and coverage based on an individual's COAs for that period using the least cost kernel utilization distribution (lcUD) method (Laffan and Taylor 2013). Similar to Brownian bridge kernel utilization distributions, lcUDs account for the inherent temporal autocorrelation present in telemetry data by incorporating the trajectory taken by individuals between consecutive detections (Horne et al. 2007; Laffan and Taylor 2013). However, unlike Brownian bridge kernels which assume direct trajectories between points, lcUDs utilize least cost trajectories to account for physical barriers to animal movements (i.e., river boundaries) (Laffan and Taylor 2013). To do this, a 50 × 50 m raster of the study system was generated with areas corresponding to suitable habitat for crocodile movement (i.e., river and tributaries) set to a value of 1. To exclude potential shortcuts across land, areas of unsuitable habitat for crocodile movement (i.e., dry land) were set to an arbitrary value of 1000, indicating that it is 1000 times more difficult to move through non-habitat than habitat. The least cost trajectories between consecutive detections were then calculated using the *gdistance* (van Etten 2015) R package. Kernel utilization distributions for both the least cost trajectories and COAs were calculated using *VTrack*. The lcUD was then calculated as the mean between both of the resulting utilization distributions, with the resulting mean utilization distribution then clipped using the *raster* (Hijmans 2016) R package to constrain the home range estimate within the boundary of the river system (Laffan and Taylor 2013). The 95% lcUD volume contour was then used as the home range estimate of individuals. To determine the appropriate smoothing parameter (*h*) with which to generate IcUDs, we performed a sensitivity analysis whereby our smoothing parameter was set as the minimum value that the extent of activity space (km^2) of a subset of tagged crocodiles from each movement strategy began to plateau (Supplementary Figure 1). A minimum of 10 COA from at least three unique locations was required to determine the home range of each individual per month. Any crocodiles who did not have enough data to generate at least one home range estimate was excluded from the analysis.

Determining home range overlap

To quantify both intra- and inter-individual overlap in home range extent, we estimated the overlap of our monthly crocodile home range estimates using the volume intersection (VI) method (Seidel 1992) following Dwyer et al. (2020). This provided a simple measure of overlap between individuals ranging from 0 (when two home ranges have no overlap) to 1 (when two individuals have identical home ranges) (Seidel 1992). As an individual's social environment is composed of all the conspecifics they may interact with (or avoid) during their normal activities (Bonnell et al. 2017; Strickland and Frère 2017; Strickland et al. 2018), we quantified the social environment of individual's as the VI between conspecifics using their monthly home range estimates. All home range and VI calculations were conducted using the Animal Tracking Toolbox extension in the *VTrack* R package (Udyawer et al. 2018). To examine how crocodile movement tactic or season (mating/non-mating) may influence the proportion of overlap between conspecifics we created a linear mixed effect model (LME) using the *lme4* (Bates et al. 2015) R package. The proportion of home range overlap between dyads was the response variable, with both movement tactic and season as the predictor variables and dyad ID as the random effect. To improve the homogeneity of the model, the proportion of home range overlap was square-root transformed. To examine between movement tactic and season differences in home range overlap, a Tukey post hoc test using least square means was performed using the *emmeans* (Lenth et al. 2021) R package. The mating season was set between August and November, as nesting in estuarine crocodiles typically begins in October (Baker et al. 2019), with courtship and mating behaviors beginning up to two months prior to this (Webb and Manolis 1989; Grigg and Kirshner 2015). To prevent potential biases in VI estimation and the number of overlapping tagged conspecifics due to the low sample size of tagged individuals during the beginning of the study, only data from August 2010 to August 2019 was included in our analysis.

Do crocodiles exhibit spatial structure?

To determine whether crocodiles displayed spatial structure, (i.e., the presence of non-random organization in space (Peres-Neto and Legendre 2010)), we calculated the repeatability of dyadic spatial overlap based on monthly and annual variation in home range overlap estimates. Here, repeatability is a measure of the total variation of a trait that is attributable to the variance among dyads estimated using the intra-class correlation coefficient (ICC) (Bell et al. 2009). This was calculated using the following equation:

$$\mathrm{ICC} = \mathrm{VAR}_{\mathrm{DYAD}}/(\mathrm{VAR}_{\mathrm{DYAD}} + \mathrm{VAR}\varepsilon)$$

where $\mathrm{VAR}_{\mathrm{DYAD}}$ is the variance explained by between-dyad variation and $\mathrm{VAR}_{\varepsilon}$ is the residual within-dyad variance. To obtain these variances, we constructed a mixed effect model with spatial overlap (VI) as the response variable, with no fixed effects assigned and dyadic identity as the random effect within a Bayesian framework using the *brms* (Bürkner 2017) R package. To examine the influence of movement strategy, separate models were constructed for each possible combination of crocodile movement tactics, with dyads only included for the months they were observed (min = 1, max = 55 months). Models were run with two chains for 3000 iterations, with a warm-up period of 500 iterations and uninformative priors. ICCs were then calculated for each model. To determine whether our observed repeatability patterns differed significantly from random chance, we created a spatially explicit null model to compare against the observed movement data. Spatially explicit null models are a commonly used approach in behavioral, movement, and spatial ecology to examine if individuals exhibit non-random space use and/or non-random social behavior (Best et al. 2014; Farine 2017; Strickland et al. 2017). For this, we constructed a spatially explicit random walk model (spatial RW model), which simulated crocodile movement sequences throughout the study river based on the number and temporal structure of their observed movements. Here, the starting point for each simulation was set as the first observed detection of an individual within the acoustic hydrophone array and the number of steps within each movement sequence was fixed to reflect that of the observed data. As the observed movements of our tagged crocodiles were restricted to the water course by snapping the COA-derived points to the river, so to were the movements of our simulated individuals with simulated data points resampled until they fell within the boundary of the river system. The proportion of upstream and downstream movements of the simulated crocodiles was based on the observed data but the order randomized. Step lengths were selected at random from a normal distribution based on the mean and standard deviation of an individual's observed movements. We ran 100 iterations of the spatial RW model. We then generated a random distribution of ICCs by calculating the ICC for each of the 100 simulated datasets. We estimated the significance of the observed repeatability by calculating a *P* value as the proportion of times that random repeatability estimates were larger than the observed (Ruxton and Neuhäuser 2013).

Are spatial overlaps consistent through time?

We calculated the lagged spatial overlap rate (LSOR) from the observed home range overlaps to examine if individuals are maintaining home range overlaps with tagged conspecifics between months and across years. The LSOR is based on the lagged association rate originally proposed by Whitehead (1995), which determines the probability of two individuals associating at time *t* when they have been observed together in the past. Thus, the LSOR represents the probability of two individuals overlapping spatially based on previous observations. To determine if movement tactic influenced how individuals maintained home range overlap with tagged conspecifics, the LSOR was calculated for each combination of crocodile movement tactics (i.e., nomadic-nomadic, nomadic-resident) using the *ansipe* (Farine 2013) R package. To reduce the potential impact of tag loss and failure, LSOR analyses were restricted to a maximum duration of five years, as this was found to be the period in which 75% of acoustic tags successfully transmitted (Supplementary Table 1). To determine if individuals were maintaining spatial overlaps through time, we calculated the null spatial overlap rate (NSOR) for each movement strategy combination using the 100 spatial RW simulations. This was done by first calculating the LSOR of each of the simulated movement datasets following the methods above. The NSOR was then determined as the mean LSOR across our RW simulations. Thus, the NSOR represents the expected LSOR under the assumption that tagged crocodiles move randomly within the environment and do not exhibit spatial structure. We would expect the observed LSOR to be greater than the NSOR if individuals were actively maintaining spatial overlaps through time, but less than the NSOR if individuals were actively spatially avoiding conspecifics. Statistical significance was set at $\alpha = 0.05$ and values reported as mean ± SE, with all analyses completed within the R statistical environment (R Core Team 2019; version 3.6.1).

RESULTS

Between August 2008 and September 2018, 176 crocodiles (0.84–4.64 m TL) were captured along the Wenlock River. Of these individuals, 63 male (1.22–4.64 m TL) and 42 female (0.84–3.22 m TL) crocodiles exhibited the minimum number of COA per month required for inclusion within the study (i.e., a minimum of 10 COA across three different locations in a month). On average, the home range size of crocodiles was 5.06 ± 0.22 (SE; 0.19–56.12) km^2, based on 28 ± 34 (SD; 1–124) COA per month (Supplementary Table 1). Crocodiles were monitored for 3.7 years on average (±2.8 years; SD), with 13 individuals being tracked for greater than 8 consecutive years (Supplementary Table 1).

Classifying crocodile movement tactics

Crocodiles were categorized into three distinct movement classes based on their monthly movements: *nomadic males*, *resident males*, and *females*. These movement tactics were found to significantly dictate both the monthly distance travelled (LME, $df = 2$, $F = 56.10$, $P < 0.001$) and monthly home range (95% lcUDs) size of individuals (LME, $df = 2$, $F = 29.36$, $P < 0.001$). *Nomadic males* ($n = 13$, 3.01–4.30 m TL) travelled greater distances per month and had larger home ranges (Supplementary Figure 2) than both resident males (Tukey, $df = 128$, $t = 5.15$, $P < 0.001$; Tukey, $df = 96$, $t = 7.11$, $P < 0.001$ respectively) and female crocodiles (Tukey, $df = 131$, $t = -9.51$, $P < 0.01$; Tukey, $df = 109$, $t = -6.05$, $P < 0.001$ respectively). *Resident males* ($n = 50$, 1.27–4.64 m TL) were also found to travel greater distances per month compared with females (Tukey, $df = 116$, $t = -7.30$, $P < 0.001$; Supplementary Figure 2). However, no differences in home range size were present between resident males and females (Tukey, $df = 108$, $t = 1.18$, $P = 0.47$; Supplementary Figure 2). The proportion of spatial overlap an individual had with its preceding month's home range was similar across the three different movement tactics (LME, $df = 3$, $F = 0.51$, $P = 0.61$).

Home range overlap

Crocodiles were found to overlap with an average of nine tagged conspecifics (min = 1, max = 21) per month, overlapping 26.6 ± 22.2% (mean ± SD; 1–99%) of their home range with each tagged conspecific (Figure 2). A significant interaction between movement tactic and season (LME; $df = 5$, $F = 4.46$, $P < 0.001$) was found to influence the proportion of home range overlap between conspecifics. During the non-mating season (December to July), we observed no difference in the proportion of home range overlap between movement tactics (Figure 3). Overall, individuals were found to increase their proportion of home range overlap with conspecifics during the mating season (August to November), however only Resident-Resident and Female–Female dyads displayed significant differences between the seasons (Tukey, $df = \text{Inf}$, $Z = 3.29$, $P = 0.047$; Tukey, $df = \text{Inf}$, $Z = 5.01$, $P > 0.001$; respectively). Male crocodiles overlapped more with conspecifics that displayed the same movement pattern (Resident–Resident, Tukey, $df = \text{Inf}$, $Z = -4.16$ $P = 0.002$; Nomadic–Nomadic, Tukey, $df = \text{Inf}$, $Z = 6.08$, $P > 0.001$), with this difference being more pronounced during the mating season (Figure 3). The proportion of home range overlap with that of a female crocodile was also influenced by a male's movement tactic (Tukey, $df = \text{Inf}$, $Z = -4.14$, $P = 0.002$). During the mating season, resident males maintained their home range overlap with female crocodiles, while nomadic males decreased their home range overlap with females (Figure 3).

Do crocodiles display non-random spatial overlaps?

We found substantial differences in the repeatability of home range overlap between dyads according to sex and male crocodile movement tactic. Resident male–resident male, resident male–female dyads, and female–female dyads displayed significantly higher levels of repeatability compared with the null model. The repeatability of nomadic male–nomadic male dyads, resident male–nomadic male dyads, and nomadic male–female dyads were found to not be different from the null model (Table 1). We also observed considerable differences in the repeatability estimates between movement tactics. Repeatability estimates for dyads containing resident males and/or females ranged between 0.23–0.46 and 0.21–0.69 respectively, whereas estimates containing nomadic males ranged between 0.06 and 0.23 (Table 1).

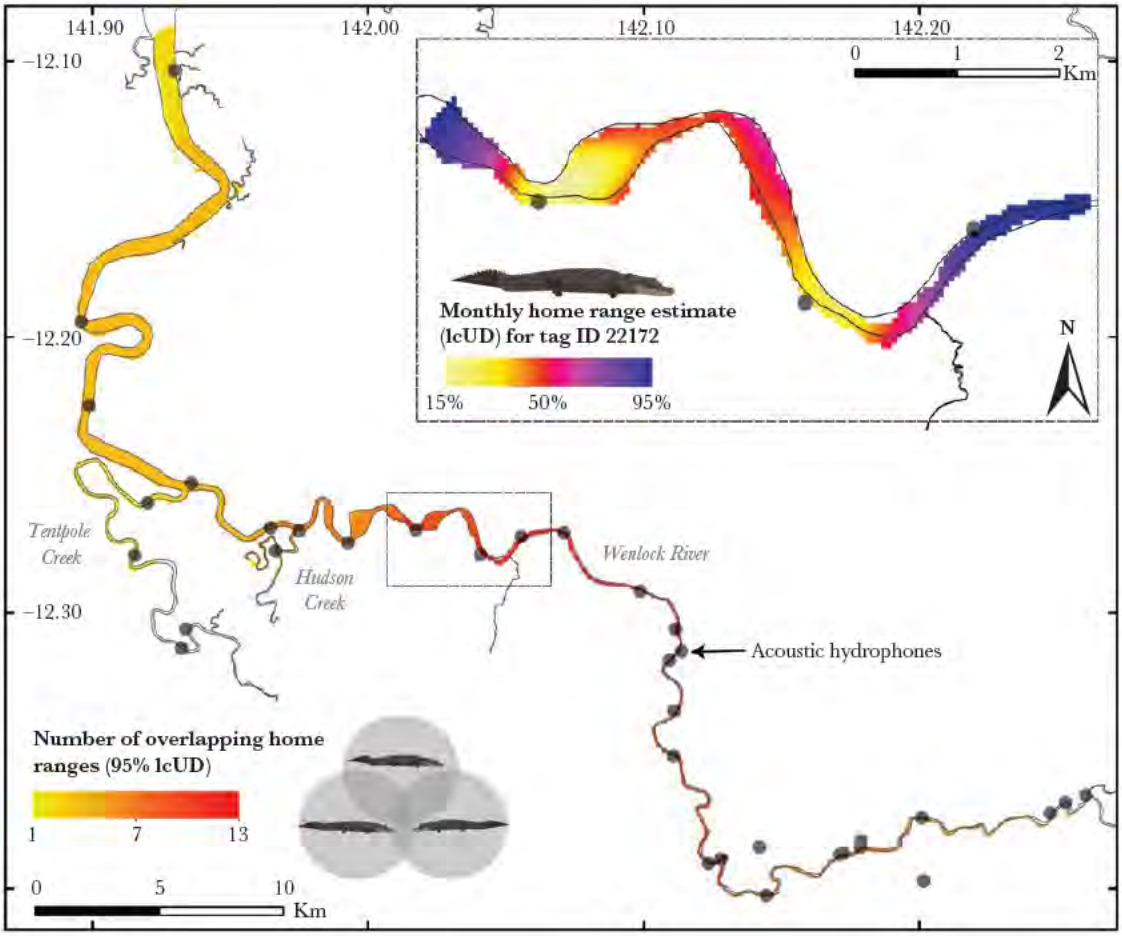

Figure 2
The number of overlapping estuarine crocodile *Crocodylus porosus* home range estimates (95% least cost utilization distribution) within the Wenlock River, Queensland, Australia for September 2019. Darker colours represent more overlapping individuals. Insert map displays the monthly 95% extent home range estimate of Tag ID 22172 for September 2019.

Are spatial overlaps consistent through time?

Resident males were found to form long-term temporally stable spatial overlaps with conspecifics, irrespective of a conspecific's movement tactic. While the spatial overlaps of resident males with conspecifics appeared random for the first ~8 months, indicating that overlaps between conspecifics begin by random chance, any spatial overlaps that persisted past this period were then actively maintained above that expected by random chance for up to 5 years (Figure 4a, d, e). In comparison, the spatial overlaps of both nomadic males and females displayed little evidence of temporal stability, with the probability of individuals overlapping in space not differing from the null model and falling to 0 after 2.5 years (Figure 4b, c, f). Regardless of movement tactic a distinct cyclic pulse was also present in the observed LSORs, where high and low estimates of LSORs corresponded to the mating and non-mating seasons respectively (Figure 4).

DISCUSSION

By tracking 105 estuarine crocodiles, cohabiting within a single river system over nine consecutive years, we discovered that both male and female crocodiles exhibited high consistency with which conspecifics they spatially overlapped with. This spatial structure was present both over the short term (months) and over the long term (up to five years), with site philopatric males maintaining the most consistent spatial overlaps with conspecifics throughout the year. Our results show that rather than being "asocial", estuarine crocodiles instead live within relatively stable social environments across extended periods of time. Estuarine crocodiles have traditionally been considered to be the most agonistic and least social of the extant crocodylians (Lang 1987), with dominant males (resident males > 4 m) having year-round exclusive home ranges, through the expulsion of other males (Messel et al. 1981; Messel and Vorlicek 1986; Lang 1987). However, animal telemetry studies have shown that even large male estuarine crocodiles can have a high proportion of home range overlap (Kay 2004; Brien et al. 2008; Campbell et al. 2013). Consistent with these later studies, we found no evidence for the formation of exclusive home ranges in estuarine crocodiles with up to 99% overlap observed between the home ranges of conspecifics. Furthermore, this proportion of monthly home range overlap increased during the crocodile mating season (August–November) possibly reflecting increased competition for mates during this period.

By remotely monitoring the movements of 105 individuals across multiple consecutive years (median = 3 years), we were able to show that individual crocodiles maintained spatial overlaps with conspecifics for at least five years. However, the stability of these spatial overlaps beyond this period is currently unknown. While our

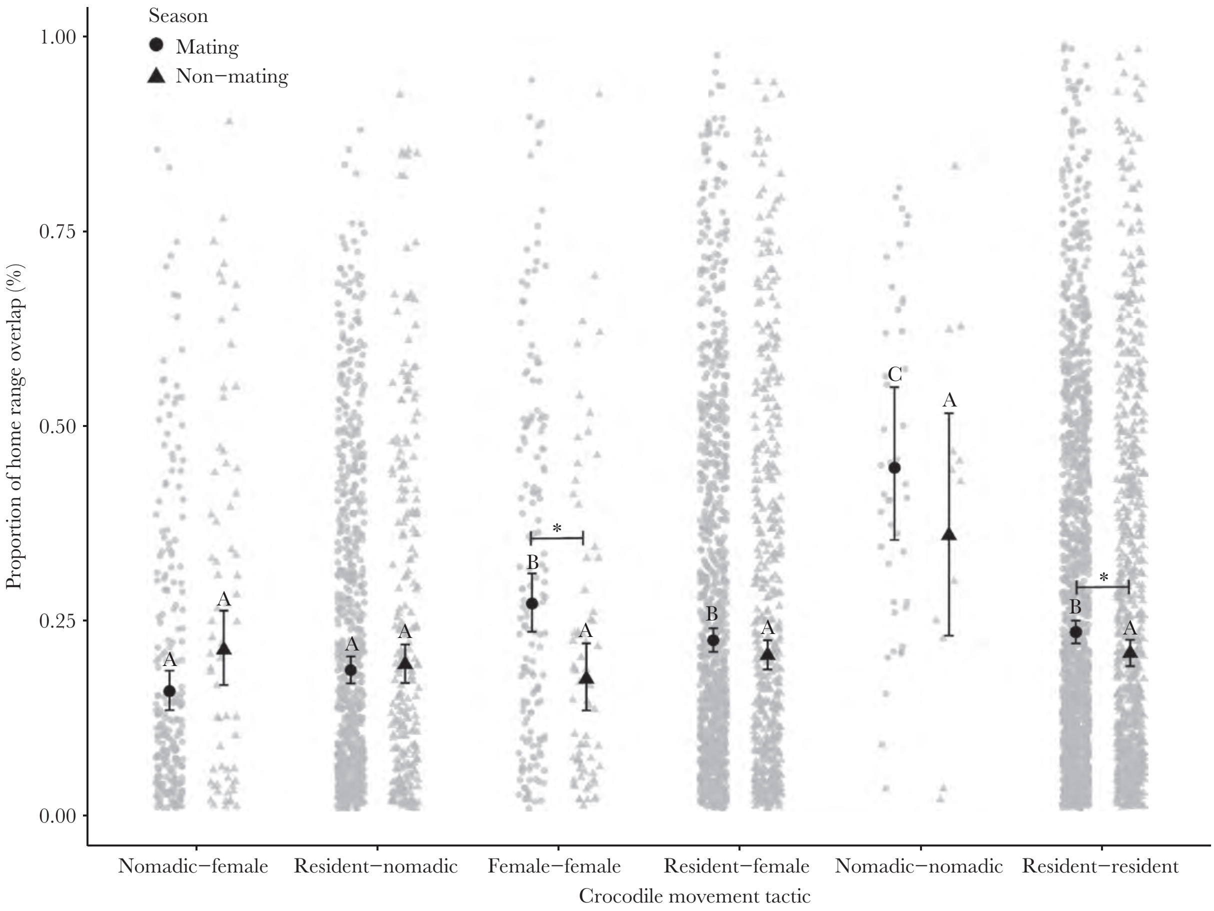

Figure 3

The proportion of home range overlap between conspecifics. Circles represent the mating season, while triangles represent the non-mating season. Within each season (mating or non-mating), movement tactic combinations with different letters above them are significantly different from each other. Significant differences between seasons for each movement strategy combination were indicated as asterisks. The raw data are represented by the grey points, while the least square model predictions are in black. Error bars represent the 95% confidence intervals.

Table 1

Differences in spatial overlap repeatability estimates between estuarine crocodile *Crocodylus porosus* according to sex and movement tactic

	Observed	Null model	
Movement tactic dyad	R	R_{DIST}	*P*-value
Resident male–resident male	0.45	0.09–0.23	**0**
Nomadic male–nomadic male	0.06	0.05–0.60	0.94
Resident male–nomadic male	0.23	0.06–0.29	0.07
Female–female	0.45	0.05–0.47	**0.02**
Resident male–female	0.46	0.10–0.40	**0**
Nomadic male–female	0.21	0.04–0.76	0.37

Observed spatial overlap repeatability (R). Distribution of random repeatability estimates (R_{DIST}) generated using a spatially explicit random movement model. *P* values calculated as the proportion of times the randomized repeatability was larger than the observed. Significant results in bold.

methods quantified the degree of social tolerance at a lower spatial and temporal resolution than typically used in studies of sociality (which typically rely on fine-scale focal observations (Frère et al. 2010; Wakefield 2013; Best et al. 2014), we were able to reveal that crocodiles display greater tolerance towards conspecifics sharing the same spatial areas than previously thought (Lang 1987). We also demonstrate how long-term tracking studies and home range metrics can provide basic insight into the social behaviors of solitary species. However, further studies observing the actual interactions of conspecifics within overlapping home ranges are required to fully quantify the social structure and examine potential drivers (e.g., sex, body size and condition, movement tactic) and consequences (e.g., access to resources and reproduction, disease transfer, physical injuries) of these interactions.

Within gregarious species, site fidelity and temporal consistency in the spatial overlap between conspecifics are often prerequisites for sociality, providing foundations on which the social structure of the population is built (Wolf et al. 2007), and influencing the emergence of social preferences (Mourier et al. 2012) and aversions (Strickland et al. 2017). For example, in Galápagos sea lions *Zalophus wollebaeki*, the high site fidelity of females and their offspring during the mating season was found to form the structural backbone of the population's social structure, on which the territories and associations of the remaining individuals within the population were superimposed (Wolf et al. 2007). Similarly in red squirrels *Tamiasciurus hudsonicus,* site fidelity has also been observed to increase familiarity with conspecifics resulting in the formation of stable "neighborhoods", reducing the costs associated with territorial defense and increasing individual fitness (Siracusa et al. 2017;

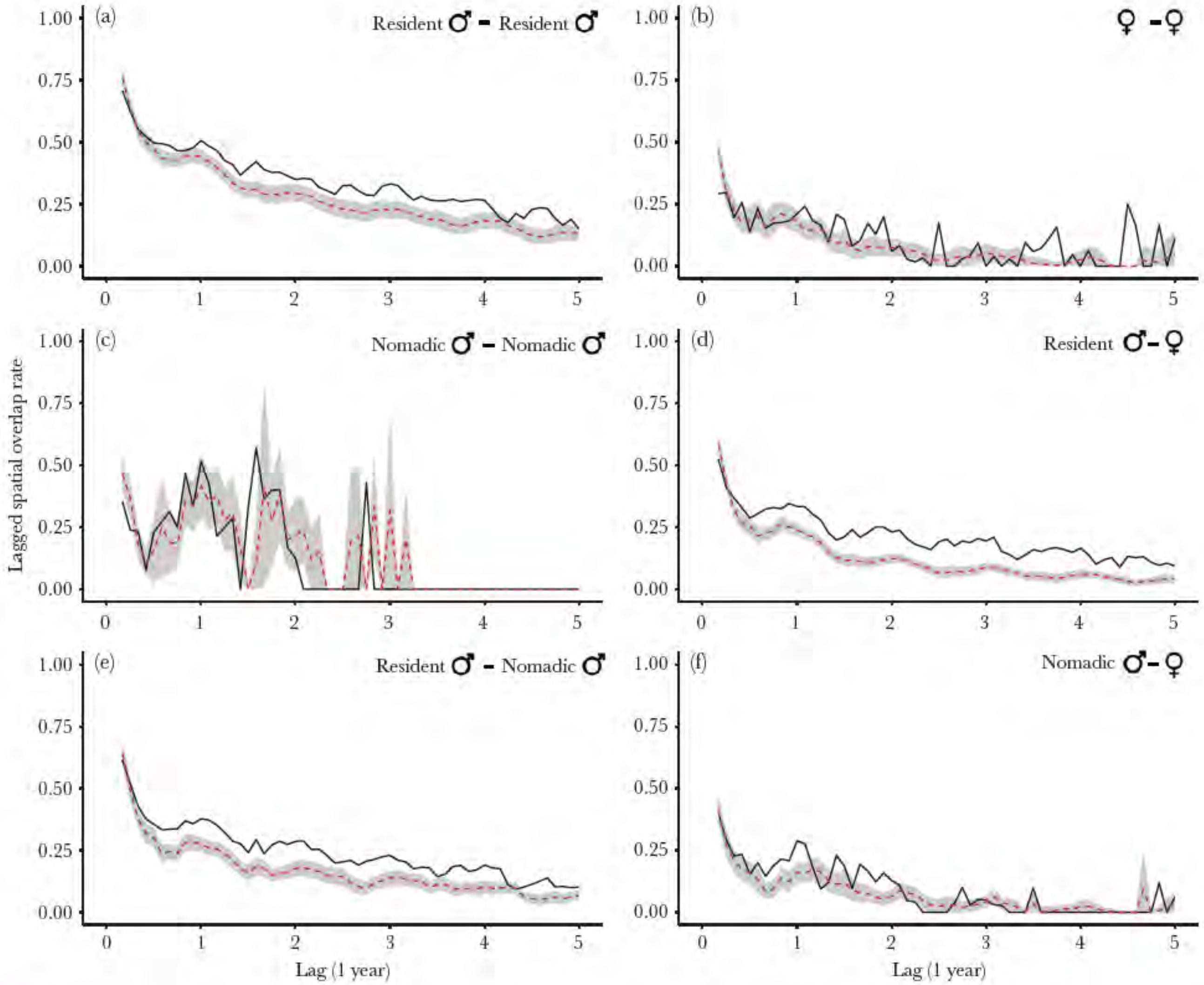

Figure 4

Lagged spatial overlap rate (LSOR) estimating the probability that estuarine crocodiles will continue to spatially overlap with tagged conspecifics across extended periods of time. LSOR estimates were created separately for (a) resident male dyads, (b) female dyads, (c) nomadic male dyads, (d) resident male and female dyads, (e) resident male and nomadic male dyads, and (f) nomadic male and female dyads. The black line represents the observed LSOR, the red dashed line represents the null LSOR with the grey fill representing ± standard deviation of the null LSOR.

Siracusa et al. 2021). Consistent with this, we found that those male crocodiles with high site-fidelity displayed the most stable and consistent social environments, while females and nomadic males displayed a greater degree of plasticity in the conspecifics they overlapped with. These findings suggest that resident male crocodiles may act as nuclei in the formation of distinct communities along the river system and could help to form the basis for social structure within the population. Further study is required to examine how movement behavior and body size influences an individual's position and connectedness within the population, as well as experimental and simulation studies examining how the removal of specific individuals might influence the social and spatial structure of crocodile populations.

While many studies have examined how the social behavior of individuals differ according to sex or with ontogenetic shifts (e.g., Frère et al. 2010; Bonanni et al. 2017; Strickland and Frère 2017; Perryman et al. 2019), few have examined how intrasexual differences in movement behavior may influence an individual's social decisions. We found that those males which were more site philopatric were found to not only display high proportions of overlap with conspecifics, but they were maintaining these overlaps both within and across multiple years. In contrast, males which were less site-attached displayed more dynamic social environments; with individuals only maintaining high spatial overlaps with conspecifics during the mating season, while the probability of overlapping with conspecifics decayed across successive years. Such understanding of fine-scale site fidelity can enhance the predictability and stability of an individual's social environment, through the mediation and reduction of aggression between conspecifics (Jaeger 1981; Wolf et al. 2007; Brena et al. 2018). Such stabilization of the social environments is particularly important for large-bodied predators such as crocodiles, where fights between individuals often result in injury and even death (Webb and Manolis 1989). Furthermore, long term familiarity with neighboring conspecifics decreases the costs associated with maintaining and defending territories (Siracusa et al. 2019). However, the benefits of adopting a more philopatric vs a more nomadic tactic likely depends on an individual's position within the social hierarchy. In freshwater crocodiles *Crocodylus* *johnstoni* larger dominant individuals have been observed chasing and preventing sub-dominant individuals from accessing basking sites, resulting in the decreased growth and physiological performance of those sub-dominant individuals (Seebacher and Grigg 2001). Thus, the two behavioral phenotypes exhibited by the crocodiles in this study likely represent alternative behavioral tactics which individuals adopt to maximize fitness while navigating the potential costs and benefits of their social environments. Further study is required to assess how stable these strategies are for this species across other river systems, and how these behavioral traits vary according to body condition, ontogeny, and familiarity with neighbors.

Unlike males, which generally prioritize access to females, female movement patterns tend to be more influenced by environmental factors, including access to resources such as food, nesting, and basking sites (Dammhahn and Kappeler 2009; Frère et al. 2010). As a result, females regardless of species often display more dynamic social environments in comparison to males, due to individuals altering their social decisions (whether to interact or not with conspecifics) in response to environmental fluctuations (e.g., seasonal food availability, access to nesting sites) (Koski and Burkart 2015; Strickland and Frère 2017). Consistent with this, we found that female crocodiles displayed highly dynamic social environments, with females rarely maintaining spatial overlaps with conspecifics (regardless of sex) between months. However, the highly restricted movements of female crocodiles during the dry season (mean home range size = 3 km^2), potentially reduced our ability to consistently obtain monthly home range estimates for these individuals as these movements were often between the detection fields of adjacent acoustic receivers (Dwyer et al. 2015). As such, we are unable at this stage to determine why female crocodiles display highly dynamic social environments. Examining how female crocodiles interact with conspecifics within the spatial overlaps we have identified, and how these interactions shift in response to resource availability and time of year (e.g., the mating vs. non-mating season) would provide interesting avenues of study to better understand the interplay between the physical and social environments of females.

By combining techniques commonly used in movement ecology and socioecology, we provide new insights into the social environment of estuarine crocodiles based on the spatial structure of this population over a 10-year period. We found that crocodiles were more social than previously thought, where an individual's degree of site fidelity influences the stability and degree of spatial overlaps between conspecifics. These findings add to the growing body of literature demonstrating the importance of understanding the underlying spatial structure of populations, for gaining insights into the social organization and structure of wild populations.

SUPPLEMENTARY MATERIAL

Supplementary data are available at *Behavioral Ecology* online.

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AUTHOR CONTRIBUTIONS

CB, CHF, CEF, HC and RD conceived the ideas and designed methodology; CB, RD, HC, TI and CEF collected the data; CB and RD led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Conflict of Interest: We declare we have no competing interests.

Data availability: Analyses reported in this article can be reproduced using the data provided by Baker et al. (2021). All R code supporting the analyses reported in this article is available from GitHub: (https://github.com/Cameron-J-Baker/Supporting-code-Baker_et-al).

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Home Range Utilisation and Long-Range Movement of Estuarine Crocodiles during the Breeding and Nesting Season

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Abstract

The estuarine crocodile (*Crocodylus porosus*) is the apex-predator in waterways and coastlines throughout south-east Asia and Australasia. *C. porosus* pose a potential risk to humans, and management strategies are implemented to control their movement and distribution. Here we used GPS-based telemetry to accurately record geographical location of adult *C. porosus* during the breeding and nesting season. The purpose of the study was to assess how *C. porosus* movement and distribution may be influenced by localised social conditions. During breeding, the females (2.92 ± 0.013 metres total length (TL), mean ± S.E., $n=4$) occupied an area <1 km length of river, but to nest they travelled up to 54 km away from the breeding area. All tagged male *C. porosus* sustained high rates of movement (6.49 ± 0.9 km d^{-1}; $n=8$) during the breeding and nesting period. The orientation of the daily movements differed between individuals revealing two discontinuous behavioural strategies. Five tagged male *C. porosus* (4.17 ± 0.14 m TL) exhibited a 'site-fidelic' strategy and moved within well-defined zones around the female home range areas. In contrast, three males (3.81 ± 0.08 m TL) exhibited 'nomadic' behaviour where they travelled continually throughout hundreds of kilometres of waterway. We argue that the 'site-fidelic' males patrolled territories around the female home ranges to maximise reproductive success, whilst the 'nomadic' males were subordinate animals that were forced to range over a far greater area in search of unguarded females. We conclude that *C. porosus* are highly mobile animals existing within a complex social system, and mate/con-specific interactions are likely to have a profound effect upon population density and distribution, and an individual's travel potential. We recommend that impacts on socio-spatial behaviour are considered prior to the implementation of management interventions.

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Introduction

Animals generally confine their movements within discrete areas. The size, placement and shape of the activity space has been termed the home range, and reflects the animals' behavioural repertoire as it searches to procure food, shelter, and mates [1]. For many species social conditions influence the size of the home range, and consequently, the abundance and distribution of the population. Understanding home range dynamics is essential for the pragmatic management of any species [2], but is particularly important in managing top predators because of their influence upon lower trophic levels [3,4,5].

The estuarine crocodile (*Crocodylus porosus*) is the apex predator in its environment and will feed upon a variety of prey items [6]. The species has a wide distribution across northern Australia, occurring in coastal areas, estuaries, rivers, inland swamps, billabongs, and off shore islands [7,8,9]. Unlike a vast majority of the world's apex predators, the Australian *C. porosus* population has undergone significant growth over the last 30 years. Once in risk of imminent extinction the current Australian population is estimated to be greater than 75 000 non hatchling individuals [10,11,12,13]. Although the population density varies considerably between river systems [14], such a large growth in population is likely to be altering the dynamics of the wider community and ecosystem [5]. This will occur not only by the consumption of lower trophic animals but also through the alteration of prey species' behavioural ecology [3].

Crocodylus porosus are generally considered to be highly territorial animals, with dominant males excluding con specifics from their home range [15]. More recently however, telemetry studies have recorded large adult male *C. porosus* living in close proximity to each other, thereby refuting previous claims of *C. porosus* as an exclusively territorial species [8,16]. Understanding which of these social conditions is most apparent is of profound importance towards management because the former would result in social conditions altering population density, dispersal, and distribution whilst the latter would not.

Previous estimates of home range upon *C. porosus* have relied upon either visual sightings or the manual collection of location data via VHF radio telemetry [8,16]. We suggest that the home range estimates of these studies may have been biased by serial autocorrelation because temporal irregularities occurred in the period between location fixing [17]. Furthermore, these studies and others upon crocodilians have defined the home range using mid stream linear distance or the minimum convex polygon method [18,19]; whilst these techniques provide a measure of the full extent of the area visited by an individual they ignore patterns of selection within the home range. This is important if we are to assess the difference between an individual's daily usage of an area compared to an area that is merely passed through or only frequented occasionally. In order to make this assessment, kernel utilisation distributions (KUDs) are convenient analytical tools, because they calculate density based upon the entire sample set of relocations during the period of interest rather than the emphasis being on the most outward location points [20]. It was the aim of this study to use KUDs to assess the relationship between daily movements and area utilisation distribution in male and female *C. porosus*. We selected to monitor the crocodiles during the breeding and nesting season (September February) as the effects of social conditions upon movement and space use were expected to be most apparent during these periods.

To apply kernel utilisation distribution plots it is important to collect accurate location data at a sufficiently high frequency and regularity [21]. To achieve this, we utilised high precision global positioning system (GPS) based telemetry data loggers, which had an inbuilt capacity to parse the collected location data through the ARGOS satellite system. In the light of previous telemetry studies upon *C. porosus* [8,16], we hypothesised that there would be profound differences in space use between males and females and the home ranges of individuals would overlap within and between the sexes. Furthermore, due to the high temporal resolution and spatial accuracy of the GPS based location data, we suspected that new insights into crocodile movement, interaction, and space use would also be revealed.

Materials and Methods

Study site and animals

Trapping was conducted on the Wenlock River, Cape York Peninsula, Australia during August 2010 (Fig. 1). A field camp was run from the Steve Irwin Wildlife Reserve (142.18°N, 12.38°E). The trapping occurred from the freshwater tidal reaches of the river down to the macro tidal brackish water, between 20 and 60 km from the river mouth. The bank vegetation in the lower reaches of the trapping zone was mangrove palm (*Nypa fruticans*) changing to *Melaleuca* dominated forests. It has been suggested that out of all the river systems along the western side of Cape York Peninsula the Wenlock system provides the most suitable nesting habitat for estuarine crocodiles [22].

Adult *Crocodylus porosus* (males 3.91±0.14 m total length, mean±S.E, n 8; females 2.93±0.13 m total length, n 4) were captured between the non tidal freshwater reaches of the Wenlock River through to the macro tidal brackish (Fig. 1). The traps were floated on the water surface or placed at the water edge along the river bank. Each trap was baited with wild pig (*Sus scrofa*) and the trap door was sprung by the crocodile when pressure was applied to the bait, via a trigger mechanism [23]. Once captured, crocodiles were removed from the trap and manually restrained. Total length (TL) and snout vent length (SVL) measurements were taken and a local anaesthetic (5 ml of Lignocaine, Troy laboratories, Smithfield, Australia) was injected under the nuchal rosette. Once the anaesthesia had taken effect, a single hole was drilled in each of the four raised osteoderms of the nuchal rosette [24]. Stainless steel multi strand, plastic coated wire (80 kg breaking strain) was inserted through the drilled holes and laced into attachment points on the GPS based satellite transmitter (in 2009 5×GPS units Sirtrack, Hamilton, New Zealand; in 2010, 13×TGM 410, Telonics, Arizona, U.S.A.). The GPS units were secured onto the dorsal surface of the crocodile with aluminium crimps threaded onto the stainless steel wire (Fig. 2). The process of removing the crocodile from the trap to eventual release took approximately 60 min. The crocodiles were released at the point of capture. To avoid any bias in crocodile behaviour occurring from the baited traps or increased boat traffic during the trapping period, only GPS based location data obtained after 01 September were used in the final analysis.

Data analysis

The devices utilised the global positioning system of satellites to determine geographical location twice daily (0800 h and 1800 h). The location data were stored on board the unit and parsed to the ARGOS satellite system between 1000 h 1600 h every other day. For each of the GPS based location fixes, the accompanying satellite dilution of precision (SDOP) value was used to define the positional resolution and precision. Stationary logging tests (7 d) prior to the study were used to pre determine the average degree of error for each GPS unit. All units performed equally and an SDOP of≤3 had a mean accuracy of error 12.1±1.1 m. All location fixes with an SDOP≤3 were excluded from the final analysis.

To assess home range size, we adopted the fixed kernel (FK) method [21]. Kernel density estimators are known to be sensitive to their choice of the smoothing parameter (h) [25]. The least squares cross validation (LSCV) method has been suggested as the most accurate way of estimating the appropriate smoothing parameter [25], it was not however suitable for the present study because it resulted in the delineation of numerous small disjunct contours, excluding connecting stretches of river. A second commonly used smoothing estimator, the reference bandwidth method [26], resulted in large areas beyond the outermost locations being included in the utilisation distributions. To ensure a contiguous home range boundary extending throughout the length of the river and accurately represent the outermost locations, we selected a smoothing parameter of h 750 m. For each individual, the 95% and 50% volume contour of the KUD (hereafter the KUD 95% and KUD 50%, respectively) were determined using the 'adehabitatHR' package [27] implemented in the statistical software R [28]. To examine temporal variation in home range use volume contours were constructed for six time periods (01 September 30 September, 01 September 31 October, 01 September 30 November, 01 September 31 December, 01 September 31 January and 01 September 28 February). Crocodile movement was constrained within the river channel, and therefore, the area produced by the FK method was considered over representative of the actual area utilised by *C. porosus*. Stretches of river intersecting the volume contours were consequently extracted to ensure that habitat inaccessible to *C. porosus* were not included in the final home range estimates. A high resolution spatial polygon of the Wenlock and Ducie River catchment was constructed using satellite imagery data (Fig. 1) and converted to a 50×50 m raster object using ARCGIS 10 (ESRI, Redlands, California, U.S.A). Areas of river contained within the KUD 95% and KUD 50%, and the corresponding centroid within the KUD 50%, were obtained using functions contained within the 'sp' [29], 'rgdal' [30] and 'rgeos' [31] R packages. This river intersection method reduced the KUD 95% by 90.7±4.1% and the KUD 50% by 71.4±3.2%.

To explore the finer scale movements in tagged *C. porosus*, two measures of directional movement were investigated. The first measure, the distance moved from the KUD 50% centroid during the period 01 September 30 September, would reveal exploratory

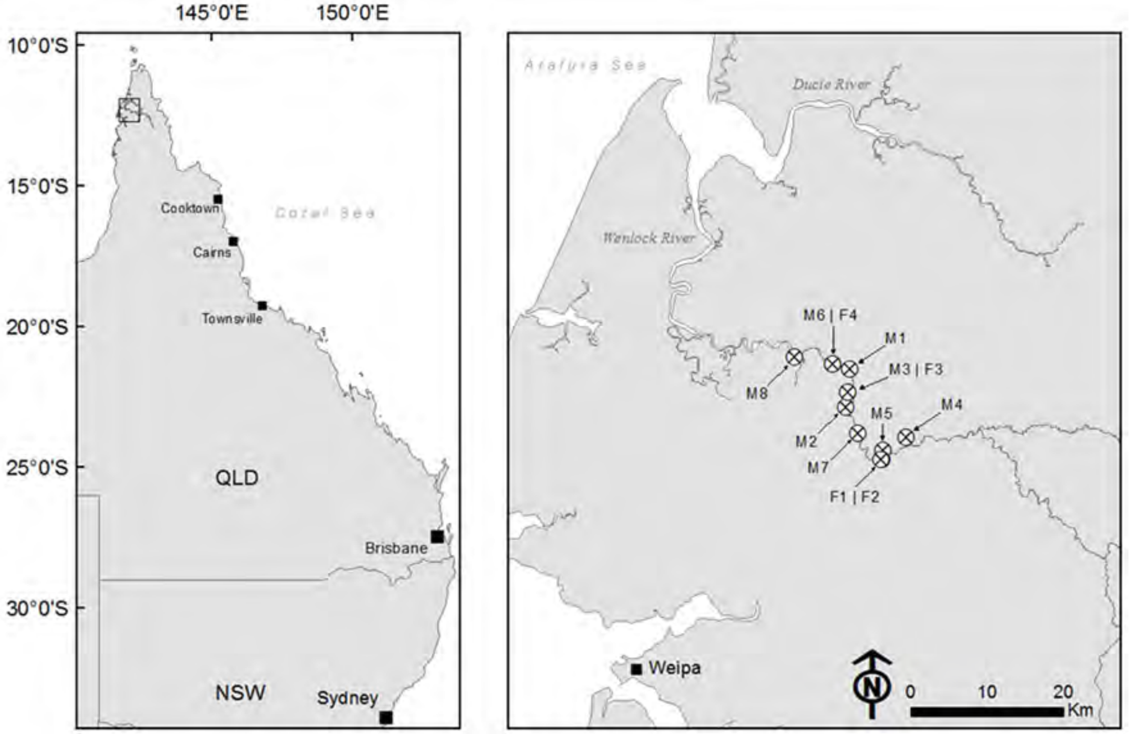

Figure 1. The Wenlock and Ducie River, Cape York, QLD, Australia. The capture locations of each *Crocodylus porosus* tagged for the study are displayed.
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movements from the centre of the home range. The second measure, the minimum distance between two locations in series, would reveal periods of activity. As crocodile movements were limited by the trajectory of the river, the minimum distance moved between two locations was calculated along the trajectory of the river using the 'raster' [32] and 'gdistance' packages [33] in R.

A general linear mixed model (GLMM) was used to assess the influence of body size and sex on movement patterns in *C. porosus*. Daily rate of movement (ROM) was included as the response variable, with days from 01 September (date) and body mass (extrapolated from SVL using the conversion factors in [34]) as covariates, sex as a factor, and crocodile ID as random effect. A second model assessed the relationship between the daily distance each individual was located from the centroid of its KUD 50%, with date and body mass as covariates, sex as a factor, and crocodile ID as random effect. Due to the correlation between body mass and sex the interaction between these variables was included in our model. Analysis was undertaken in Statistica 10 (Statsoft Inc, Tulsa, USA) and $P<0.05$ was considered significant.

Figure 2. ***Crocodylus porosus*** **with GPS based satellite transmitter attached to the nuchal rosette.**
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Results

The majority of the crocodiles tagged in this study remained within the Wenlock River for the duration of the study, but one male travelled to the adjacent Ducie River system, and some males and females moved into seasonal creeks located far upriver. Location data were collected twice daily for eight male and four female *C. porosus* from the 01 September 2010 until the 28 February 2011 (Table 1). 7.1±0.4% of location fixes did not have a sufficiently low SDOP for inclusions in the analysis and were therefore removed from the analysis.

Male Movements

The application of kernel density estimators to the location data and calculation of the cumulative home range illustrated that the movement patterns of the eight males could be grouped into two discrete categories. The 'nomadic' males ($n = 3$) were defined by the fact they did not demonstrate a stable KUD 95% during the 6-month study (Fig. 3a), whilst 'site fidelic' males ($n = 5$) displayed a KUD 95% which remained stable throughout the study (Fig. 4a).

The 'nomadic' males ($n = 3$) travelled extensively throughout the Wenlock and Ducie River catchments (Fig. 3a). They did not confine their movements to a discrete area on the area, and therefore the KUD 50% comprised only a fraction (13.6±4.9%,) of their total KUD 95% (Table 1). Because there was no defined home range, the location fixes rather than the KUDs were plotted on the maps to illustrate space use (Fig. 3a). The 'nomadic' males rate of movement averaged $384.3\pm29.1\ \text{m h}^{-1}$ during darkness and $233.4\pm56.3\ \text{m h}^{-1}$ during daylight hours (Table 1). During the six months of tracking the 'nomadic' males moved many

Table 1. Summary statistics for four female and eight male *Crocodylus porosus* tracked by GPS-based telemetry between 01 September 2010 and 28 February 2011.

Croc ID	Total Body Length (m)	Day ROM (m/h)	Night ROM (m/h)	Total distance moved (km)	KUD 95% (km^2)	KUD 50% (km^2)	Max distance from centroid
M1	3.2	301	352	824	34.2*	6.6*	73.2
M2	3.7	153	428	1054	42.1*	6.4*	69.2
M3	3.9	245	373	1269	72.5*	4.7*	165.4
M4	4.3	290	589	1179	9.0	4.2	19.2
M5	3.9	67	118	173	7.3	3.5	12.2
M6	3.7	84	248	197	8.7	3.6	27.9
M7	4.1	166	447	964	11.2	5.1	9.6
M8	4.5	200	270	324	7.1	4.2	8.07
F1	3.0	123	56	258	12.8	3.9	54.3
F2	2.9	17	39	127	7.2	2.2	54.8
F3	3.2	34	92	165	4.9	0.8	33.1
F4	2.6	27	23	154	1.1	0.5	22.5

*indicates that the monthly kernel utilisation distribution (KUD) had not stabilised by the end of the study.

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hundreds of kilometres and on average travelled 102.6±40.8 km from the KUD 50% centroid (Fig. 3b). The mean total length of the 'nomadic' males was 3.6±0.2 m (mean ± S.E.).

As the name implies the 'site fidelic' males (n 5) exhibited a stable KUD 50% in which they confined their movements during the 6 months of study (Fig. 4a). The KUD 95% and KUD 50% were comparable across the group (Table 1), and the KUD 50% comprised a large component of the total KUD 95% (48.1±2.8%). There was overlap in the KUD 50% between males, but this was never greater than 47.1% (35.1±6.1% mean±S.E., n 8). The 'site fidelic' males moved a minimum river distance of 334.4±83.7 m h ^{1} during darkness, decreasing to 161.4±41.2 m h ^{1} during daylight hours (Table 1). Although the average hourly rate of movement for the 'site fidelic' males was less than exhibited by the 'nomadic' males, there was no significant difference in the daily distance travelled between the two groups throughout the study (Table 2). The 'site fidelic' males moved back and forward within their home range and therefore the daily distance they were located away from the KUD 50% centroid closely matched the daily rate of movement (Fig. 4b). The maximum river distance the 'site fidelic' males were located away from the KUD 50% centroid averaged 15.4±3.7 km for the group (Table 1). The mean total length of the site fidelic males was 4.1±0.18 m.

Female movements

The four tagged female *C. porosus* were of a similar size range and were smaller than the tagged males (Table 1). All females occupied the main trunk of the river and exhibited a defined KUD 95% that was stable between 01 September and 01 December (Fig. 5a). The KUD 50% of two females overlapped at 32.1 and 34.4% area, whilst the other two females held discrete KUD 50% in close proximity. The daily rate of movement for females was much lower than recorded for the males (night 52.5±13.4 m h ^{1}; daylight 50.3±22.2 m h ^{1}), and they did not exhibit the male preference for nocturnal activity (Table 1).

During December and January, each female showed an approximate 30% expansion of their KUD 95%. This increase in the KUD 95% and KUD 50% was due to a sharp increase in daily activity and a lengthening of the distance the female was located away from the KUD 50% centroid (Fig. 5b). F1 travelled upriver whilst F2, F3 and F4 travelled downriver, and within a 24 h period all females were located a considerable distance from the KUD 50% centroid. It seemed logical due to the timing that these long range movements exhibited by the females were towards nesting areas. F2, F3 and F4 remained at the new location for less than 48 h before travelling back to the KUD 50% centroid within a 24 h period. They remained within their original KUD 50% for 1 2 weeks before undertaking the same journey back to the nesting location. Once at the nesting location for the second time, they remained there until the end of the study (28 February). F1 did not show this repetitive movement and undertook a single long distance movement in January, remaining at the new location until the end of the study.

GLMM

The general linear mixed effects model showed that body mass had no significant effect upon the daily rate of movement (ROM) or the river distance an individual was located away from its KUD 50% centroid (Table 2). Sex did have a significant effect upon ROM but not distance from the KUD 50% centroid and date had a significant effect upon both ROM and distance from the KUD 50% centroid. Crocodile ID exerted a significant effect within the model upon both ROM and distance from the KUD 50% centroid, but classifying males into either 'nomadic' or 'site fidelic' groups accounted for the significant effect of crocodile ID ($F_{1,9}$ 67.4, $P<0.01$).

Discussion

Male movements

We recorded two distinct behavioural tactics exhibited by tagged male *C. porosus* throughout the six month study. The daily rate of movement was not significantly different between groups exhibiting either behavioural tactic, but the temporal directionality of movement defined each group. Males exhibiting a 'nomadic' tactic ranged throughout the Wenlock and Ducie River catchments; their movement along the river were typically unidirectional upon consecutive days and confined only by river geography. In contrast, males exhibiting a 'site fidelic' tactic

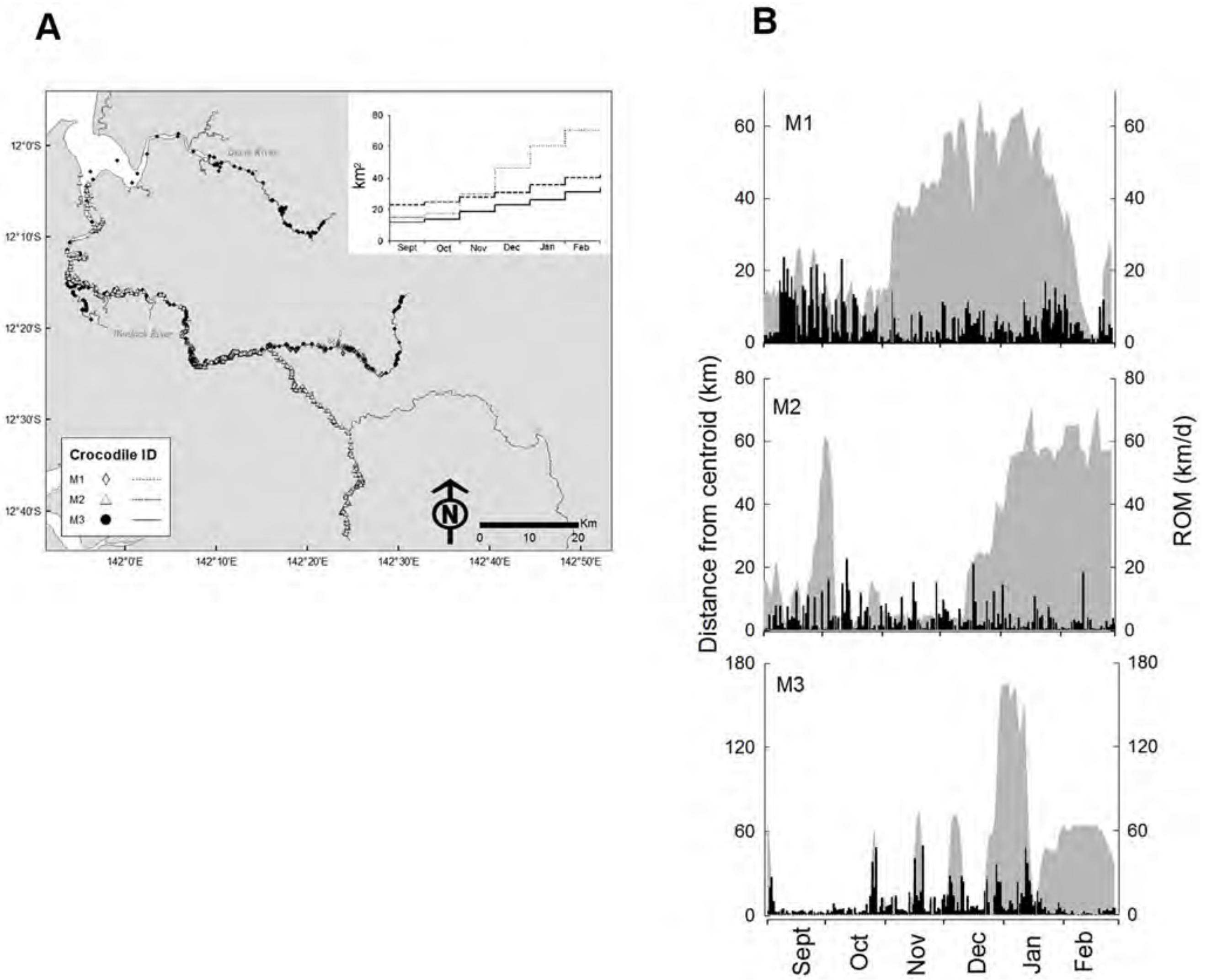

Figure 3. Movement patterns of 'nomadic' male Crocodylus porosus. (a) GPS location fixes obtained twice daily between 01 September and 28 February (n = 3). Inset line graph shows the monthly cumulative KUD 95% for each individual. (b) The relationship between daily rate of movement (ROM) and daily distance from the KUD 50% centroid (grey = primary y axis; black = secondary y axis).
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confined their movements within a discrete stretch of river. Each individual male maintained its selected behavioural tactic throughout the breeding and nesting season.

The patterns of movement recorded by GPS based location fixing and defined by KUD home range analysis strongly reflected territorial patrolling behaviour and mate defence [35,36]. Tagged con specifics were located inside the home range of the 'site fidelic' males, but the rate of movement of these individuals would have resulted in them passing through the home range quickly, and the lack of total exclusion may simply be a function of the large home range area and the high mobility of the con specifics. It is likely that the 'nomadic' males passed through the territories of many other untagged 'site fidelic' males during this period.

The present study was undertaken during the breeding and nesting season and all tagged males would have been of reproductive age. Body size is a good surrogate of social status in *C. porosus* [37], and although behavioural strategy was not significantly segregated by size in this study, we argue that it is the most likely determinate between a 'nomadic' or a 'site fidelic' lifestyle. Certainly, the dichotomy of movement patterns were strongly reflective of the 'fighting' or 'sneaking' alternative reproductive tactics often displayed within polygamous mating systems [38,39]. That is, dominant males maximise their reproductive success by defending mating rights with co habiting females, whilst subordinate males maximise their chance by 'sneaking' copulations with unguarded females. Further support for this theory in *C. porosus* populations comes from the genetic analysis of eggs collected from nests in the wild, which showed multiple paternity is widespread with some clutches having more than two sires [40].

A surprising observation that contradicts much of the literature [6,15] was the sustained high daily rates of movement exhibited by all the tagged *C. porosus*. Even the site fidelic males travelled hundreds of kilometres during the study, albeit within a discrete area. Translocated male *C. porosus* have been previously reported to have travelled over hundreds of kilometres in a quest to return home [16,41,42]. These were however, considered extreme rates of movement, undertaken by the individual only because of the manipulated conditions and a strong homing instinct. On the contrary, high frequency GPS based location sampling revealed

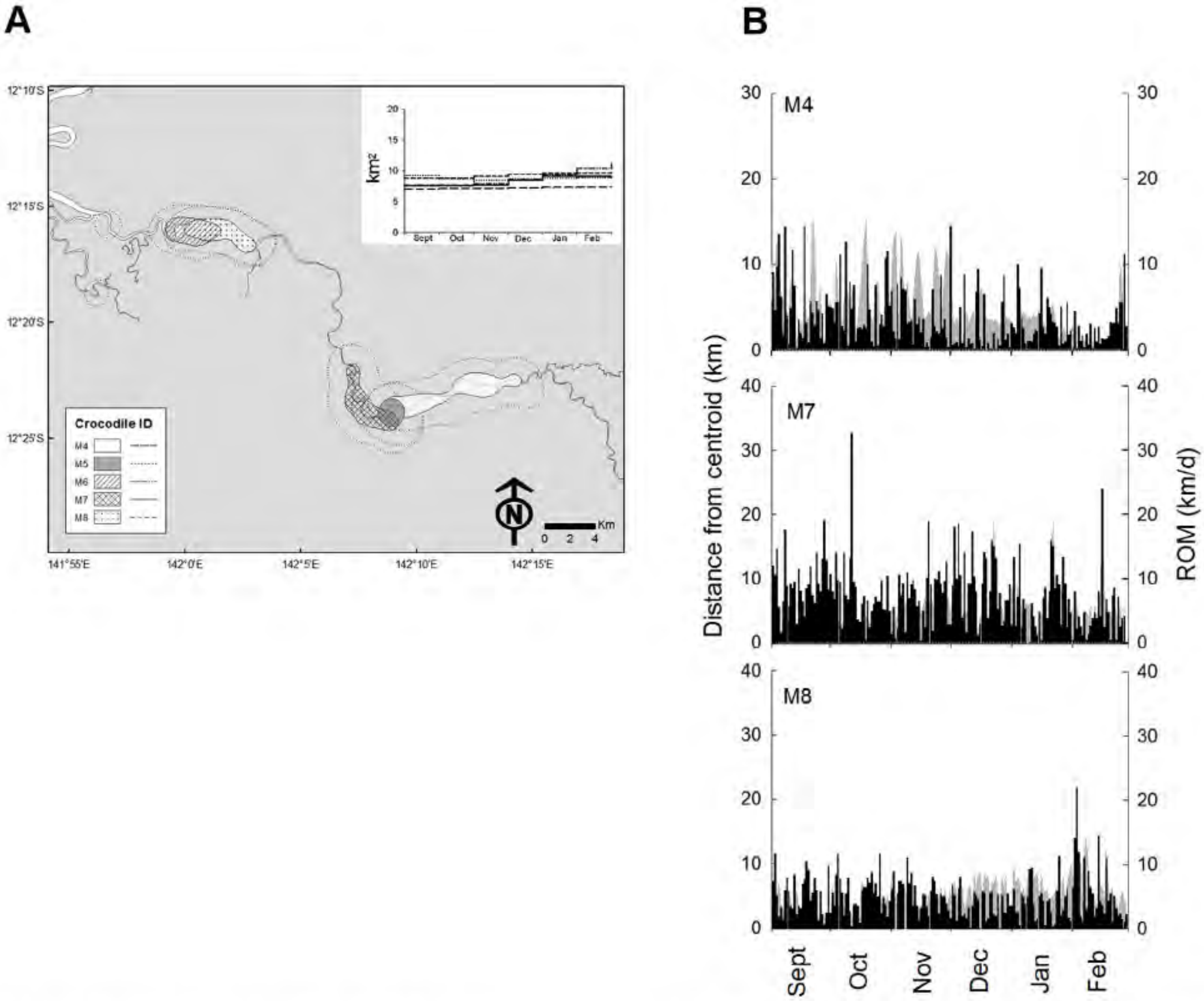

Figure 4. Movement patterns of 'site fidelic' male Crocodylus porosus. (a) KUD 50% and KUD 95% (dotted boundary) calculated from GPS location fixes recorded between 01 September and 28 February (n = 5). Inset graph shows the monthly cumulative KUD 95% for each individual. (b) The relationship between daily rate of movement (ROM) and daily distance from the KUD 50% centroid (grey = primary y axis; black = secondary y axis).
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that adult male *C. porosus* are extremely active animals routinely moving many kilometres per day. Presumably, it is because dominant males move back and forth within the confines of a territory that lower rates of location sampling or anecdotal observations have given the impression of far lower potential for movement in *C. porosus*.

Table 2. The results from two general linear mixed-effects models to examine the covariates and factors influencing daily rate of movement (ROM) and site-fidelity for *Crocodylus porosus* (male = 8; female = 4).

		Daily ROM		Daily distance from KUD 50% centroid	
	DF	**F**	**P**	**F**	**P**
Sex	1,9	19.67	0.001	0.99	0.76
Body mass	1,9	0.29	0.6	1.3	0.27
Date	1,2158	4.8	0.02	629	0.0001

doi:10.1371/journal.pone.0062127.t002

Female movements

In northern Australia, *C. porosus* nest from November through until March [43]. The time between copulation and the laying of eggs in captive *C. porosus* is between 4 to 6 weeks [6], and therefore, courtship and mating may occur anywhere between the end of September and early December. During this period our tagged female *C. porosus* confined their movements within a few kilometres of the main trunk of the river. It has been suggested previously that female *C. porosus* remain close to the nesting location throughout the year [43]. This was not the case in the present study however, and all our tagged females travelled considerable distances (up to 54 km) to a location where we presume they nested (based upon movements that were representative of attentive nest guarding). Such large movement between the breeding and nesting site has

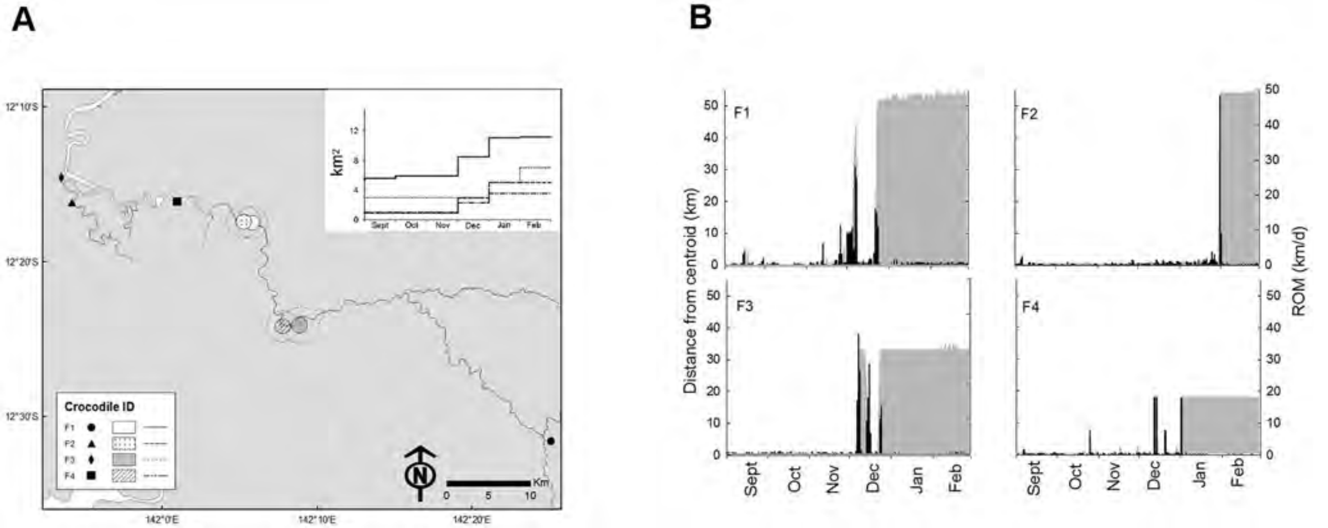

Figure 5. Movement patterns of female Crocodylus porosus. (a) The KUD 50% and KUD 95% (dotted boundary) calculated from GPS location fixes recorded between 01 September and 28 February (n = 4). Inset graph shows the monthly cumulative KUD 95% for each individual. (b) The relationship between daily rate of movement (ROM) and daily distance from the KUD 50% centroid (grey = primary y axis; black = secondary y axis).
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not been reported previously for female *C. porosus*, and may be reflective of the local environment.

The females that were captured and tagged in this study inhabited the tidal freshwater reaches of the river. In this area, the river is relatively narrow and bordered by steep sandy banks sparsely covered with *Melaleuca* trees. The river would be fast flowing through this section in the wet season, and this location does not contain good nesting habitat for *C. porosus*. Prior to nesting, three out of the four tagged females travelled downstream to a much wider, saline brackish, section of the river. In this stretch, the river is bordered by thick stands of mangrove, *Nypa* palms and salt marsh; vegetation and habitat that is much more suited for *C. porosus* nesting [44]. Moreover, this section of the river contains a disproportionally high density of hatchling *C. porosus* compared to other stretches of the river [10]. This suggests that female migration into this area may be a common behavioural strategy within the local population. One of our tagged females did however; migrate over 40 km upstream from the breeding area to the nesting location. This area did not appear to be ideal *C. porosus* nesting habitat [44], but there was a large permanent freshwater swamp in close proximity.

It seems reasonable to assume that the tagged female *C. porosus* travelled long distances to a nesting location because of better nest building materials, access to freshwater, and a reduced likelihood of the nest being flooded during the wet season [44]. What is less clear is why the females did not breed in the locality of the nesting areas and save themselves from these energetically expensive journeys. A possible reason is that the breeding area had better resources than at the nesting areas. Over a four year period we have laid numerous traps throughout a 60 km stretch of the Wenlock River but only caught females of breeding size within a few discrete locations (Campbell, personal observation). The GPS location data revealed that during the breeding period the females exhibit high site fidelity to these areas. We argue that these breeding areas are located within productive sections of the river, and the females select these areas in order to build up fat stores for egg gestation and nesting. If this is true then it suggests that *C. porosus* have a social system based upon resource based mate choice. That is, the females select areas containing the best resources and the males defend territories around these areas to maximise their mating opportunities [45,46]. Further investigation is required to confirm this social structure, which would have profound influence upon population density and distribution.

A novel observation of this study was that three out of the four tagged females travelled to the locality of the nest site a few weeks prior to the actual nesting movement. These journeys would have required considerable energetic expenditure, and therefore are likely to have offered some advantage to the offspring. We can only speculate on what this may have been, and the motivation for this repeated movement so close to nesting remains an avenue of future investigation.

Effects upon the ecosystem

The movements of the 'nomadic' and the 'site fidelic' males would have resulted in very different feeding opportunities and likely required disparate foraging strategies. The 'nomadic' *C. porosus* would need to select a variety of prey items from freshwater and saline brackish ecosystems, whilst 'site fidelic' *C. porosus* would need to take prey whenever it was available within the limits of their home range. Consequently, *C. porosus* are likely to vary in their degree of individual specialisation across spatial scales. Stable isotopic studies upon the tissues of American alligators (*Alligator mississippiensis*) in the Florida Everglades revealed a population composed of both generalist and specialist feeders [46]. There was a strong correlation between ingested prey items and broad scale movements, and we argue that alternative behavioural tactics driven by social status may have underpinned the observed diet selection by individuals.

When highly mobile predators move rapidly between habitats and feed on a variety of prey species, they create habitat linkages which transport nutrients and energy between systems [5]. A predator that rapidly moves between habitats and switches prey will stabilise the ecosystem by increasing pressure upon one channel of energy whilst freeing up a depleting energy channel from strong predatory pressure [3]. In contrast, a sessile predator may take food whenever available, resulting in negligible transport of energy or nutrients. The dichotomy of movement strategies observed in this study for adult *C. porosus* would result in very different top down regulation upon trophic interactions and the coupling of ecosystems and habitats. Consequently, understanding the relationship between *C. porosus* density, spatial movement, and home range dynamics are important in defining the wider community and ecosystem effects of a growing *C. porosus* population.

Implications for management

Since the legislated protection of *C. porosus* there has been a general increase in population abundance across northern Australia. Within some rivers, crocodile density has remained stable for the last 10 to 20 years whilst total crocodile biomass has continued to increase, whereas other rivers are increasing in crocodile density but with no matching increase in total biomass [14]. The social dynamics of the *C. porosus* in this study may aid to explain some of these observed trends. For example, the theory of female resource based mate choice [47,48] in *C. porosus* would serve to stabilise population density in areas of good crocodile habitat, and because displacement is unlikely to be achieved by a smaller rival, total crocodile biomass of the area would increase over time. Conversely, rivers or areas with fewer resources would not be selected by females, and dominant males would not hold territories around these areas. Therefore, the population in these poorer quality habitats is primarily composed of smaller subordinate crocodiles, with density but not biomass increasing over time.

Estuarine crocodiles pose a potential risk to the public and a management intervention implemented across northern Australia is to remove crocodiles from around urban centres and areas of high human visitation [48]. A high majority(>75%) of the *C. porosus* captured in permanently set traps are males between 2 and 3 m total length (Yusuke Fukuda, Scott Sullivan, personal communication), and the high rates of movement exhibited by the subordinate males in this study explains this capture bias. Although implemented less frequently, the removal of dominant male *C. porosus* is also considered as a viable management intervention to reduce crocodile density in particular areas. We recommend that the impact of this management intervention is thoroughly evaluated because, as has been shown for other vertebrate species, dominant male removal can cause social perturbations and can increase movement and immigration from neighbouring areas [49,50,51]. Only by thorough evaluation of each management intervention, taking into account any consequences of social perturbation, can the desired outcome be achieved in the management of *C. porosus*.

Acknowledgments

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Author Contributions

Conceived and designed the experiments: HAC CEF. Performed the experiments: HAC TRI CEF. Analyzed the data: HAC RGD. Wrote the paper: HAC RGD.

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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 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 ($r^2 = 0{\cdot}92$, $P < 0{\cdot}0001$).

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 km^2 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 rivers 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 downriver 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 sutra; 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 collated 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/oceancurrents/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

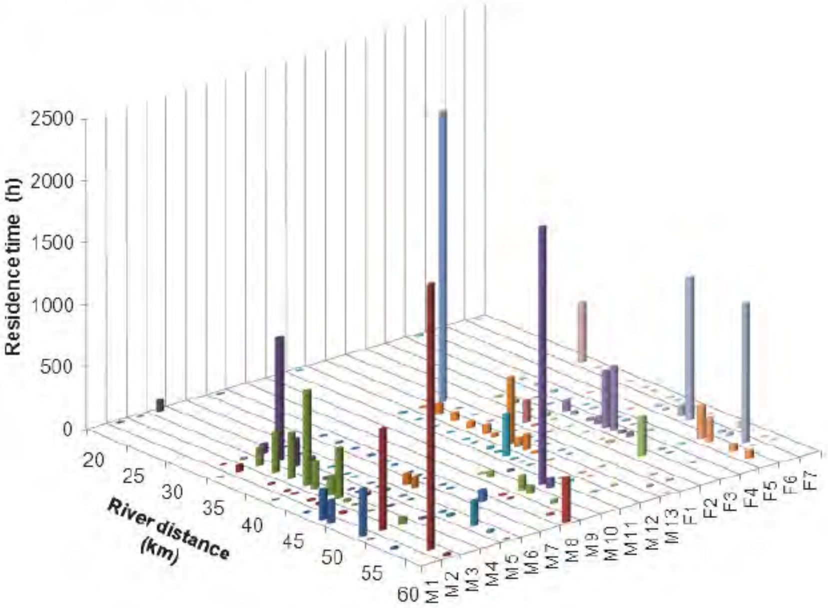

Fig. 1. The amount of time (h) that each acoustically tagged *Crocodylus porosus* (n 20) spent at discrete locations along the Kennedy River. River distance is expressed km from the River mouth. Crocodile ID is on the z axis (M, male; F, female), Crocodiles M2, M3, M5, M7, M11, F4 & F7 all undertook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

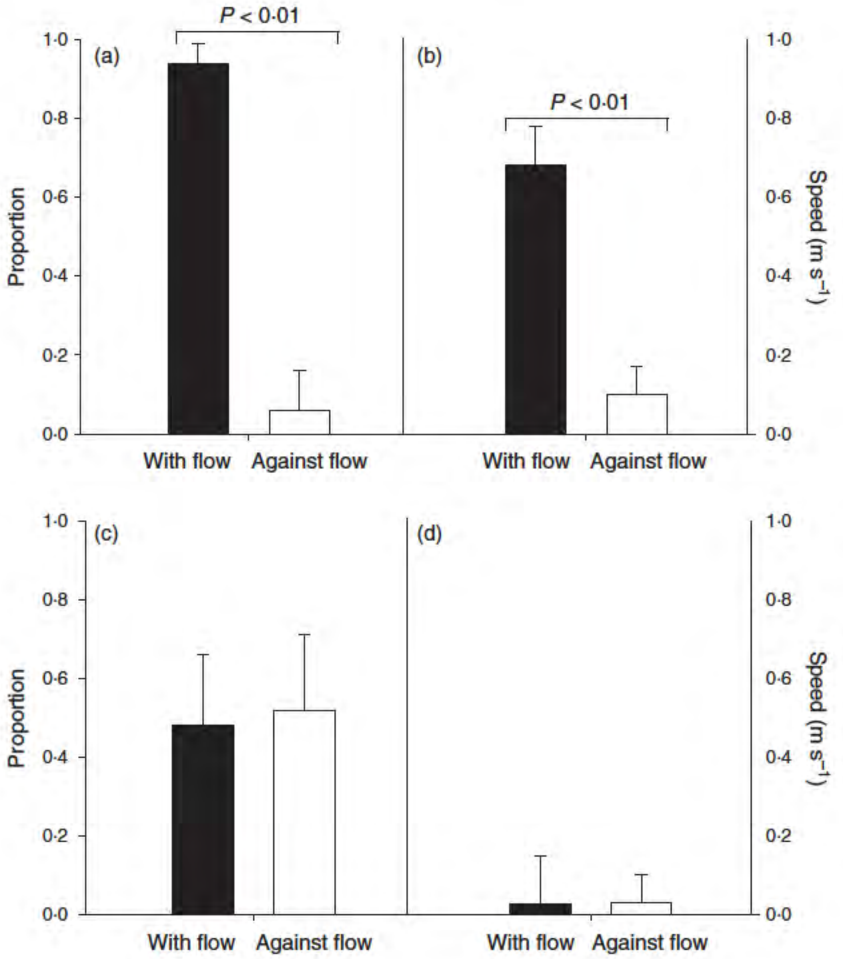

Fig. 2. The effects of current directional flow on movement during long and short distance travel in *Crocodylus porosus* (n 8). The black bars show movement when the current was flowing in the same direction as the travelling crocodile and the clear bars demonstrate movement when the current was flowing 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 ± 0·10 m s^{-1} and the rate of movement upstream was 0·58 ± 0 05 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 equilibrated 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 ± 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

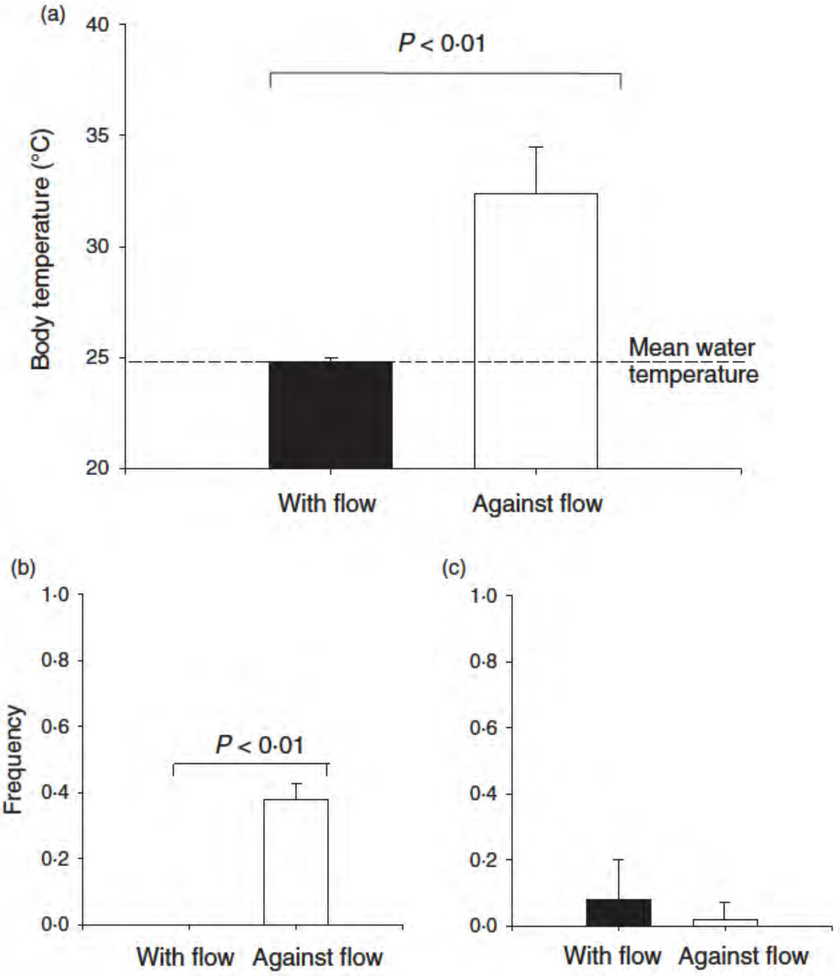

Fig. 3. The effect of current flow direction on river exiting in *Crocodylus porosus*. (a) The maximum body temperature recorded for each hour during long distance journeys (n 42, N 2). (b) The proportion of time spent out of the water when engaged on journeys when the daily distance travelled was > 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 ± S.E., n 127), but dives could last up to 1 h. During periods of unfavourable tidal flow the crocodiles spent 42% ± 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 significant 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

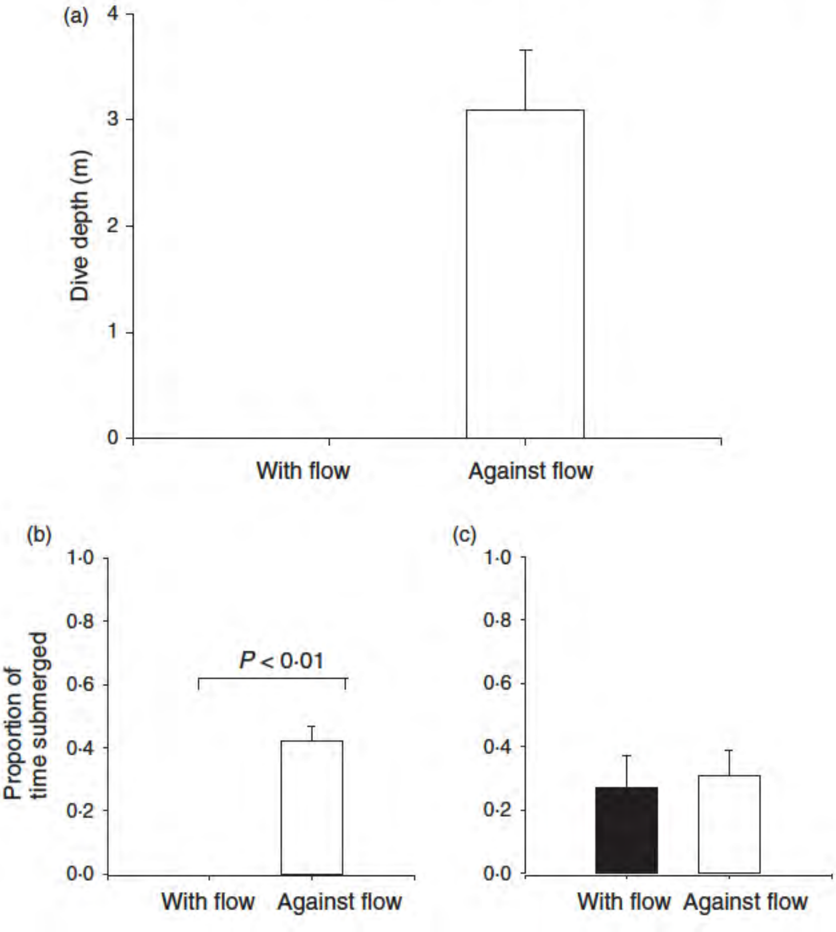

Fig. 4. The effect of current flow direction on diving in *Crocodylus porosus*. (a) The maximum depth dive attained during each hour during long distance travel (n 190, N 6). (b) The amount of time spent submerged when engaged on journeys when the daily distance travelled was >10 km in a constant direction. (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.

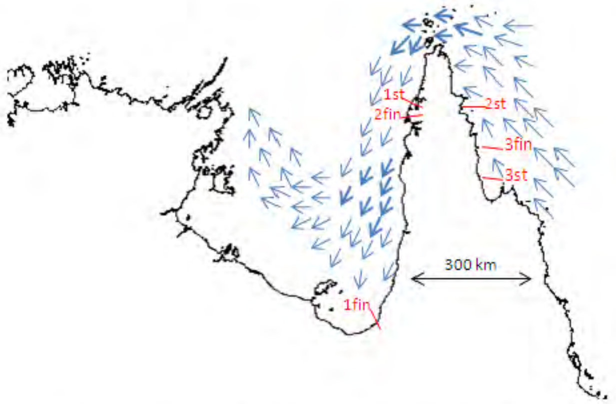

Fig. 5. Schematic diagram showing the coastal travel by three adult *Crocodylus porosus* around Cape York Peninsula, Northern Australia. Start (st) and finish (fin) locations for each journey are shown for crocodile: (1) a 3·84 m male travelled between the 18th December, 2004 to 11th January, 2005; (2) 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 m s^{-1}, thick arrows >0·3 m s^{-1}).

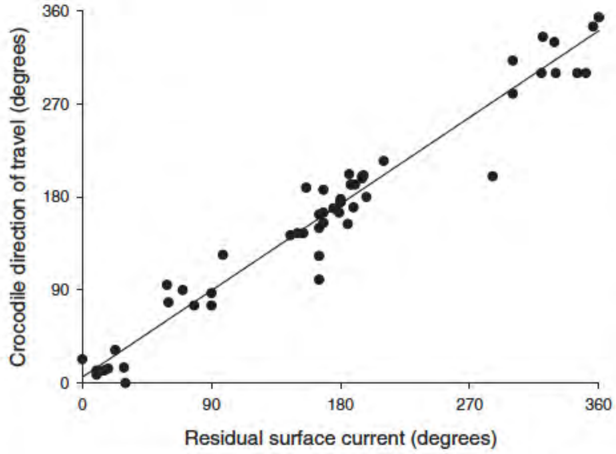

Fig. 6. The relationship between residual surface current direction and the bearing in which *Crocodylus porosus* moved between consecutive satellite fixes (n 56, N 3,). Y 0·91X + 10·4, r^2 0·92.

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 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 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 km in 19 days, the average speed of movement between successive satellite fixes was 0·41 ± 0·08 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 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. novaeguneae, 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 km^2, 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.

Acknowledgements

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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.

Summary of Worldwide Crocodilian Attacks for 2015

Article · January 2016

Brandon Sideleau
Charles Darwin University

Proceedings of 23rd CSG Working Meeting (Louisiana, USA; May 204) now available

The Proceedings of the 23rd CSG Working Meeting (Lake Charles, Louisiana, USA, May 2014) are now available as an electronic version (www.iucncsg.org - under Publications) and hard copy.

Registered participants who attended the Working Meeting will receive a complimentary copy of the Proceedings. Additional copies are being offered at $US35, to help cover the costs of postage. Please contact Dr. Mark Merchant directly (mmerchant@mcneese.edu) for further information.

Tom Dacey. *CSG Executive Officer (csg@wmi.com.au)*.

SUMMARY OF WORLDWIDE CROCODILIAN ATTACKS FOR 2015. At CrocBITE (www.crocodile-attack.info) we compile records of crocodilian attacks worldwide from all time periods. For 2015 we recorded 323 attacks resulting in 151 deaths from 37 different countries (Tables 1-4) and 13 different crocodilian species (Table 5). While each year our methods and sources for obtaining crocodilian attack records improve, there are still some notable gaps in our data. Much of the range of the Nile crocodile (*Crocodylus niloticus*) has generally poor reporting in regards to attacks. In many of these countries (eg Burundi, Ethiopia, Somalia) reporting is virtually non-existent, while in other countries (eg Democratic Republic of the Congo, Malawi, Mozambique, Uganda) the small number of records we find or receive are a small fraction of the attacks that actually occur. Namibia, South Africa, Zambia, and Zimbabwe are exceptions, and a wealth of attack data have been identified for these regions. For the Saltwater crocodile (*C. porosus*) the entire island of New Guinea (particularly the Indonesian provinces of Papua and West Papua) continues to be problematic in regards to attack data collection. A source in the Purari River Delta of Papua New Guinea provides some records for Gulf Province every year (and suggests attacks are frequent) and a few reports from the islands of New Britain and Bougainville usually reach the media but the vast majority of attacks are not reported or are only reported at a local level. The same is true of the Solomon Islands, and in 2015 we did not find or receive a single attack record from the archipelago, although it seems likely that attacks occurred. In addition, Timor-Leste is no longer reporting crocodile attacks

Table 1. Crocodile attack statistics for Africa in 2015.

Country	Fatal	Non-fatal	Total
Angola	3	4	7
Botswana	1	3	4
Dem. Repub. of Congo	8	0	8
Guinea-Bissau	2	0	2
Kenya	3	1	4
Madagascar	2	1	3
Malawi	6	0	6
Mozambique	5	1	6
Namibia	8	1	9
South Africa	1	1	2
Sudan	1	0	1
Swaziland	0	1	1
Tanzania	1	3	4
Uganda	3	0	3
Zambia	7	7	14
Zimbabwe	7	6	13
Totals - Africa	**58**	**29**	**87**

Table 2. Crocodile attack statistics for Asia in 2015.

Country	Fatal	Non-fatal	Total
Brunei	1	0	1
India	20	38	58
Indonesia	26	38	64
Malaysia	13	8	21
Nepal	1	1	2
Philippines	1	3	4
Sri Lanka	10	3	13
Timor-Leste	2	1	3
Totals - Asia	**74**	**92**	**166**

Table 3. Crocodilian attack statistics for the Americas in 2015.

Country	Fatal	Non-fatal	Total
Argentina	0	1	1
Brazil	3	6	9
Colombia	1	2	3
Costa Rica	0	2	2
El Salvador	0	1	1
Guyana	0	1	1
Jamaica	0	1	1
Mexico	7	20	27
Panama	0	1	1
Peru	0	2	2
USA	3	7	10
Totals - Americas	**14**	**44**	**58**

Table 4. Crocodile attack statistics for Oceania in 2015.

Country	Fatal	Non-fatal	Total
Australia	0	7	7
Papua New Guinea	5	2	7
Totals - Oceania	**5**	**9**	**14**

Table 5. Crocodilian attack statistics by species for 2015.

Species	Fatal	Non-fatal	Total
Crocodylus niloticus	56	29	85
Crocodylus porosus	55	61	116
Crocodylus palustris	21	33	54
C. porosus or *C. palustris*	3	0	3
Crocodylus acutus	5	17	22
Crocodylus moreletii	2	8	10
C. acutus or *C. moreletii*	0	1	1
Crocodylus suchus	2	0	2
Crocodylus johnstoni	0	3	3
Melanosuchus niger	3	7	10
Alligator mississippiensis	3	7	10
Caiman crocodilus	1	1	2
Caiman latirostris	0	2	2
Caiman yacare	0	1	1
Tomistoma schlegelii	0	4	4

on a consistent basis (the fisheries website appears to have stopped adding attacks in early 2014; http://peskador.org/incident.php) despite attacks continuing to be frequent; most reports now come from social media (eg photos of victims and/or crocodiles killed in retaliation posted on Facebook) or on rare occasions a Tetum language media source. In contrast, reporting from Indonesia appears to be improving and even attacks from remote provinces such as Maluku and North Maluku are now reaching the media. However, even given the increased level of news media reports, recent HCC surveys we conducted in the Kupang and Malaka regencies of West Timor, East Nusa Tenggara province revealed that only 54.5% of attacks from the 2007 through 2015 period were reported in the news media, with the remainder being recorded through village surveys and through contacting the local BKSDA offices. This suggests that a potentially high number of attacks continue to go unreported even in the Indonesian provinces for which we have records, particularly in the more remote provinces where online news media reports remain our only source of information.

There were several notable attacks and attack trends this year, including record worst years for fatal attacks in two areas and a fatal attack by what is generally considered to be an inoffensive species in another area. 2015 was the worst year on record for fatal *C. porosus* attacks in Sarawak (Malaysia) with a total of 13 attacks resulting in 9 deaths (the previous worst was in 2013 when 12 attacks resulted in 7 deaths).

It was also the worst year on record for fatal attacks in Mexico with a total of 27 attacks, resulting in 7 deaths. The Mexican attacks were attributed to the American crocodile (*C. acutus*) (16 attacks resulting in 5 deaths) and Morelet's crocodile (*C. moreletii*) (10 attacks resulting in 2 deaths); in one non-fatal case the culprit species was undetermined as both species were present in the immediate area. Of particular note is the very high level of conflict with *C. acutus* in the Lazaro Cardenas area of Michoacan State, particularly within the Barra de Santa Ana Estuary where 4 attacks resulting in 2 deaths were reported (one of the fatal attacks was caught on video); the total number of attacks for the Lazaro Cardenas area was 8 (including the 4 attacks in Barra de Santa Ana). In addition, a fatal *C. acutus* attack was reported from Nichupte Lagoon in the popular tourist destination of Cancun in Quintana Roo State; this is the first death we have recorded from the area, although non-fatal attacks are not uncommon. The fatal *C. moreletii* attacks occurred in Tabasco State (Balancan) and Quintana Roo (near Chetumal and the Belizean border).

This was also a particularly notable year for *C. porosus* attacks in East Kalimantan Province of Indonesia, where 11 attacks resulting in 8 deaths were reported. These attacks ranged from Balikpapan north through the Mahakam River Delta (Kutai Kartanegara regency) into East Kutai regency (particularly the Sangatta and Bengalon Rivers). Apparently, a large number of crocodiles were killed in East Kutai regency in response to the increased attack frequency (Rima News). The total number of reported attacks in Borneo (including Brunei, Kalimantan and Malaysia) in 2015 was 34 resulting in 22 deaths. Interestingly, for the 2007-2015 period the Malaysian state of Sarawak (in western Borneo) and East Kalimantan (Indonesian eastern Borneo) have the same number of fatal attacks reported (37 each), although it is possible some fatal attacks were unrecorded for East Kalimantan during the earlier years prior to active compiling of data (2007-2010). This is unlikely to be the case in Sarawak as attacks are believed to be comprehensively recorded within the state (CrocBITE 2016).

In a small number of cases worldwide each year it is difficult to determine exactly which species is responsible for an attack. This is most often the case when two potentially dangerous species inhabit the same area. In 2015 there were 3 fatal attacks reported from the Eastern Province of Sri Lanka in areas where both *C. porosus* and the Mugger (*C. palustris*) are present. Both species have been responsible for many fatal attacks in Sri Lanka in recent years, so this made identifying the culprit very difficult; these attacks took place in Panama, Pottuvil and Batticaloa (CrocBITE 2016). No crocodile surveys have been conducted in Sri Lanka's Eastern Province, although both species are known to be present in each area. Although older maps of the *C. porosus* distribution in Sri Lanka limit the species to the western and southern coasts, this is not the case and the species is actually found along the eastern coast from Panama to as far north as Trincomalee (Samarasinghe 2014; Rom Whitaker, pers. comm.).

In January an infant was reported to have been killed by a crocodilian in the Issa Oristuna reservation area of Sabanas de San Angel municipality in Magdalena, Colombia. All evidence suggested the culprit in the attack was likely a Spectacled caiman (*Caiman crocodilus*) (CrocBITE 2016). While this may be surprising given the maximum size of the species and the general view that it does not pose a threat to humans, a small infant is well within the size range of adult caiman prey items (www.crocodilian.com 2016). While this is the first fatal incident we have recorded for the species, there are numerous records of non-fatal incidents (both provoked and unprovoked), particularly within Colombia. From 2007 to 2015 we recorded 20 attacks involving *C. crocodilus* (including the aforementioned incident), mostly from Brazil and Colombia, but also single incidents from Suriname and Trinidad. While many of these incidents involved fishermen accidentally stepping on caiman and being injured by defensive attacks, some cases appeared to be unprovoked and even involved people walking on land (of particular note is an incident in 2009 in Trinidad when a woman sustained serious injuries when she was attacked by a caiman while crossing a bridge en route to her place of employment) (CrocBITE 2016).

The first fatal American alligator (*Alligator mississippiensis*) attacks since 2007 also occurred in 2015, with 3 deaths reported, including the first fatal attack ever recorded in Texas. On 3 July 2015 a 28-year-old man named Tommie Woodward was killed by a 3.4 m alligator at a location known as Adam's Bayou in Orange County, Texas. He had apparently ignored warning signs and warnings from local residents and proceeded to swim in the early morning hours. The other two fatal attacks occurred in Florida - one on 19 October within the St. John's River of Blue Springs State Park and the other on 13 November at a pond in Barefoot Bay; neither of these attacks was witnessed and death by alligator attack was determined postmortem (CrocBITE 2016).

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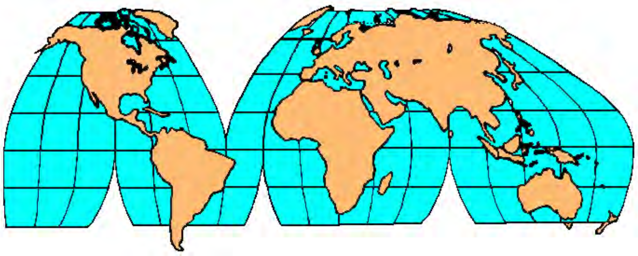
Regional Reports



West and Central Africa

THIRD REGIONAL WEST AND CENTRAL AFRICA REGIONAL MEETING. The 3rd West and Central Africa (WACA) Regional Meeting was held in Côte d'Ivoire on 8-10 December 2015. The meeting was convened at the University of Nangui-Abrogoua in Abidjan, and brought together a dynamic group of over 50 crocodile scientists from the region.

The theme for the meeting was "Crocodile Management Issues Across a Complex Landscape", and, the presentations reflected the diversity of research and approaches to conservation from Guinea in the west of the region to the Democratic Republic of the Congo in the east.

A successful fundraising drive ensured that sufficient funds were available to bring delegates to the meeting from 15 regional countries (Benin, Burkina Faso, Cameroon, Central African Republic, Côte d'Ivoire, Democratic Republic of Congo, Gabon, Ghana, Guinea, Liberia, Niger, Nigeria, Senegal, Sierra Leone,Togo), representing government institutions, NGOs, universities and research institutions, and the private sector.

In addition, key crocodile conservation experts from beyond the African continent also attended the meeting, including CSG Chairman Professor Grahame Webb (Australia), CSG Regional (WACA) Chairmen, Dr. Samuel Martin (France) and Dr. Matt Shirley (Gabon/Cote d'Ivoire), CSG Regional (WACA) Vice-Chairman Christine Lippai (South Africa/USA), CSG IUCN Red List Authority Dr. Perran Ross (USA), and a full complement of CSG members from Europe and the USA. A full list of all participants will be available in the Proceedings.

Presentations dealt with various topics, including: the interaction between crocodiles and people; livelihoods and bush-meat trade; land-use planning and ecotourism; and, community management of wetlands. These are all key issues identified as common concerns throughout the region. An additional common issue revolved around the need for National Crocodile Conservation Strategies, which many believed would assist with crocodile management and conservation in their respective countries.

Selected key discussion points included the following:

- Bushmeat trade: this is a big issue in Nigeria and Gabon. In Nigeria, a rapid assessment was carried out to obtain

Queensland Estuarine Crocodile Monitoring Program 2016–2019

Key Findings Report

#32064

Queensland Government

Introduction

In Queensland, the estuarine crocodile (*Crocodylus porosus*) occurs in a coastal strip from Gladstone northwards along the east coast, throughout the Cape York Peninsula, and across the Gulf of Carpentaria to the Northern Territory border. Estuarine crocodiles are not uncommon on offshore islands of the Great Barrier Reef and Torres Strait. Queensland has some of the most diverse crocodile habitat in Australia.

In the previous century, unregulated hunting of estuarine crocodiles for their skins led to a decline in the population and effective commercial extinction of the species, resulting in full legal protection by 1974. The crocodile population in Queensland has since increased, but the species is still listed as Vulnerable under state conservation laws. Current threats to Queensland's population arise from illegal killing, incidental mortality, destruction of nesting habitat by feral pigs, and land development.

Since 1975, there have been 46 estuarine crocodile attacks on humans in Queensland, 16 of which have been fatal. The average of 0.3 fatalities per year is much lower than deaths from sharks – 1.1 deaths per year (West, 2011). Most of these attacks occurred along the coast between Townsville and the Daintree River, and as in the Northern Territory, the majority impact local, adult males (Brien et al. 2017). Each fatality is a tragedy and makes balancing the responsibilities of conservation and public safety more challenging.

From 2016 to 2019, the Department of Environment and Science conducted a comprehensive monitoring program of the estuarine crocodile population across its range in Queensland. During 2020, the department compiled and analysed data collected through this program and compared these to historic data to assess how the population had changed in size, distribution, density, and size class structure over time–using results collected from as far back as 1979.

Summary of key findings

The size of the estuarine crocodile population in Queensland is currently estimated at 20,000–30,000 non-hatchlings, with an average of 1.7 crocodiles and 36kg of crocodile biomass[1] per kilometre of river surveyed.

For comparison, the population of estuarine crocodiles in the Northern Territory is three to four times larger (100,000), three times more abundant (5.3/km) and has a ten times higher biomass per kilometre (388kg/km) than in Queensland (Fukuda et al. 2011, 2020).

The population started from a very low base and recovery has been relatively slow and highly variable across the state.

The spatial distribution of crocodiles in Queensland has not changed over time, and there is no evidence of a southward expansion of their range.

The number and density of crocodiles are highest in northern Cape York Peninsula (3.0/km) and decline southward, with 1.2/km in the Gulf of Carpentaria and the Cairns region, down to 0.2/km in the Fitzroy River, Rockhampton.

That section of coastline from Cooktown to Rockhampton accounts for around 20% of the Queensland crocodile population.

The crocodile population in Queensland is highly unlikely to reach the size or density of the Northern Territory due to the lack of suitable habitat.

While the crocodile population has continued to increase relatively slowly along the east coast between Cooktown and Ayr, the average size of crocodiles has reduced in this area. This is likely to be a consequence of the regular removal of 'problem crocodiles' under the Queensland Government's crocodile management program.

Queensland has seen the recovery of a threatened species that is a large predator, while at the same time seeing a reduction in the risk to public safety.

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[1] Biomass refers to the mass of crocodiles in a particular section of waterway as opposed to the number (density) of individuals

Methods

Figure 1. State-wide survey effort showing areas covered in 2016-2019 by: boat-based spotlight surveys (56), including 42 rivers and covering 2200km; and helicopter surveys (14), including 27 rivers covering 2500km.

In 2016, the Department of Environment and Science embarked on a comprehensive crocodile monitoring program involving systematic spotlight and helicopter surveys in carefully selected, previously surveyed areas of river systems throughout the state.

During the 2016-2019 program a total of 56 boat surveys were conducted in 42 rivers covering 2,200 km, and a total of 14 helicopter surveys were conducted in 27 rivers covering 2,500 km (**Figure 1**). This included rivers as far south as Maryborough on the east coast, through to Cape York Peninsula and the Gulf of Carpentaria.

The survey teams consisted of highly skilled departmental officers who were selected through a rigorous competency-based testing process and received intensive training from highly experienced crocodile biologists, who also provided ongoing support and quality control for the program.

This was the most comprehensive crocodile population monitoring program to be carried out in Queensland for more than a decade, with previous state-wide surveys occurring in 1979, 1984-89, and 1994-2003. The results of these historical surveys were compared and analysed with those of the current program.

The design of the program and subsequent analyses were peer reviewed and endorsed by members of the International Union for the Conservation of Nature (IUCN) Crocodile Specialist Group, which includes the world's leading experts on crocodilian biology and monitoring.

Overall population trends (numbers, density, biomass, and trajectory)

The size of the estuarine crocodile population in Queensland is currently estimated at 20,000 – 30,000 non-hatchling[2] crocodiles, with an average of 1.7 crocodiles and 36 kg of crocodile biomass[3] per kilometre of river surveyed.

There has been an increase in the crocodile population over time. However, there is no evidence of a 'large increase' now or into the future. Estimated doubling times[4] for crocodile numbers in Queensland range from 36 years on Cape York Peninsula, along the Gulf of Carpentaria and in the Cairns region, to up to 100 years in the Fitzroy River, Rockhampton.

The population started from a very low base due to previous hunting, and recovery has been relatively slow and highly variable across the state. For example, while numbers in some rivers appear to have stabilised as early as the 1980s (e.g. Wenlock River, north-western Cape York), some others continue to increase (e.g. Norman River, Gulf of Carpentaria).

The contemporary population of estuarine crocodiles in the Northern Territory is approximately 3-4 times larger (100,000), 3 times more abundant (5.3/km), and 10 times higher in biomass/km (388kg/km) than in Queensland. The population in Queensland is highly unlikely to reach the size or density of the Northern Territory due to the lack of suitable crocodile habitat across the state.

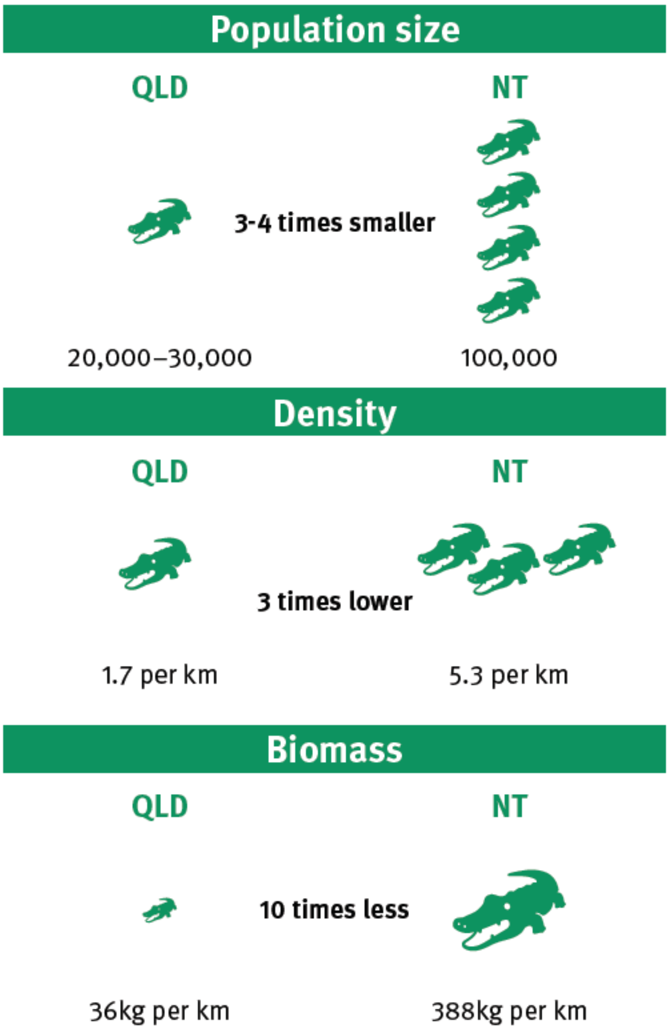

Figure 2. The contemporary population of estuarine crocodiles in the Northern Territory is 3-4 times larger (100,000), 3 times more abundant (5/km), and 10 times heavier/km (388kg) than in Queensland.

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[2] Only non-hatchling crocodiles >60cm in length are included in density estimates, as crocodiles smaller than this have very low survivorship

[3] Biomass refers to the mass of crocodiles in a particular section of waterway as opposed to the number of individuals per kilometre of waterway (density)

[4] The estimated time in years required for a doubling of the local population density

Results from the populated east coast management area (Cooktown to Ayr)

Management of estuarine crocodiles in Queensland is the responsibility of the Queensland Department of Environment and Science under the *Nature Conservation Act 1992* and Nature Conservation (Estuarine Crocodile) Conservation Plan 2018. The Queensland Crocodile Management Plan provides the current framework for the state-wide management of public safety risks associated with crocodiles. Under the management program, crocodiles that pose a threat to public safety are targeted for removal from the wild by the department or its contractors.

While the crocodile population continues to increase relatively slowly along the populated east coast between Cooktown and Ayr, the average size of crocodiles in this region has been reduced, which is likely to be a consequence of the Queensland Government's crocodile management program, with ~460 crocodiles (>2m; average: 2.3m) having been removed between 2004-2019.

While the absolute rate of non-fatal attacks (0.9 per year) in Queensland has increased over time, there has been no increase in the rate of fatal attacks (0.3 per year; Brien et al. 2017). The removal of larger crocodiles (~4m), capable of causing fatalities, from in and around populated areas on the east coast has likely contributed to this lack of increase in fatalities.

Distribution and range in Queensland

The spatial distribution of estuarine crocodiles in Queensland has not changed since the 1980s and there is no evidence of a southern expansion of their range. The crocodile population in Queensland is primarily riverine, with over 90% of the population existing below 20m elevation above sea level.

The number and density of crocodiles are highest in northern Cape York Peninsula (3.0/km) and decline southward, with 1.2/km in the Gulf of Carpentaria and Cairns regions, down to 0.2/km in the Fitzroy River, Rockhampton (Figure 4). This southerly reduction is a likely consequence of lower temperatures and less suitable habitat.

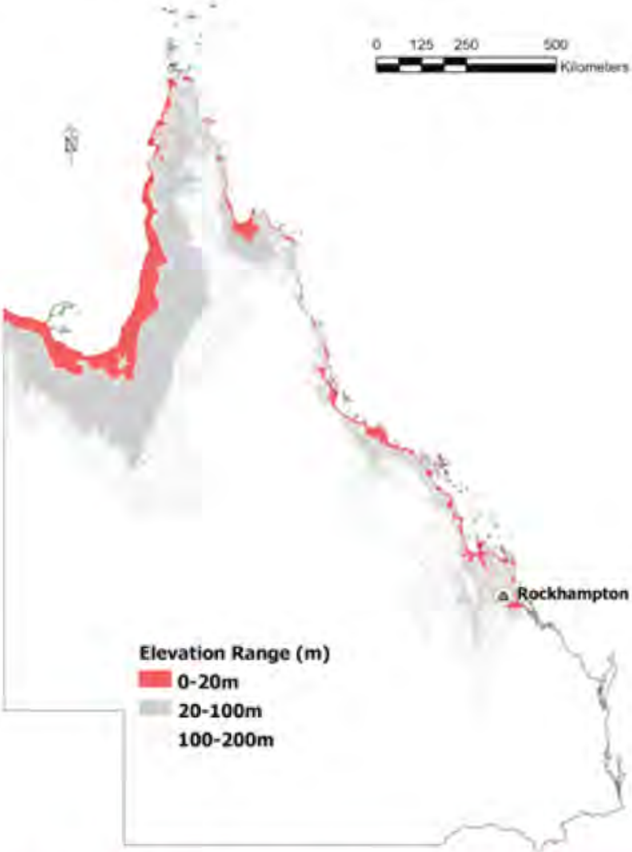

Figure 3. The majority (>90%) of the estuarine crocodile population in Queensland exists below 20m elevation above sea level, with a further ~9% at 20-100m elevation and ~1% at 100-200m elevation.

Regional variations

- North-western Cape York Peninsula is the most important source of nesting and recruitment in Queensland and contains almost 40% of the state's estuarine crocodile population.
- The Proserpine River, in the Whitsundays region, has the highest density of crocodiles (5.5/km) in Queensland, for reasons that are yet to be fully understood.

No crocodiles were detected in waterways south of the Fitzroy River, Rockhampton, during the monitoring program. While crocodiles are known to occur in waterways south of the Fitzroy River, they occur as individual animals rather than established populations and are best considered vagrants or non-breeding residents.

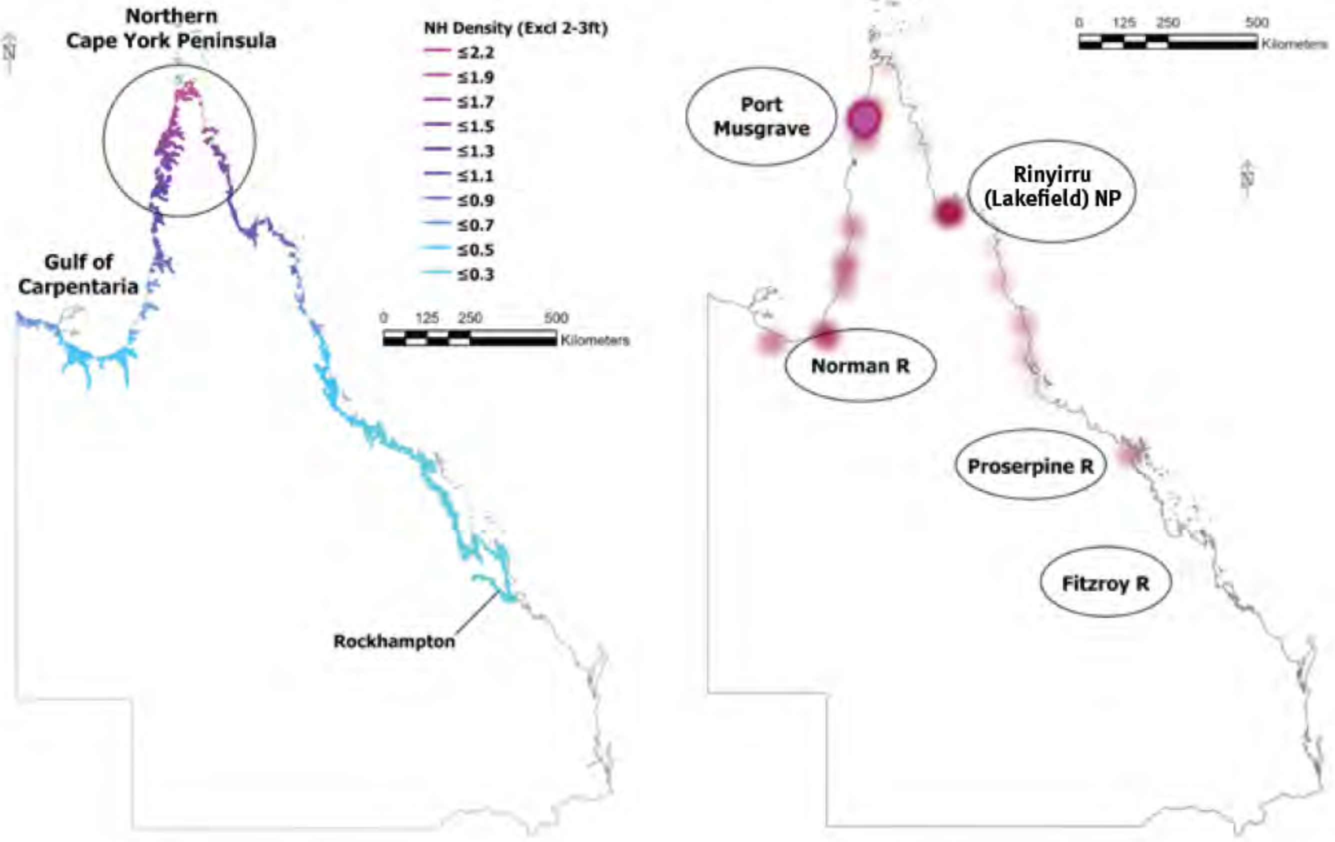

Figure 4. a) Crocodile densities are highest in northern Cape York Peninsula and decline southward; b) The far north-west of CYP contains 40% of the population, while Rinyirru (Lakefield) National Park and the Norman River are also key areas for nesting and recruitment. The Proserpine River has the highest density of any river in Queensland – 5.5/km, while the Fitzroy River represents the southern-most breeding population.

Where to from here?

Human-crocodile conflict will continue into the future. However, the modest growth rate of the crocodile population and the low to very low density of crocodiles across much of their range should allow for continuing effective management into the future. Key to this is the adoption and promotion of Crocwise behaviour.

The Department of Environment and Science will continue to actively monitor crocodiles into the future. It forms a key knowledge source to inform actions that improve both conservation and public safety outcomes. Rigorous and comprehensive monitoring allows future management models to become more responsive to population trends. This includes taking a proactive approach by identifying key areas for future management efforts and critical research.

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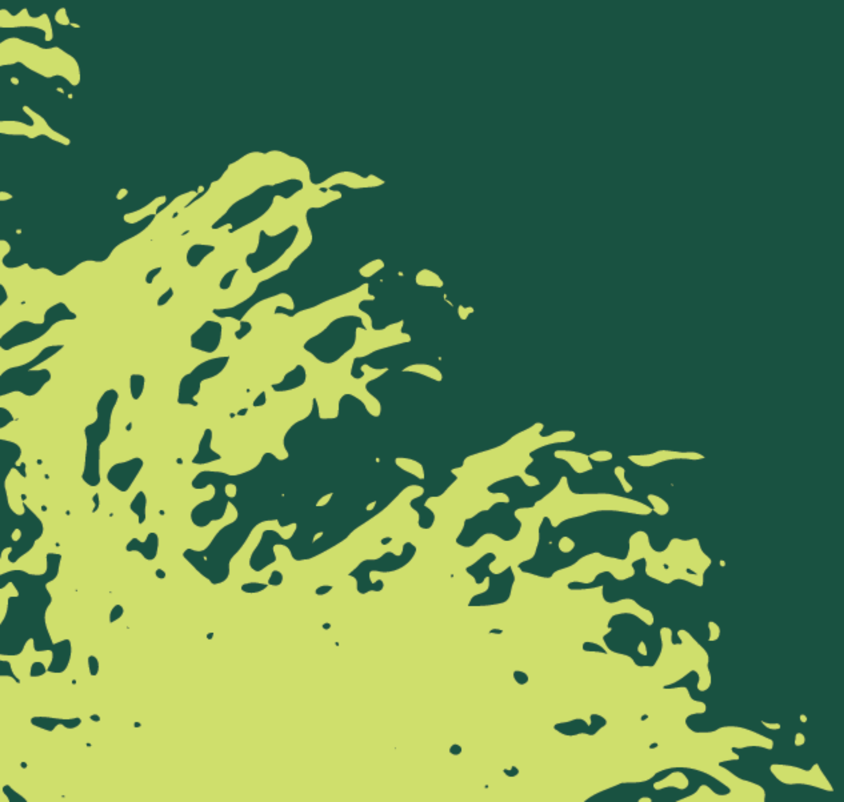

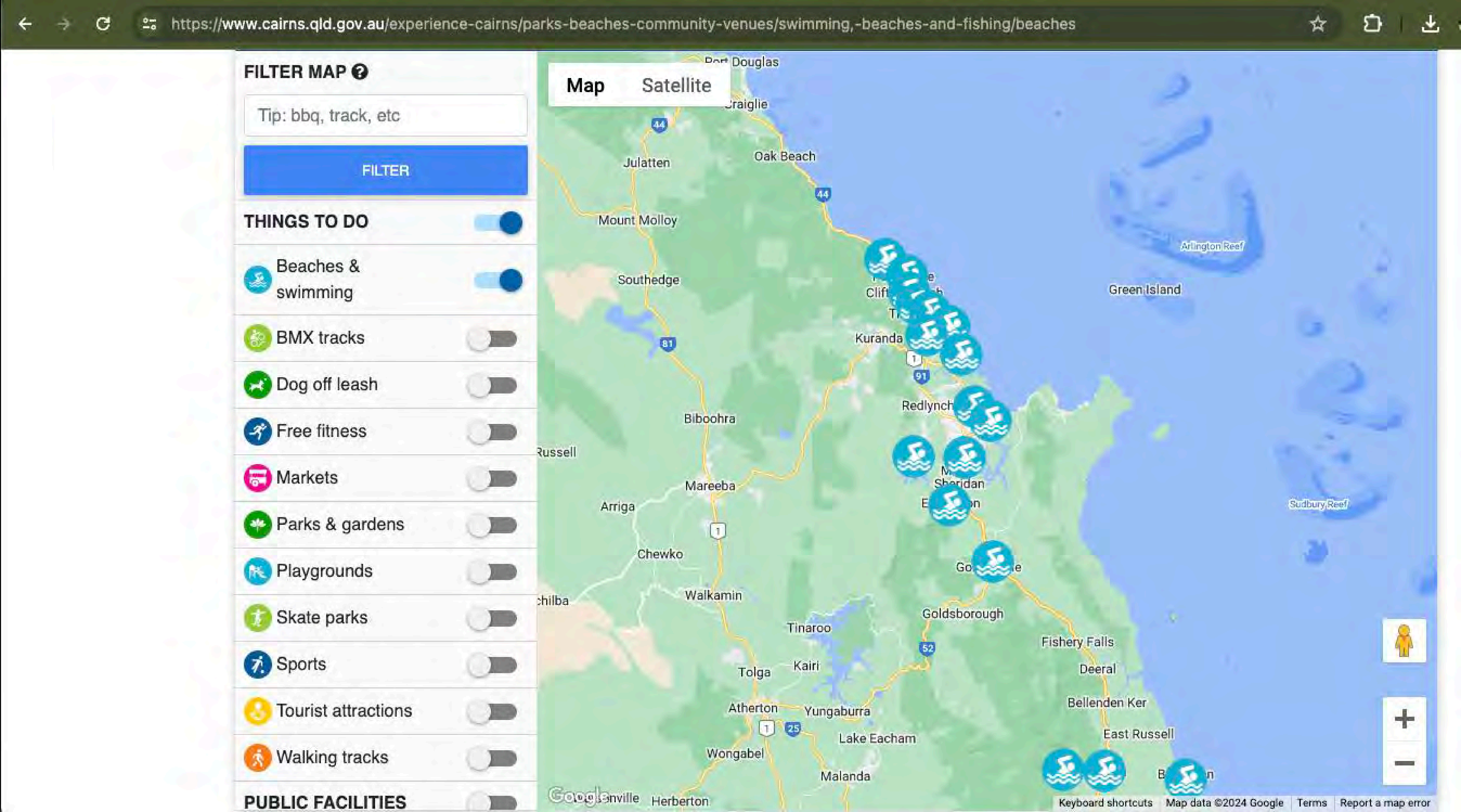

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Predicting the probability of large carnivore occurrence: A strategy to promote crocodile and human coexistence

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Predicting the probability of large carnivore occurrence: a strategy to promote crocodile and human coexistence

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Keywords
large carnivore; top predator; estuarine crocodile; maximum likelihood; acoustic telemetry; human–wildlife conflict; population estimation.

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Abstract

Preserving large carnivores that perceive humans as prey brings conservation values into direct conflict with human security. Informing when and where humans and large carnivores occupy the same space may reduce attack frequency and promote coexistence. Here, we demonstrate a methodology to better understand the spatiotemporal relationship between a population of large carnivores and humans. The carnivore of study was the estuarine crocodile *Crocodylus porosus*, a large semi-aquatic predator responsible for 705 recorded human attacks over the last 20 years. Crocodiles were captured every August over 3 years and individuals greater than 2.5 m in length were implanted with an acoustic transmitter ($n = 84$). The transmitter emitted a coded pulse detected when in proximity to underwater hydrophones deployed throughout the river. The telemetry data informed which previously captured crocodiles were present during subsequent trapping episodes and adult population size was estimated using a closed-population model. Over 3 years, 24 of the tagged crocodiles were detected 269 times moving through a shallow-water area where humans frequently entered the water. The tagged crocodile presence was extrapolated to the population level to provide a probability of adult crocodile presence across a range of temporal scales. The results showed that between September and December, the probability of crocodile presence within the human entry zone was 0.97 ± 0.01 during darkness but decreased to 0.07 ± 0.01 during daylight, except around periods of high tide when it increased to 0.71 ± 0.02. Human visitors confined their activity to shallow water during daylight hours, but no consideration was given to the significant rise in crocodile presence with season and tide. The observed patterns in crocodile and human behaviour, around this shallow-water river crossing, exhibited parallels with historical incidences of crocodile attack.

Introduction

Human population expansion is a major cause of species decline and biodiversity loss. Large carnivores are particularly vulnerable to human population expansion because of their feeding habits directly conflicting with humans and their resources (Jackson & Nowell, 1996; Woodroffe, 2000; Treves & Karanth, 2003). In places where large carnivores and people coexist, there are significant societal and political challenges for conserving these potentially dangerous species and persecution is widespread (Rasker & Hackman, 1996; Treves & Karanth, 2003; West, 2011). This includes direct killing by local communities (Kissui, 2008) as well as government-sponsored harvesting and eradication schemes (Barnett & Baston, 2013). Direct killing, as a consequence of human–wildlife conflict, remains the greatest threat to the persistence of many large carnivore populations (Weber & Rabinowitz, 1996; Woodroffe & Ginsberg, 1998).

Human attitudes towards large carnivores have, however, considerably changed in recent decades. This has occurred because of aesthetic reasons but also because the elimination of large carnivores has been shown to alter ecosystem structure and function (Estes *et al.*, 2011; Hines & Gessner, 2012), with trophic cascades being unleashed after the resident carnivore population was removed (Terborgh *et al.*, 2001; Ripple *et al.*, 2013). As a consequence, the preservation of large carnivores throughout their range is becoming of central concern to conservation managers (Metz *et al.*, 2012; Steinmetz, Seuaturien & Chutipong, 2013) and large carnivores are receiving protective status with prosecution of those who carry out retaliatory killings. Thus, what was once a simple relationship between carnivore and prey has turned into a political conflict between locals, conservationists, resource managers and policymakers (Löe & Röskaft, 2004; Treves *et al.*, 2006).

A suitable example of a species that generates discord, disagreement and controversy between local inhabitants, government and those seeking to preserve the population is the estuarine crocodile *Crocodylus porosus*. This ancestral archosaur is the world's largest reptile and the top predator within coastal, estuarine, freshwater and marginal terrestrial ecosystems from East India throughout Southeast Asia to Northern Australia, Fiji and the Solomon Islands (Webb & Manolis, 1989). Intensive hunting of crocodiles in Australia between the 1940s and 1970s severely depleted the population and concerns for its long-term viability resulted in the Australian Government affording the species protective status. This intervention has allowed the estuarine crocodile population to recover substantially across Northern Australia and the population size is now estimated to be over 150 000 non-hatchling individuals (Read *et al.*, 2004; Fukuda, Whitehead & Boggs, 2007; Fukuda *et al.*, 2011). The estuarine crocodile recovery is a remarkable success story in an age when many large carnivores are in decline (Ripple *et al.*, 2013). Estuarine crocodiles do however, occasionally attack and kill humans, their pets, and livestock; thus, they are reviled by many who live within their geographical range.

Archiving and analysis of estuarine crocodile attacks in Australia have shown that the majority of attacks have been carried out upon local residents swimming or wading in waters known to be inhabited by estuarine crocodiles (Caldicott *et al.*, 2005; CrocBITE, 2013; Fukuda *et al.*, 2014). In Australia, government agencies erect signage to warn of crocodile presence and education schemes have been carried out to warn of the potential dangers around crocodile habitat. Regardless, human attacks continue to track with the growing estuarine crocodile population across Northern Australia, resulting in government schemes for selective removal and public outcries for widespread culling (Leach, Delaney & Fukuda, 2009).

The purpose of this project was to better understand the spatiotemporal relationship between human and estuarine crocodile occurrence. We aimed to reveal aspects of human behaviour that could be modified around waterways to reduce the likelihood of a close encounter with an adult estuarine crocodile. We employed underwater acoustic telemetry to estimate crocodile population size and monitor their activity, integrating these data to assess the probability of crocodile occurrence around a shallow-water river crossing in Northern Australia. We also instigated a human-based survey of visitors to the area to understand if humans behaved in a manner that minimized their risk of crocodile attack.

Methodology

Crocodile capture and tagging

Between 2008 and 2013, 20 crocodile traps were deployed throughout a 47-km stretch of the Wenlock River (Fig. 1). This system has one of the healthiest crocodile populations in Queensland, Australia (Read *et al.*, 2004). The traps were situated on the river banks or floating on the water surface. They were placed in the same location each year for 21 days during August. Each trap was baited every fourth day with wild pig *Sus scrofa* and sprung by a trigger-pin mechanism attached to the bait line (Walsh, 1987). The crocodiles primarily entered the traps during darkness and were processed the following morning. Crocodiles were removed from the trap using noosed ropes around the top jaw and then manually restrained. The total length and sex of each crocodile were recorded. Surgical methodology has been reported elsewhere (Franklin *et al.*, 2009). In brief, a local anaesthesia (Lignocaine, Troy Laboratories, Smithfield, New South Wales, Australia) was injected into the area of soft skin and muscle immediately behind the left forelimb and a ventral to dorsal incision (8 cm) was made using a scalpel. A pocket was created between the epidermis and the underlying muscle layer by blunt dissection and an acoustic transmitter (VR16 VEMCO, Halifax, Nova Scotia, Canada) was inserted. The transmitter was positioned so that it was not in immediate contact with the wound and in a lateral position with the crocodile's body. The wound was closed using four to six interrupted sutures of cat-gut (2-0 gauge – Ethicon, Newark, NJ, USA). The acoustic transmitters had a projected battery life of 7 years. All crocodiles captured that were >2.5 m in total length were acoustically tagged for this study and a passive integrated transponder tag was inserted into the fleshy base of the tail.

Every captured crocodile was carefully assessed to determine if it was a recaptured individual. First, a mobile acoustic receiver (VR100, VEMCO) was passed over the animal to detect for the presence of an acoustic transmitter; second, a microchip reader was passed across the base of the tail to detect for the presence of a microchip and finally, the nuchal rosette, dimensions and distinguishing marks/scars were checked against a photograph database. If the crocodile was a recapture, it was released; otherwise it underwent the tagging procedure.

In order to detect for tagged crocodile presence, an array of static underwater acoustic receivers (VR2-W, VEMCO) was deployed throughout the study area from September 2010 until August 2013 (Fig. 1). A total of 30 receivers were placed *c.* 2 to 5 km apart and these receivers detected the presence of the tagged crocodiles if they were within ~200 m line of sight radius. Each receiver was attached to a concrete anchor (20 kg) and situated ~2 m from the river bank and ~1 m below the water surface. River depth varied between 3 and 7 m throughout the study area in the dry season. The detection range of each receiver was determined by towing an activated tag behind a boat up and down river away from the VR2W receiver location. A VR100 receiver (VEMCO)

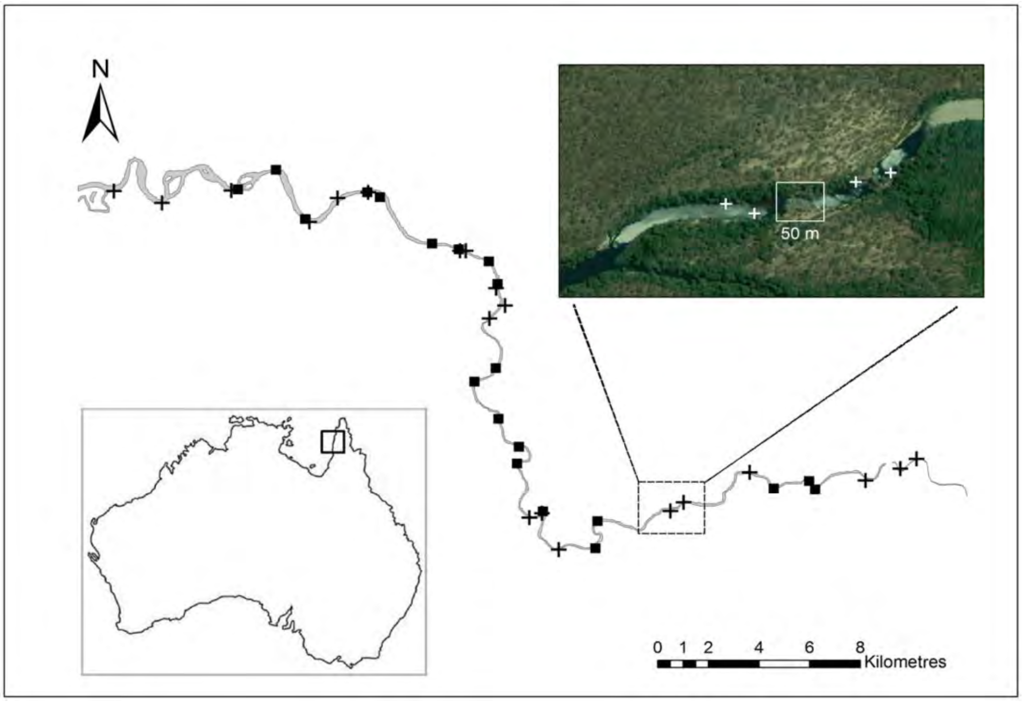

Figure 1 The Wenlock River, Cape York Peninsula, Queensland, Australia. Direction of flow runs from south-east to north-west. The location of underwater acoustic receivers (+) and crocodile traps (■) throughout the river are illustrated. Enlarged aerial image (ESRI ArcGIS BaseMap) is of the frequent human-visitation site, white crosses (+) denote acoustic receiver location and the white box the human water-entry area.

aboard the boat was used to provide location of the boat by the Global Positioning System when each transmission was emitted. The log records between the VR100 and VR2W were compared to determine which locations were out of range of the VR2W receiver. Detection radius was generally between 200 and 300 m. The river width was typically less than 40 m. The pulse transmission rate of the transmitters was set between 90 and 120 s and based upon crocodile rates of travel (Campbell *et al.*, 2010*a*, 2013), it was highly unlikely that a tagged crocodile could pass by a receiver without being detected.

A site of frequent human-visitation study was located within the centre stretch of the trapping area (12°23′14’S, 142°10′24’E) in an area of fresh (but tidal) water. Locals and tourists frequently visited this area for fishing, swimming and camping. This section consists of a stretch of shallow water (~50 m long and ~30 m wide with a maximum depth of ~0.8 m) with two deep pools (minimum depth ~ 5 m, maximum width ~30 m) immediately upstream and downstream. Two underwater acoustic receivers were anchored within each of these pools and it was highly unlikely that an acoustically tagged crocodile could be present or move into the shallow-water stretch without being detected. Depth recorders (Star_Oddi, Reykjavik, Iceland) placed within the shallow water recorded a 42-cm difference in water depth between mean low and high water spring tides.

Human dimensions study

In April 2013, a survey by questionnaire was undertaken upon the inhabitants of Weipa (12°39’S, 141°51’E). This township is the closet urban centre to the human-visitation site used in this study. The purpose of the survey was to establish what proportion of locals visited the monitored site, what water-based activities they participated in and what measures, if any, they undertook to reduce the risk of crocodile attack. Participation in the survey was voluntary and each participant was provided with a one-page cover letter outlining the survey rationale. The survey was designed to take less than 5 min to complete and consisted of 18 multiple choice and two open-ended questions (Supporting Information Appendix S1). The survey was advertised in the local paper as well as emailed to local businesses. Participants could access it on the Internet and a lottery style draw was instigated to encourage participation.

Data analysis

Movement and residence of adult crocodiles

When a tagged crocodile was within the detection radii of an underwater receiver, the acoustic transmissions from the implanted tag were detected by the receiver and stored on-board. Acoustic receivers were retrieved and downloaded during September of each year and the data were divided into three separate years for analysis. Calculation of crocodile presence and movement from the acoustic detections was undertaken using the V-Track software (Campbell *et al.*, 2012) in R (R Development Core Team, 2010). Using the residence function, the software was used to define periods when a tagged individual was located within the detection radii of each receiver and when it moved between the detection radii of adjacent receivers. A residence event was assigned as the last detection at a receiver if no other detection was received within a timeout window of 10 min (allowing a maximum of 10 acoustic transmissions to be missed before a timeout was scored) or if the succeeding tag transmission was detected by another receiver.

Analysing temporal patterns in activity

It was possible to demonstrate that a crocodile moved through the human frequented site by its detection on receivers placed upstream and downstream of the shallow-water zone (acoustic detections could not pass over). The time taken from leaving one receiver detection radii and appearing at the next showed the time individuals spent within the shallow-water zone. To determine if the timings of tagged crocodile movements through the human frequented site were significantly different from values from random expectations, we used Monte Carlo randomizations. Date and times occurring between 1 September 2010 and 31 August 2013 were sampled to create a series of random movements which equalled the number of actual movements across the monitored site. These actual and random movements were then paired with data sheets containing the timings of high and low tide and sunrise and sunset according to the time of the movement event. Tidal readings were obtained from The Tidal Unit Maritime Safety Queensland collected by the tidal gauge site located at Weipa, Queensland (Station Number 070021A; 12°40’S, 141°52’E) and calibrated according to a time depth recorder located immediately upstream and downstream of the closely monitored site. Sunrise and sunset times for the area were obtained from the Astronomical Applications Department, US Naval Observatory.

A generalized linear model (GLM) with a binomial error structure and logit link function was used to determine whether actual movements across the monitored site differed from what would be expected if crocodile movements across the monitored site were random. In this model, our response variable was the actual (=1) or random movement (=0) of tagged crocodiles across the monitored site. Our dependent variables were month names (September–August) and time of day (day vs. night) as factors and hours from high tide (0–12 h) as a covariate. The GLM was run 10 000 times using different permutations of randomized movements and significance was assigned if the upper 95% confidence interval (CI) of P fell below 0.05 (Good, 2006). Because all crocodiles above 2.5 m are considered dangerous to humans, regardless of sex, we did not discriminate between male and female crocodiles when assessing temporal patterns in behaviour.

Estimating crocodile abundance

To assess the size of the local adult crocodile population and determine if it remained constant during the study, a maximum likelihood approach was taken (Hilborn & Mangel, 1997). It was possible to use this closed-population model because the acoustic telemetry array detected the number, the number of previously captured crocodiles present in the river during each sampling episode. Assuming a constant population size in the river (N), the likelihood (L) of observing our capture and recapture data was:

$$L = \prod_{i=1}^{x} \binom{T_i}{CT_i} p_i^{CT_i} (1 - p_i)^{(T_i - CT_i)} \tag{1}$$

where i is the year, x is the total number of years within the study period, p_i is the probability of catching a crocodile given it is in the river (p_i = number caught in year i, C_i/total population in river, N), T_i is the total number of tagged crocodiles in the river and CT_i is the number of tagged crocodiles caught. The likelihood was maximized (or the negative log likelihood was minimized) using:

$$\begin{aligned} \min -lnL = -\sum_{i=1}^{3} ln\binom{T_i}{CT_i} + CT_i ln\left(C_i/N\right) \\ + (T_i - CT_i)\ln\left(1 - \left(C_i/N\right)\right) \end{aligned} \tag{2}$$

where the only unknown in this equation was N and the minimum was found by numerically simulating different values of N. As this dataset is relatively small, we modelled this equation using a simple C program and searched over all whole population size estimates from $n = 28$ to $n = 300$. Using the likelihood ration test, 95% CIs are the range of parameters for which the negative log likelihood is within 1.92 of the minimum value (Hilborn & Mangel, 1997).

If we assume a non-constant population size, then the value of N in equations (1) and (2) needs to be replaced by N_i, the population size in each year ($i = 1$ to 3). There are now three unknown parameters (N_1, N_2, N_3). These were all varied simultaneously to find the values that minimized the negative log likelihood (equation 2). As each year is now independent of the other, this is exactly equivalent to using the Lincoln-Petersen estimator (Southwood & Henderson, 2000). The two models (constant population size and different population each year) were then compared using the change in Akaike information criterion (AIC) score for each model. To be significant, the change in AIC score from the one-parameter model (constant population size) to the three-parameter model (non-constant population size) had to be greater than twice the difference in the number of parameters or sampling periods (i.e. >4).

Probability of crocodile presence

To determine temporal patterns in the probability of any crocodile (tagged and untagged) being present at the monitored site (p_{FHV}), the probability of a tagged crocodile being present (calculated from the acoustic detection data) was scaled by the total population size in the river using the following equation:

$$p_{FHV} = 1-\left(1-\left[1-(1-p_T)^{1/T}\right]\right)^N = 1-(1-p_T)^{N/T} \qquad (3)$$

where p_{T} is the probability of a tagged crocodile being present, T is the total number of tagged crocodiles in the river and N is the total crocodile population size in the river.

Results

Capture information

A total of 84 adult estuarine crocodiles (64 males and 20 females) greater than 2.5 m in total length were captured in all 20 of the set traps (Table 1). The sex ratio of male to female crocodiles captured was similar to that captured in other Australian *C. porosus* population studies (Fukuda *et al.*, 2013). Crocodiles were captured and tagged up to 10 km upstream and 40 km upstream and downstream of the human-visitation site and only three crocodiles were captured within 1 km of the monitored site. In each capture year, a proportion of crocodiles that had been captured on previous years and implanted with transmitters were recaptured (Table 1).

Population estimation

Population estimates and 95% CIs were: 56 (39 104), 106 (51 332) and 73 (44 157) crocodiles for the 3 years that recapture data were available (2010, 2012 and 2013). The constant population model (AIC = 7.77) was a more parsimonious fit to the data than our non-constant population model (AIC = 10.92). Therefore, probability estimates for each year were undertaken using the constant population model, 71 (52 108) crocodiles >2.5 m in length.

Crocodile presence at the monitored site

A total of 269 crocodile presence events were recorded within the area of frequent human visitation over the 3-year study. These events comprised 24 of the 84 tagged crocodiles. Male ($n = 19$) and female ($n = 5$) tagged crocodiles were detected moving through the shallow-water area and details about these crossings for each year are shown in Table 2. Prior to moving into the shallow water, the crocodiles remained within adjacent deep water pools for extended periods. These ranged from 18 min to 27 h and averaged 9.9 ± 2.5 h and 9.5 ± 5.9 h for the upstream and downstream pools, respectively. Once into the shallow water, the crocodiles travelled fairly quickly, taking 14.0 ± 2.7 min to travel from the downstream pool to the upstream pool and 10.8 ± 1.6 min to move in the downstream direction.

The results from our GLM showed that the timing of tagged crocodile movement through the shallow water at the monitored site differed significantly from what would be expected if movements were random. Crocodile presence around the monitored site was an order of magnitude greater between September and December than at other times of the year [$P < 0.001$, 95% CI ($< 0.001, < 0.001$); Fig. 2a]. The majority of movements through the shallow-water area were embarked upon and completed after sunset and before sunrise [day|night coefficient (± SE) = 1.02 (± 0.32); $P = 0.009$; 95% CI (0.007, 0.011)], with 13% of

Table 1 The capture data for *Crocodylus porosus* during four trapping episodes over 3 years

	2010	2011	2012	2013
Total number of captures	28	15	17	19
Number of captured crocodiles present	16	21	25	27
Number of recaptures	8	0	4	7
Annual estimate of population size	56 (39 104)	–	106 (51 332)	73 (44 157)

Population size was estimated for each year using the maximum likelihood ratio based upon the number of new captures, recaptures and the number of previously captured animals present in the river during the trapping episode. The 95% confidence intervals for the population estimates are shown in parentheses.

Table 2 The detection of acoustic tagged *Crocodylus porosus* movement through shallow water at the monitoring site

	Year 1	Year 2	Year 3
Number of presence events detected	116	77	76
Predicted number of presence events	430	240	219
Number of tagged individuals detected	12	16	19
Predicted number of individuals	58	49	54
Time to cross shallow water (min)	33.9 ± 1.2	16.9 ± 0.9	23.1 ± 0.3
Time spent in deep water (h)	9.6 ± 2.5	9.5 ± 3.9	9.8 ± 2.1
Crocodile length	3.52 ± 0.60	3.38 ± 0.41	3.43 ± 0.34

Values for acoustic tagged crocodiles have been scaled to predict values for a fixed local population of 71 individuals greater than 2.5 m in length (mean ± SE).

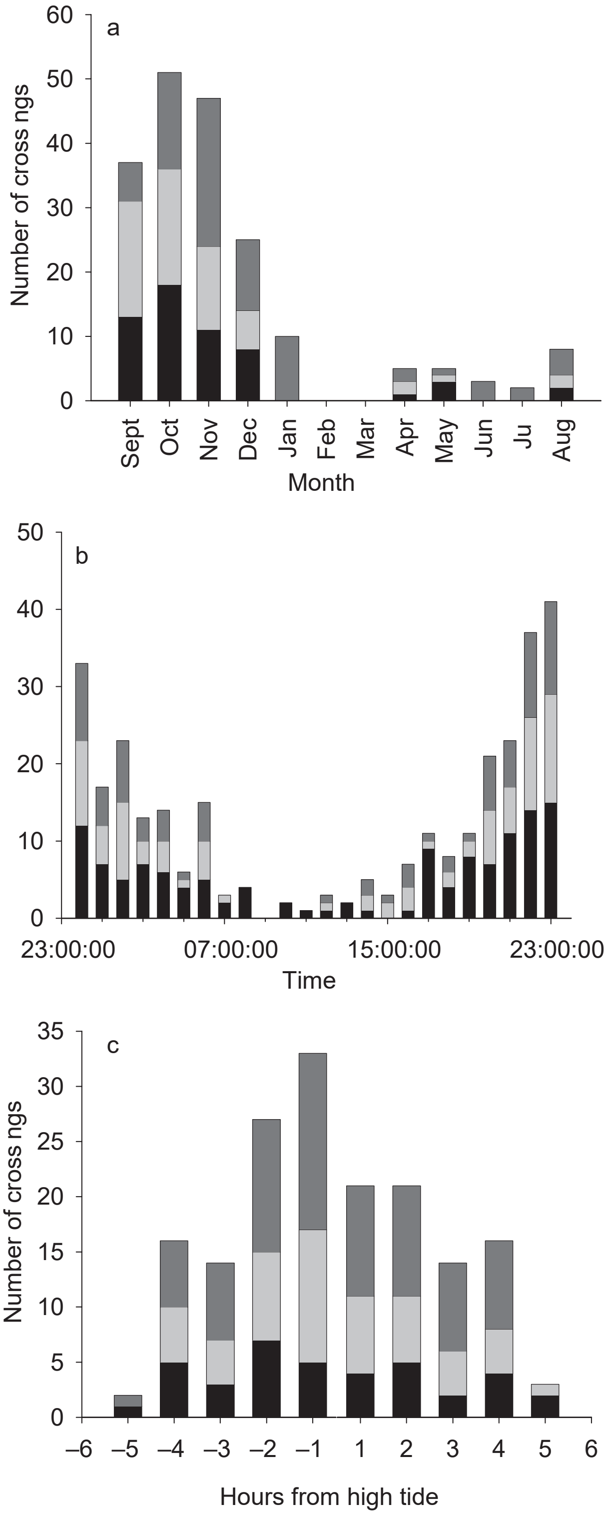

Figure 2 The temporal distribution: (a) months of the year, (b) hours of the diel cycle, (c) hours of the tidal cycle of estuarine crocodile movements through the shallow-water study area. The bars are separated into movements through the shallow water undertaken in year 1 (black), year 2 (light grey) and year 3 (dark grey) of the study.

shallow-water movements occurring during daylight (Fig. 2b). Crocodile movement through the shallow water was significantly increased when tidal height was high (hours to high tide coefficient ± SE = −0.27 ± 0.002; $P = 0.006$; 95% CI [0.005, 0.007]; Fig. 2c).

The probability of any crocodile (tagged and untagged) being present at the monitored site was calculated from scaling up the acoustic detection data to the estimated local population (78 individuals). This revealed that the actual number of adult estuarine crocodiles moving through this area was potentially three- to fourfold greater than those tagged and detected (Table 2). Estimation of temporal patterns in the probability of crocodile presence showed that there was a very high probability of a crocodile being present in the deep water pools between September and December but low throughout the rest of the year (Table 3). During this season, there was a high probability of a crocodile moving through the shallow water during darkness and during periods around the high tide (Table 4).

Human survey

Our voluntary Internet survey was completed by 13% of the Weipa township adult population (129 females, 180 males). Out of those surveyed, 188 individuals (61%) regularly visited the site monitored for crocodile presence in this study (Table 5). Out of this group, a vast majority stated that they would not enter the water if they saw a crocodile either on the bank or in the water. Nevertheless, ~80% regularly waded in the shallow water with ~30% engaging in swimming activity. The majority of visitors would not enter the water during darkness with ~17% saying that they had entered the water during darkness previously.

Table 3 The seasonal and diel probability of *Crocodylus porosus* presence within deep water at the study site

January–August	Year 1	Year 2	Year 3
0600–1800 h	0.03	0.11	0.08
1800–0600 h	0.12	0.21	0.18
September–December			
0600–1800 h	0.51	0.82	0.71
1800–0600 h	0.78	0.96	0.81

Table 4 The seasonal and diel probability of *Crocodylus porosus* moving through shallow water at the study site

January–August	Year 1	Year 2	Year 3
0600–1800 h	<0.01	<0.01	<0.01
1800–0600 h	<0.01	<0.01	<0.01
High tide (± 3 h)	<0.01	<0.01	<0.01
Low tide (± 3 h)	<0.01	<0.01	<0.01
September–December			
0600–1800 h	0.02	0.09	0.06
1800–0600 h	0.96	0.98	0.96
High tide (± 3 h)	0.71	0.78	0.65
Low tide (± 3 h)	0.26	0.38	0.28

Table 5 The behaviour of humans around the study site

Behaviour around the shallow-water river crossing	Response (%)
Would not enter shallow water if saw crocodile	98.3
Stay vigilant for crocodiles	37.5
Only enter water during daylight hours	83.4
Only enter water at particular time of year	29.7
Only enter water at particular tidal height	35.0
Only wade in shallow water	39.8
Swim in shallow water	31.1
Swim in deep water	0.7
Undertake fishing activity by water's edge	31.3
Camp by water's edge	29.6
Allow children in water	7.8
Allow dogs in water	28.4

Survey results were drawn from 188 adults who frequented the area to undertake recreational activities.

Approximately 70% of visitors did not consider that their exposure to crocodile attack was altered by the season or the stage of the tidal cycle. Less than 10% of those surveyed allowed children to enter the water.

Discussion

The study revealed that from September to December, there was almost a 100% probability that an estuarine crocodile, greater than 2.5 m in length, was within deep water pools adjacent to the shallow-water human entry zone. The crocodiles moved out of these deep pools and into the shallow-water zone with the onset of darkness or around the high tide. Humans regularly entered the water September to December, with the majority of visitors confining their activity to shallow water during daylight hours. Humans did not consider that crocodile presence was significantly increased during September to December or around the high tide. A small percentage of visitors had swum in the deep water pools and entered the water during darkness.

Satellite tracking studies have shown that male and female *C. porosus* increase activity and home-range size from September through until late December (Kay, 2004; Campbell *et al.*, 2013), as they search for mates and nesting sites (Webb, Messel & Magnusson, 1977; Webb & Manolis, 1989). We argue that these behaviours resulted in a high number of crocodiles moving through the shallow-water river crossing during these months. These movements primarily occurred during darkness and periods around the high tide. Crocodiles are generally more active during darkness (Campbell *et al.*, 2013), but we argue that the nighttime bias in movement through the shallow water suggested a general wariness towards the frequent presence of humans in this area. The crocodile preference for moving during the high tide may have simply been for ease of travel (Campbell *et al.*, 2010*a*). As a direct consequence of these behaviours, however, crocodiles spent prolonged periods within deep-water pools adjacent to the human entry zone. Crocodiles can remain submerged for many hours (Campbell *et al.*, 2010*b*) and in contrast to the acoustic telemetry data, the human-based survey reported that, crocodiles were not regularly sighted by visitors to this area.

In Northern Australia, shallow-water river stretches generally receive a high number of human visitors. This is due to the shallow water creating a riffle, which forms a natural crossing point of the river. They are also considered scenic areas and good fishing spots. Our surveyed locals regularly visited the shallow-water riffle on the Wenlock River with 80.6% of them entering the water. Only 37.5% of visitors remained vigilant for crocodiles, suggesting that most did not consider that there was a high probability that an adult crocodile was in close proximity. The human-based survey supports a theory that humans consider these shallow-water riffles 'safe' places to enter the water, particularly if they remain in the shallow water and only enter during daylight hours. To a large extent, this modification of human behaviour may be proficient because there have been no recorded incidences of crocodile attack at this particular river stretch, despite the high crocodile presence. However, archival data from Australia over the past 40 years do exhibit parallels with the findings of this study. These are; (1) incidences of crocodile attack are highest between September and December; (2) the victims have predominantly been locals familiar with the area; (3) the majority of attacks have occurred during daylight; (4) victims are typically wading or swimming (Caldicott *et al.*, 2005; CrocBITE, 2013; Fukuda *et al.*, 2014). Moreover, 34% of participants in our human-based survey had experienced a close encounter with an estuarine crocodile during swimming, wading, fishing or participating in boating activity. We therefore recommend that human behaviour around waterways in crocodile country be further modified, and suggest that this study be used as a framework to provide guidance.

Promoting tolerance and coexistence is an important societal challenge in the conservation of large carnivores. Only by reducing the incidence of attacks will there be continued public support to preserve them. To prevent and mitigate human–carnivore conflict, it is imperative that we first understand when and where the probability of an attack is greatest and, second, convey that message to the public so that they may adjust their behaviour accordingly. Estimates of risk to humans from large carnivores are commonly based upon archival attack records (e.g. Caldicott *et al.*, 2005; West, 2011). However, because attacks on humans by large carnivores are thankfully rare, it can be challenging to undertake robust quantitative analysis on these data. The methodologies described in this study enable the probability of large carnivore presence around a human frequented area to be quantified over a range of spatial and temporal scales. Further, we argue that the 'probability of large carnivore presence' (% likelihood of a crocodile being present at a particular point in space and time) is a comfortable approach for communicating the risk of attack to the public.

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Supporting information

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Appendix S1. Questionnaire provided to members of the public.