Crocodile Control and Conservation Bill 2024

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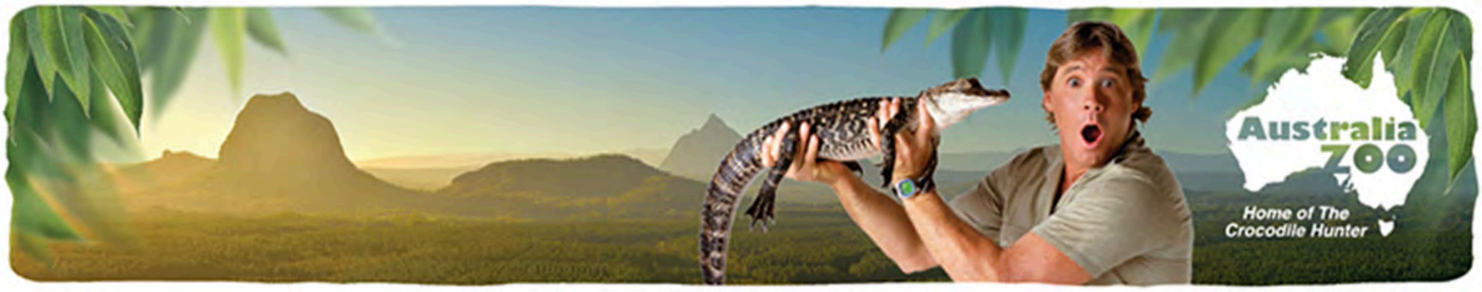


Australia Zoo's Submission to the Inquiry into the Crocodile Control and Conservation Bill 2024

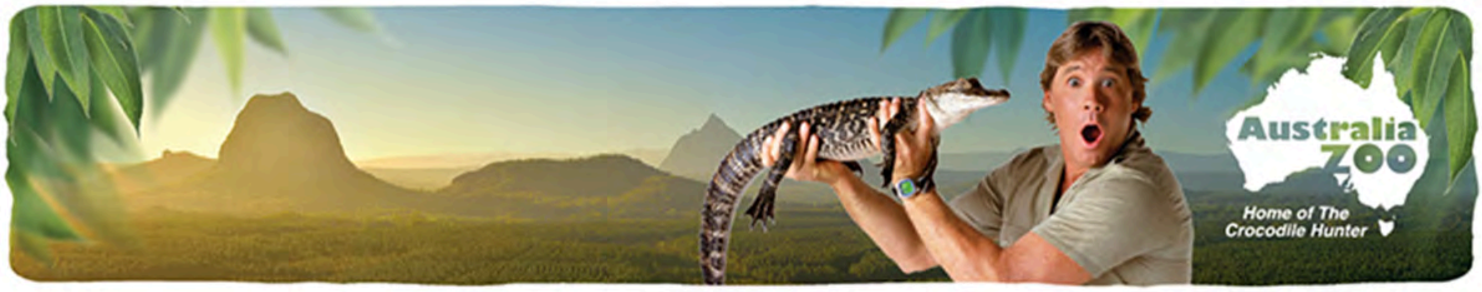
Australia Zoo wishes to formally oppose the Crocodile Control and Conservation Bill, introduced by Mr Shane Knuth MP on 22nd May 2024.

"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.

Australia Zoo and its partners, The University of Queensland and Wildlife Warriors, 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.

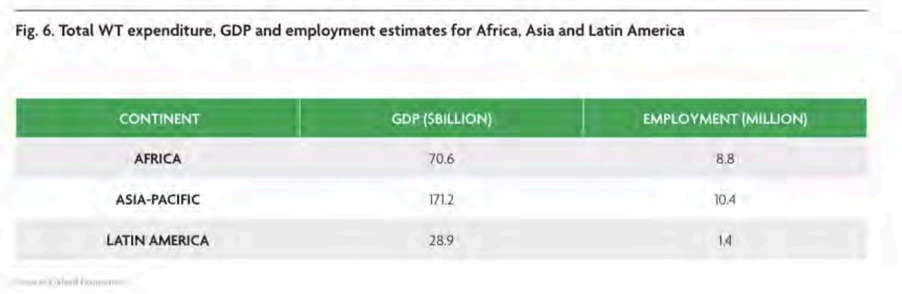
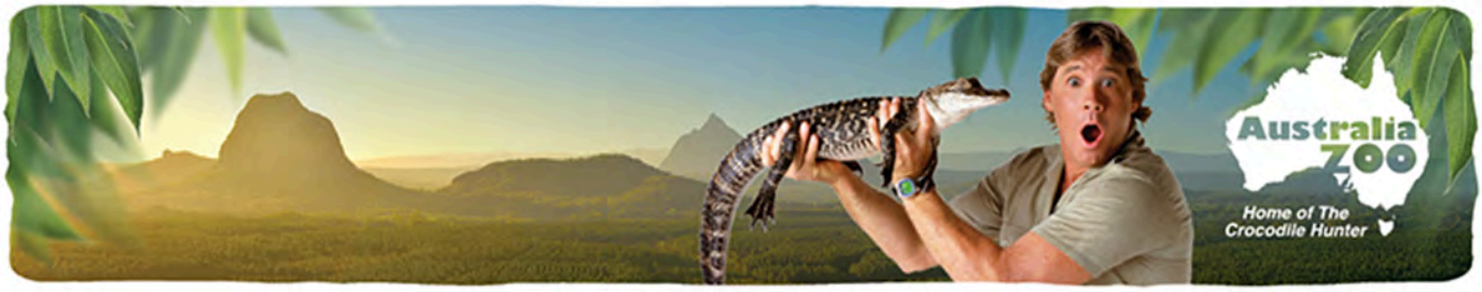


Fig. 6. Total WT expenditure, GDP and employment estimates for Africa, Asia and Latin America

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

Source: Oxford Economics

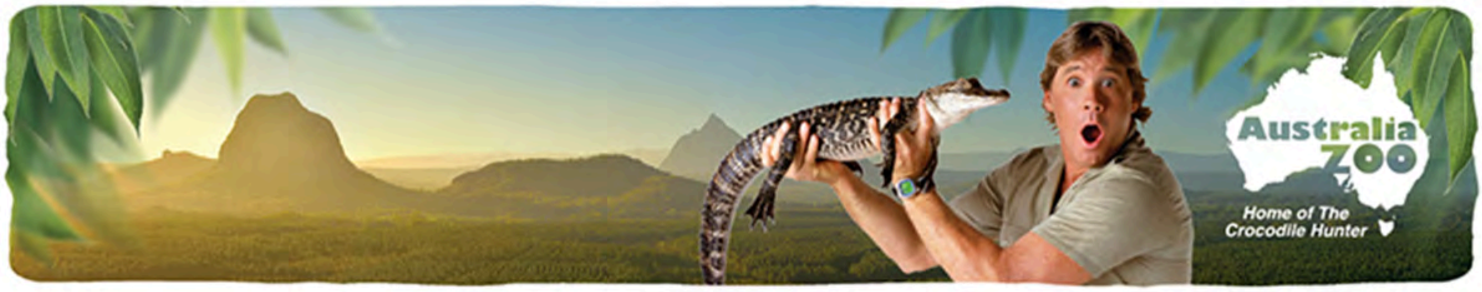


This is the future of tourism, not culling an animal so you can swim at the beach, not killing a vulnerable species for fun, people want to see and experience our beautiful wildlife, and Queensland operators can profit from it in turn. Queensland's population of estuarine crocodiles is approximately 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. Australia Zoo 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,

[redacted]

Dr Terri Irwin AM
Owner Director, Australia Zoo

[redacted]

Luke Reavley
General Manager, Australia Zoo

Summary of Worldwide Crocodilian Attacks for 2015

Article January 2016

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Brandon Sideleau
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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.

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**

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 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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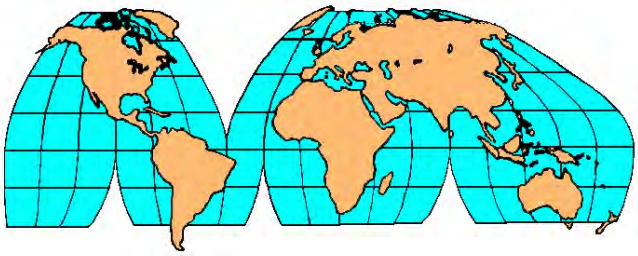
Regional Reports



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

Australia Zoo
Home of The Crocodile Hunter

Dear [redacted]

We wish to inform you of a saltwater crocodile that has been illegally shot in the Wenlock River, near Stones Crossing.

We are currently on the Steve Irwin Wildlife Reserve for our annual crocodile research trip. On Sunday 1st August, we discovered a 2.3m male crocodile that had been fatally shot in the head in the days prior.

We are currently working with Crime Stoppers to offer a reward for anyone that comes forward with information resulting in the prosecution of the criminals responsible for the shooting the estuarine crocodile, a species protected under the Nature Conservation Act 1992.

Unfortunately, this is not the first time we have witnessed unlawful crimes against crocodiles on the Wenlock River. Last year we witnessed the Gator Family gill netting across the Wenlock, resulting in the death of at least two crocodiles that were a part of our study. One crocodile was significantly important, as an old mature breeding female, which through our studies we have found to be incredibly rare. This incident was reported to both the Department of Environment and Department of Agriculture and Fisheries.

As you can imagine, these are by no means isolated incidents. As a matter of pure coincidence, we happened to come across the crocodiles involved in the above incidents. With limited policing and patrols of the Wenlock, we fear this is happening all too often, where a vulnerable species is being unlawfully killed with no repercussions.

We would welcome the Department's view on the above, and how they plan to curb the ongoing crimes against wildlife in the Wenlock River.

Out of respect to the local First Nation groups, we have informed them of the incident against their totem species.

We look forward to your response,

Yours in Conservation,

[redacted]

Luke Reavley
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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)

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BEHAVIORAL ECOLOGY – ORIGINAL RESEARCH

Ontogenetic shifts in the nesting behaviour of female crocodiles

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Abstract

Body size and age are crucial factors influencing reproductive capacity and success. As females grow, their reproductive investment and success often increase due to improved overall physiological condition and experience gained through successive reproductive events. While much of this work has been conducted on birds and mammals, surprisingly little is known on how body size affects nesting decisions in other long-lived vertebrates. We monitored the movements and nesting behaviour of 57 wild female estuarine crocodiles *Crocodylus porosus* over a 10-year period (and across consecutive nesting seasons) using externally mounted satellite tags, implanted acoustic transmitters and a network of submerged acoustic receivers. Applying Hidden Markov models to the telemetry-derived location data revealed that female nesting behaviours could be split into three distinct states: (i) ranging movements within home ranges and at nesting sites; (ii) migrations to and from nesting sites; (iii) and nesting/nest guarding. We found that during migration events, larger females migrated further and remained away from dry season territories for longer periods than smaller individuals. Furthermore, not only were migratory movements stimulated by increases in rainfall, larger females migrated to nest sites at lower rainfall thresholds than smaller females. We provide some of the first evidence of body size influencing nesting decisions in an ectothermic vertebrate, with shifts likely resulting from an increased willingness to invest in nest protection among larger and more experienced females.

Keywords Estuarine crocodile · Hidden Markov modelling · Nest-site selection · Parental investment · Telemetry

Introduction

In long-lived vertebrates, reproductive capacity and success generally increase throughout an individual's lifetime (Forslund and Pärt 1995; Tejedo 1992). While several hypotheses have been put forward to explain these reproductive shifts, the leading consensus is that younger, smaller individuals invest less in reproductive care due to poorer physiological condition and/or a lack of essential skills (Pradel et al. 2012; Snyder et al. 2016). Physiological condition can influence reproductive output such as offspring number and size (Barneche et al. 2018), as well as behavioural decisions such as how far individuals travel to nest sites (Ponsero and Joly 1998) and the timing of reproduction (Vandeperre and Methven 2007). Experience acquired progressively through successive reproductive events can also influence reproductive decisions (Curio 1983), such as the timing of oviposition/parturition (Robertson and Rendell 2001), selection of nest sites (Pärt 2001) and parental attentiveness (Snyder et al. 2016) that in turn influence offspring survival. While a significant body of work has examined shifts in reproductive behaviours and performance, studies have primarily focused on the influence of age on avian (Forslund and Pärt 1995; Pradel et al. 2012) or mammalian reproduction (Broussard et al. 2008; Snyder et al. 2016). However, in fish, amphibians and reptiles, body size rather than age is often the overarching factor determining age of first reproduction (Kozłowski 1992; Shine and Charnov 1992). While fecundity and reproductive success have both been shown to increase with body size throughout an ectotherm's lifetime (Barneche et al. 2018; Stahler et al. 2013), very little is known as to how

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body size influences nesting decisions in female ectotherms. This paucity of information is largely due to preconceived notions of a lack of parental care (Shine 1989), along with the logistical and financial difficulties in monitoring long-lived and highly mobile species in their natural environment over multiple years and across consecutive breeding seasons. However, understanding this is crucial for providing insights into the evolution of parental care and how the degree of this care may shift throughout an animal's lifetime.

When and where a female decides to reproduce can also have major impacts on reproductive success (Angilletta et al. 2009). Females often utilise a variety of environmental cues (e.g., rainfall, temperature, photoperiod) as triggers for reproductive behaviours such as the initiation of reproductive migrations (Bowen et al. 2005; Tibblin et al. 2016) and the timing and location of oviposition/parturition (Alagaili et al. 2017; Schaper et al. 2012; Tejedo 1992). By utilising external cues, females are often able to time their reproductive behaviours to coincide with periods of high resource availability in order to maximise reproductive success (Pettorelli et al. 2007; Thomas et al. 2001). Understanding the effect environmental cues have on reproductive decisions generally requires behavioural and spatial data to be collected from the same individuals before, during and after reproductive events (Bowen et al. 2005; Schaper et al. 2012). For long-lived and highly mobile species, however, obtaining these data in a natural setting can be challenging, due to difficulties observing individuals continuously and undisturbed within their natural environment. Furthermore, large numbers of individuals need to be monitored simultaneously and often across multiple reproductive events to provide confidence that the patterns observed are related to intrinsic factors such as body size and experience.

Crocodylians provide an excellent group to examine for ontogenetic shifts in nesting behaviours. Like birds and mammals, but unlike most other reptiles, crocodylians provide extended parental care (Shine 1989), including nest guarding during incubation, transportation of young from the nest to water and hatchling care (see Somaweera et al. 2013 for review). Furthermore, both male and female crocodylians exhibit apparent indeterminate growth (Briggs-Gonzalez et al. 2017; Tucker et al. 2006), with body size shown not only to tightly correlate with an animal's age (Taylor et al. 2016; Wilkinson and Rhodes 1997) but also a range of factors including fecundity (Thorbjarnarson 1996), social structure (Webb and Manolis 1989), activity space and diet (Hanson et al. 2015). Environmental factors have also been shown to influence crocodylian movements with both males and females moving in response to shifts in tidal and ocean currents (Campbell et al. 2010). Furthermore, increased rainfall has been suggested as a major factor influencing the timing of oviposition by nesting female crocodiles, a factor which is presumed to enhance reproductive success (Fukuda and Saalfeld 2014; Webb et al. 1977). However, little is known about how environmental factors influence the timing of nesting movements in female crocodiles, if these patterns are consistent across multiple consecutive nesting seasons and how the behavioural decisions vary according to animal body size.

Estuarine crocodiles *Crocodylus porosus* are the largest and most widely distributed extant crocodylian, ranging from northern Australia throughout Southeast Asia to the eastern coast of India (Webb and Manolis 1989). Over a 10-year period, we explored individual- and population-level variation in nesting behaviour among wild female *C. porosus* in a northern Australian river system. Using acoustic and satellite tracking technologies to remotely monitor crocodile behaviour, we examined (1) correlations between body size and nesting behaviours and movements of female *C. porosus;* (2) individual plasticity in the scale and timing of nesting movements; and (3) if nesting migrations are correlated with rainfall. We predicted that larger and presumably more experienced females would display increased nesting investment (i.e., distance travelled, duration at nesting sites) than smaller individuals and that rainfall would be an important factor influencing when females begin nesting. The study provides new insights into the influence of potential ontogenetic shifts in the nesting behaviours and movements of a long-lived aquatic vertebrate.

Methods

Crocodile capture and release

Between 2008 and 2017, 18–20 crocodile traps were deployed annually along a 47-km stretch of the Wenlock River, Cape York, Australia (Fig. 1). Trap placement ranged from non-tidal freshwater to macro-tidal brackish waters, with traps either floated on the water surface or placed at the high-tide mark along the riverbank. Traps were set between August and September each year, baited with wild pig *Sus scrofa* and sprung by a trigger mechanism attached to the bait. Hand capture via spotlighting with a noose was also used to capture animals < 2 m total length. Once crocodiles were restrained, their sex and total body length (TL) were recorded and transmitter(s) attached (see below) before animals were released at their point of capture.

Remote monitoring of crocodile behaviour

To remotely monitor the movements of crocodiles across multiple years and consecutive nesting seasons, we used a combination of implanted coded acoustic transmitters and a network of underwater hydrophones. Prior to tag implantation, a local anaesthetic (Lignocaine, Troy Laboratories,

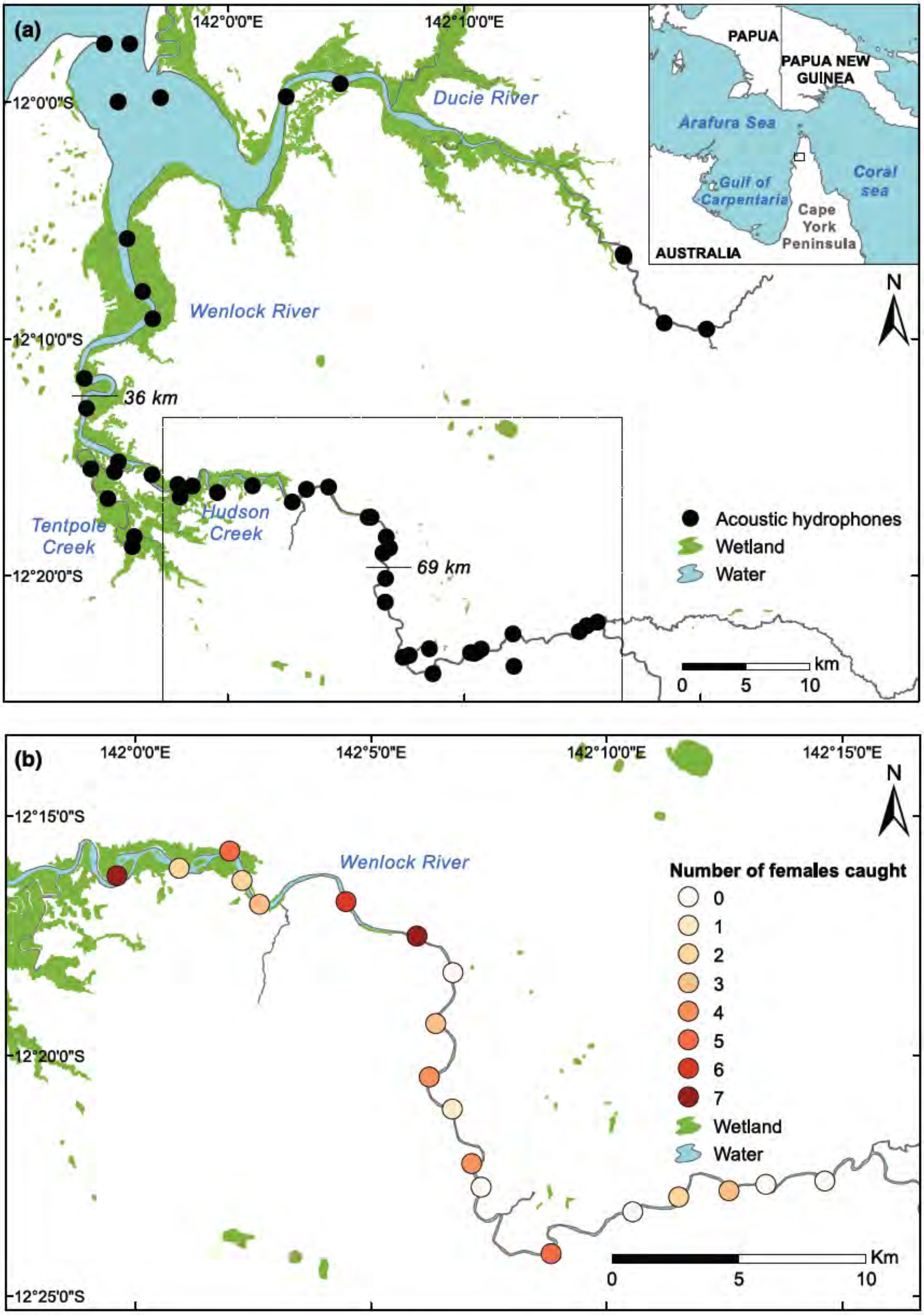

Fig. 1 The location (**a**) of the static underwater acoustic receivers throughout the Wenlock and Ducie Rivers, Queensland, Australia. The location (**b**) of the 20 crocodile trap sites and the number of females caught at each site. The lines at 36 and 69 km indicate the area of river that the majority of female estuarine crocodiles (*Crocodylus porosus*) exit the array. Colour version available online

New South Wales, Australia) was injected behind the front left forelimb and a ventral to dorsal incision (~ 4 cm) made with a scalpel. A pocket was then created between the epidermis and muscle via blunt dissection and a coded acoustic transmitter (VEMCO V16T-6x, Amirix Systems, Halifax, Nova Scotia, Canada) inserted (Franklin et al. 2009). The small size of these devices (16 mm dia.) and a projected battery life of 7–10 years permitted migratory movements to be investigated in both small and large individuals (1–4.68 m TL), and over multiple nesting seasons. In order to detect the implanted acoustic tags, a network of static underwater acoustic hydrophones (VEMCO VR2-W) was deployed throughout the Wenlock and Ducie River systems for the duration of data collection (Fig. 1a). Each hydrophone was connected to a concrete anchor placed 2–5 km apart and situated 2–20 m from the river bank and approximately 1 m below the water surface. The detection radius of each receiver was approximately 200 m and the pulse transmission rate was set randomly between 90 and 120 s, making it unlikely that a crocodile could pass by a receiver without being detected.

To examine fine-scale nesting movements and nest site selection, a subset of female crocodiles was also selected for remote tracking via satellite telemetry. As tag size was limited not only by the battery but also by the area between a crocodile's nuchal scutes, only females larger than 2.5 m total length ($n = 14$) could be tracked. Sirtrack GPS units (Hamilton, New Zealand) were utilised in 2009 and Telonics TGW-4310-3 GPS units (Arizona, USA) utilised from 2010 onwards. These transmitters recorded the GPS position approximately every 12 h and had a battery life of approximately 12–15 months. Crocodile location was acquired by remote download via the ARGOS system. Prior to transmitter attachment, a local anaesthetic (Lignocaine) was injected under the nuchal rosette. Holes were then drilled through the four-prominent nuchal scutes and the transmitter attached between the nuchal scutes via plastic-coated stainless-steel wire (Franklin et al. 2009).

Identification of nesting events

Satellite-tagged crocodiles were identified as 'nesting' if they undertook a large-scale (> 15 km) upstream or downstream movement between October and March, followed by a period of highly constrained movement indicative of nest-guarding (Campbell et al. 2013; Kay 2004). Where possible, nesting events were validated through visual inspection of the nest site in the months immediately following the nesting season (Online Appendix S1). To quantify movement behaviours of satellite-tagged females, we constructed Hidden Markov models using the moveHMM (Michelot et al. 2016) package in R (R Core Team 2015). Models were run across the pooled data for all nesting females, with two- to six-state models constructed based on the step lengths (Gamma distribution) and turning angles (von Mises distribution) of the satellite-derived tracks. Following Zhao et al. (2008), the presence of a distinct 'knee point' in the resulting AIC and log-likelihood curves (Online Appendix S2) were used to identify the most parsimonious number of behavioural states to facilitate biological interpretation and prevent model over-fitting (Dean et al. 2012). To compare how home range size varied between behavioural states, we calculated a female's 50% volume kernel utilisation distribution (KUD 50%) for each behavioural state using ZoaTrack (Dwyer et al. 2015a). These areas were then compared using a linear mixed effect model (LMM) whereby the KUD 50% was the response variable, behavioural state was the independent variable and crocodile ID was the random effect. LMMs were constructed using the nlme package in R (Pinherio et al. 2016).

While a switch in behaviour from aquatic foraging to land-based nesting could be identified by applying Hidden Markov models to high-precision satellite telemetry data, monitoring crocodile nesting behaviour via acoustic telemetry was more challenging. As acoustic tag detections were limited to occasions when a tagged crocodile swam within hydrophone detection fields (Dwyer et al. 2015b), no detections were obtained if (1) tagged individuals occupied stretches of river between acoustic hydrophones or (2) if females were on land nest-guarding. To identify potential nesting events in acoustic-tagged females, we applied a filter that identified those crocodiles that were not detected within the acoustic array for 90–240 days, with tagged animals departing the array between 01 October and 31 March. This filter was based upon published accounts of the timing and duration of nest location and construction, oviposition, nest incubation and hatchling care (Magnusson 1979; Webb and Manolis 1989; Webb et al. 1977). A nesting migration was assumed to occur when a crocodile left her dry season home range and moved up- or downstream for at least 5 km, before disappearing from the array. This distance threshold was based on previous records of female home range size (Brien et al. 2008; Campbell et al. 2013; Kay 2004) and the maximum distance between acoustic hydrophones. We then validated the selection of these parameters by comparing acoustic-derived movements with (1) satellite tracking data from dual-tagged females (i.e., females with both acoustic and GPS transmitters; $n = 14$), (2) contrasting female movements with the movements of acoustically tagged male crocodiles and (3) by running a sensitivity analysis of distance and duration filters that showed negligible influence of parameter choice on model performance (Online Appendix S3, S4).

Arrival and departure times when individuals moved between the detection fields of acoustic receivers was determined utilising the V-Track package (Campbell et al. 2012) in R. From these values, we extracted the duration in days between the last observed detection and the first observed detection following a nesting event 90–240 days later. We also extracted the duration in days females were absent from their home ranges during nesting events and the total distance migrated along the course of the river following the methods outlined in Dwyer et al. (2015b). For those females with more than 18 months of behavioural monitoring via acoustic telemetry (i.e., two complete nesting seasons), nesting frequency was calculated as the number of months between the start of the current nesting event and the start of the previous nesting event.

Environmental factors

Throughout the study period, half-hourly temperature and barometric pressure recordings were obtained from the Australian Bureau of Meteorology (Weipa airport, Station number 27045; 50 km from study area). Total daily rainfall (recorded between 0900 and 0859 AEST) and river height recordings were also collected from the Queensland Department of Natural Resources and Mines (Moreton Telegraph Station, Station number 925001A; 42 km from study area). Daily moon phases were calculated utilising the lunar (Lazaridis 2014) package in R. River height was selected as a proxy for cumulative rainfall across the catchment.

Body size and environmental correlates with on nesting behaviour

LMMs were constructed to examine possible correlations between body size and the nesting behaviour of female *C. porosus*. In these models, minimum distance migrated (km), duration from home range (days), reproductive timing (days) or frequency of nesting (months) were included as the response variables. Minimum distance migrated was natural log-transformed + 1, while frequency of nesting and duration from home range were natural log-transformed to meet the models' assumptions of normality. Total length (m) was used as the predictor variable and crocodile ID included as the random effect. To examine whether the distance migrated correlated with the duration that females were away from their home range, we constructed a generalised linear model (GLM), with duration from home range (days) as the response variable and minimum distance migrated (km) as the predictor variable. We initially utilised a Poisson distribution; however, after detection of overdispersion within the model ($\phi = 9.25$), a Quasi–Poisson GLM model was used to correct standard errors following the methods in Zuur et al. (2009).

To determine any possible correlations between environmental factors and body size on *C. porosus* nesting migrations, we constructed a GLM (binomial distribution logit link). In this model our response was whether an individual migrated (TRUE/FALSE) during the specified nesting period or not. We initially constructed our model with year nested within crocodile ID as a random effect to account for repeated measures and non-independence; however, examination of the random effect indicated no influence; thus only a GLM was used. For our predictor variables, rainfall, temperature, barometric pressure, moon phase and river height were selected a priori to reduce the risk of model overparameterisation (Grubeber et al. 2011). Akaike Information Criterion corrected for small sample size (AICc) was used to determine whether the daily minimum, maximum, mean or difference between maximum and minimum recordings of temperature, barometric pressure and river height were selected in our model investigating the influence of environmental factors on nesting migrations. Thus, total daily rainfall (mm), minimum daily temperature (°C), daily difference in barometric pressure (hPa), maximum daily river height (m) and moon phase were utilised as predictor variables. Total length (m) was utilised as a covariate to examine for potential correlations with body size. Variance inflation factor (VIF) was utilised to check for multicollinearity between predictors. Following Zuur et al. (2010), the covariate with the highest VIF value was dropped and VIFs recalculated until all were below the selected threshold of two. Model selection was completed following the Information Theoretic approach (Burnham and Anderson 2002), with a model considered 'best' if its Akaike weight was > 0.9 (Grubeber et al. 2011). If no 'best' model was achieved, a top model set compromising the 95% confidence interval (summed Akaike weights from largest to smallest until ≥ 0.95) was delimitated (Burnham and Anderson 2002). Model averaging following the zero method (Burnham and Anderson 2002) was then completed across the top model set. All model selection and averaging was performed utilising the MuMIn (Bartón 2018) package in R. Statistical significance was set at $\alpha = 0.05$ and values reported as mean ± SE.

Results

Between 2008 and 2017, 57 female crocodiles (1.13–3.23 m TL) and 101 male crocodiles (1.00–4.68 m TL) were captured on the Wenlock River in set traps and by hand. Female crocodiles were captured throughout our study area, primarily within close proximity to wetlands or side creeks (Fig. 1b). Of the 158 crocodiles captured, 24 individuals were recaptured at least once throughout the study period revealing a growth rate of 7.39 ± 1.22 cm/year.

Classification of nesting behaviours

Of the 57 females captured, 14 of the larger individuals (2.51–3.23 m TL) were fitted with satellite tags that transmitted GPS location fixes for 2–16 months. Only nine tags remained on animals throughout the identified nesting period (Table 1), with five devices ceasing during October ($n=1$), January ($n=3$) or February ($n=1$) before a nesting migration was observed. Of the nine tags that transmitted throughout this period, five individuals (2.75–3.23 m TL) were observed undertaking movements indicative of nesting (Table 1), representing a mean proportion of 42 ± 19% of the females tracked per year. These movements comprised three behavioural states (Appendix S2). The first was a 'home ranging' state (State 1; Fig. 2), categorized by moderate (0.33 ± 0.01 km) step lengths (Fig. 2a) and turning angles around 180° (Fig. 2b); second was a 'migratory' state (State 2), categorized by long step lengths (2.29 ± 0.25 km) and turning angles around 0°; third was a 'nesting' state (State 3), categorized by short (0.01 ± 0.00 km) step lengths and variable turning angles. Females were found to have a significantly greater KUD 50% during State 1 compared to State 3 (LME, $t=-6.32$ $df=6$, $P<0.001$). Nesting migrations comprised four discrete stages: the first stage consisted of the outbound migration (State 2) from their home range (State 1) to a nest site (Fig. 2c, d). The distance females migrated from a dry season home range to nesting sites ranged between 18 and 51.6 km and the duration of outbound migrations ranged between 1 and 30 days ($n=5$; 7.4 ± 5.7 days; mean ± SE; Table 1). Once at a nest location, females transitioned back to State 1 and began a period comprising fine-scale exploratory movements (< 7 km radius from the nesting location). The duration of these exploratory movements varied between 10 and 52 days ($n=5$; 34.4 ± 7.7 days; Table 1), where it is assumed that females were searching for appropriate nest sites. Females would then transition into State 3, involving highly constrained movements (< 100 m/day; state 1) indicative of nest and hatchling guarding. Nesting duration was between 125 and 127 days ($n=2$; Table 1). The final stage consisted of the return migration to their respective home ranges. The total time that females were absent from their home range for nesting movements ranged between 141 and 178 days (Table 1). Most females undertook a single migration to the nest (e.g., Fig. 2c, e); however, female 11899 (Fig. 2d, f) and female 3078 undertook two outward migrations from the dry season home-range to and from the nesting location. The number of days that each female remained at their nesting location during these 'exploratory' movements was 4 and 5 days, respectively. The four females (2.51–3 m TL) that transmitted during the nesting period, but were not identified as undertaking nesting movements, either maintained a 'home ranging' state (State 1) throughout the nesting period ($n=2$), or transitioned to a 'migratory' state (State 2) followed by a period of 'home ranging' (State 1) for 159–192 days before returning to their dry season home-range ($n=2$).

Migration frequency, distance and nesting duration

Between August 2008 and July 2017, 57 female *C. porosus* (1.13–3.23 m TL) with implanted acoustic transmitters were tracked via the hydrophone array. Females were monitored for 2.7 years on average (± 0.3 years) with one individual tracked for 9 consecutive years. When our detection filter was applied to these data, we identified 72 potential nesting events from 36 of the 57 tagged females

Table 1 Summary statistics of the reproductive movements of the 14 female estuarine crocodiles *Crocodylus porosus* tracked using satellite telemetry

Crocodile ID	Total Length (m)	Date caught	Duration tracked (months)	Evidence of nesting?	Distance migrated (km)	Migration duration (days)	Duration of exploratory behaviour (days)	Duration nesting (days)	Duration from home range (days)
3078	3.15	15-Aug-10	5	Yes	29.9	2	32	–	–
60262	3.23	16-Aug-10	7	Yes	50.7	30	52	–	–
3086	2.94	11-Aug-10	7	Yes	51.6	3	28	–	–
11899	2.75	25-Aug-16	9	Yes	31.1	1	10	127	141
12728	2.93	7-Aug-15	12	Yes	18.0	1	50	125	178
12721	2.69	30-Aug-17	2	No	–	–	–	–	–
15362	2.68	13-Aug-11	5	No	–	–	–	–	–
15356	3.11	17-Aug-11	5	No	–	–	–	–	–
3076	2.59	14-Aug-10	6	No	–	–	–	–	–
3082	3.00	10-Aug-10	7	No	–	–	–	–	–
3078	3.16	30-Aug-17	8	No	–	–	–	–	–
11893	2.93	25-Aug-16	10	No	–	–	–	–	–
15338	2.51	27-Aug-12	12	No	–	–	–	–	–
14204	2.66	31-Aug-12	16	No	–	–	–	–	–

Dash represents no data for that parameter

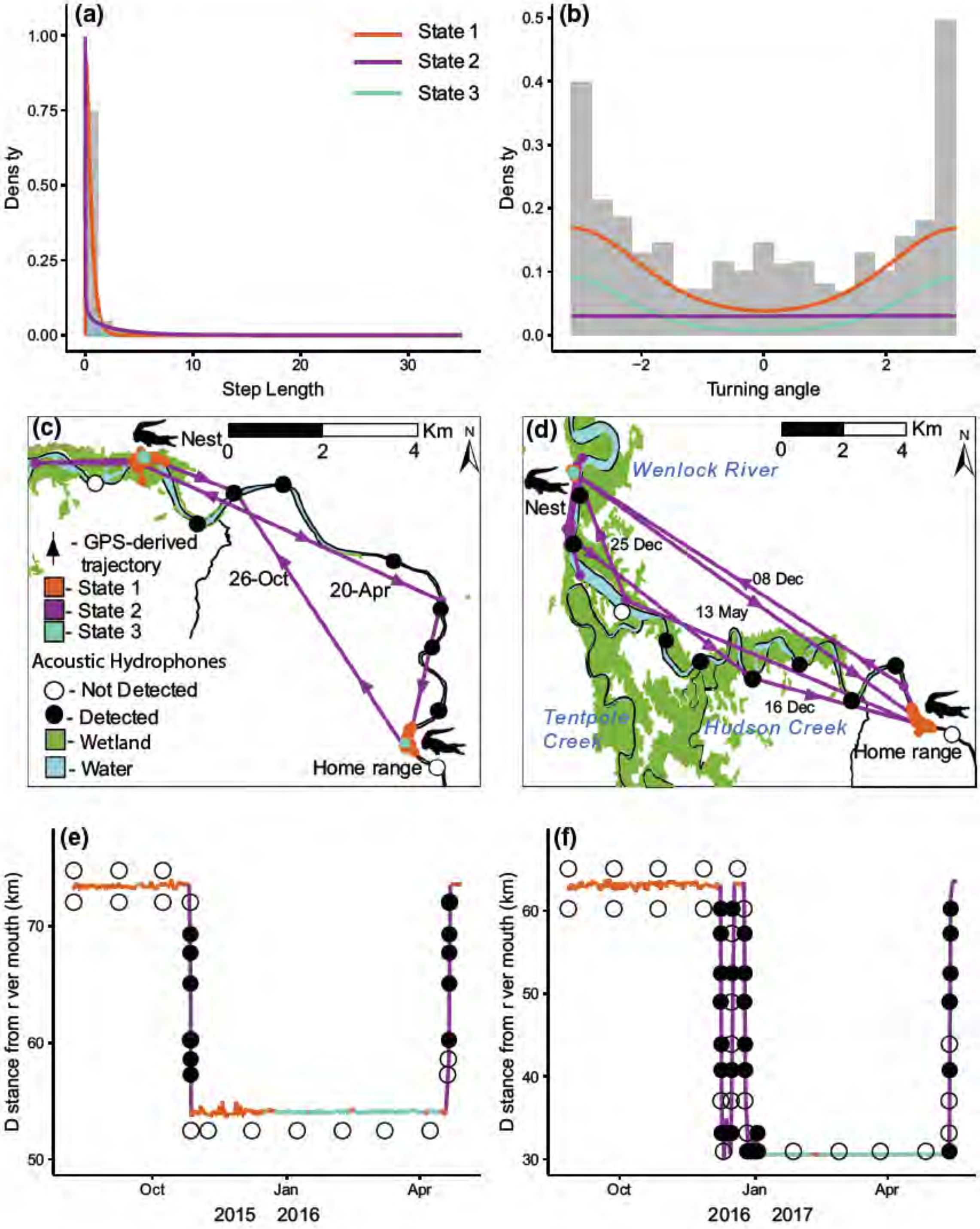

Fig. 2 The fitted state-dependent densities for step lengths (**a**) and the turning angles (**b**) estimated from the Hidden Markov modelling. Movement trajectory for (**c**) Crocodile ID 12728 and (**d**) Crocodile ID 11899 with points representing acoustic receivers or GPS-location fixes with the assigned behavioural state (State 1= 'home ranging'; State 2= 'migratory'; State 3= 'nesting') and lines showing the directional path between consecutive fixes. The distance of (**e**) Crocodile ID 12728 and (**f**) Crocodile ID 11899 from the mouth of the Wenlock River over the tracking period with the assigned behavioural states. Colour version available online

(i.e., 41.26 ± 3.64% of the tagged population each year). Only females > 1.74 m TL were identified as 'nesting' by our filter (Table 2), with the timing of these events peaking in January (Fig. 3a) when total monthly rainfall was greatest (Fig. 3b). The median duration between presumed nesting events was 12 months (min = 9 months), with up to 4 years passing between events (Fig. 3c).

Table 2 Summary statistics of the 36 female estuarine crocodiles *Crocodylus porosus* identified as nesting through acoustic telemetry

Crocodile ID	Total Length (m)	Duration tracked (years)	Number of detections	Number of nesting events	Mean distance migrated (km)	Mean time away from home range (days)
14209	1.74	3.4	2124	2	0.0	134.0
3094	1.90	2.2	242293	2	0.7	147.0
3084	1.91	2.4	6224	2	1.9	190.0
3088	2.02	2.3	14807	2	76.3	108.5
15341	2.08	5.0	293,993	1	0.0	127.0
22186	2.09	1.5	982	1	8.9	138.0
3077	2.11	1.5	5600	1	0.0	115.0
13869	2.13	1.8	18,094	2	1.9	110.0
22165	2.16	1.0	11,158	1	0.0	218.0
15339	2.17	5.0	383,310	3	0.2	140.7
14198	2.20	2.8	54,197	1	1.5	148.0
22176	2.20	1.5	6093	1	0.0	121.0
60253	2.26	4.2	6412	2	7.6	187.5
60255	2.39	3.3	1499	3	0.5	128.0
14205	2.43	2.8	55,376	1	0.0	178.0
15350	2.47	5.6	464	5	6.3	159.0
60259	2.49	8.0	80,919	4	19.5	123.5
15338[a]	2.51	5.0	45,594	2	7.9	132.0
12727	2.56	2.0	16,758	2	47.9	150.5
3076[a]	2.58	2.4	70,034	1	11.7	99.0
13888	2.61	0.6	2322	1	13.7	122.0
3074	2.62	2.7	4067	1	16.3	121.0
3079	2.64	1.9	2179	2	15.6	182.5
14204[a]	2.65	4.1	6009	2	3.0	152.5
15345	2.67	5.0	5923	1	0.0	179.0
15359	2.69	5.5	6207	3	3.0	154.3
3067	2.73	7.0	2242	1	6.8	176.0
11899[a]	2.75	0.6	70	1	16.7	141.0
60261	2.89	5.2	57,442	3	50.5	195.7
13879	2.91	2.5	3012	2	27.8	244.0
14222	2.92	2.1	207	1	7.6	147.0
12728[a]	2.93	2.0	2479	2	8.3	147.0
3086[a]	2.94	1.0	9036	1	47.0	185.0
15356[a]	3.11	2.8	2656	3	22.0	169.0
3078[a]	3.15	2.4	29,493	2	16.0	166.0
60262[a]	3.23	9.0	170,831	6	41.3	210.8

[a] Females that have been dual tagged with a GPS transmitter and acoustic tag

The majority of females (46%) migrated downstream from their home range: 19% moved upstream and 35% remained within their dry season home range. Females preferred to exit the array in areas of wetland habitat, with 50 of the 72 nesting events occurring between 35.8 and 69.1 km from the river mouth (Fig. 1a). In contrast, male movements were primarily upstream (64%), with males exiting the array along tributaries in areas of steep eucalypt dominated banks and beyond the most upstream acoustic receivers. Of the 36 acoustic-tagged females identified by our filter as 'nesting', 15 females (36 of the 72 (50%) nesting events) exited the acoustic array within 5 km of their dry season home range (Table 2). Of those females that migrated > 5 km, the minimum distance moved ranged between 6.84 and 84.2 km (15.9 ± 2.5 km; $n = 36$; Table 2). We recorded 11 instances of double migrations among acoustic-tagged females where, following a migration, an acoustic-tagged female remained at a presumed nesting site for 1–30 days (6.6 ± 2.6 days) before returning to their dry season home range and undertaking a second migration to the same area (Fig. 2f). The time taken to migrate from a dry season home range to a presumed nesting location was 4 ± 1 days, but could take as

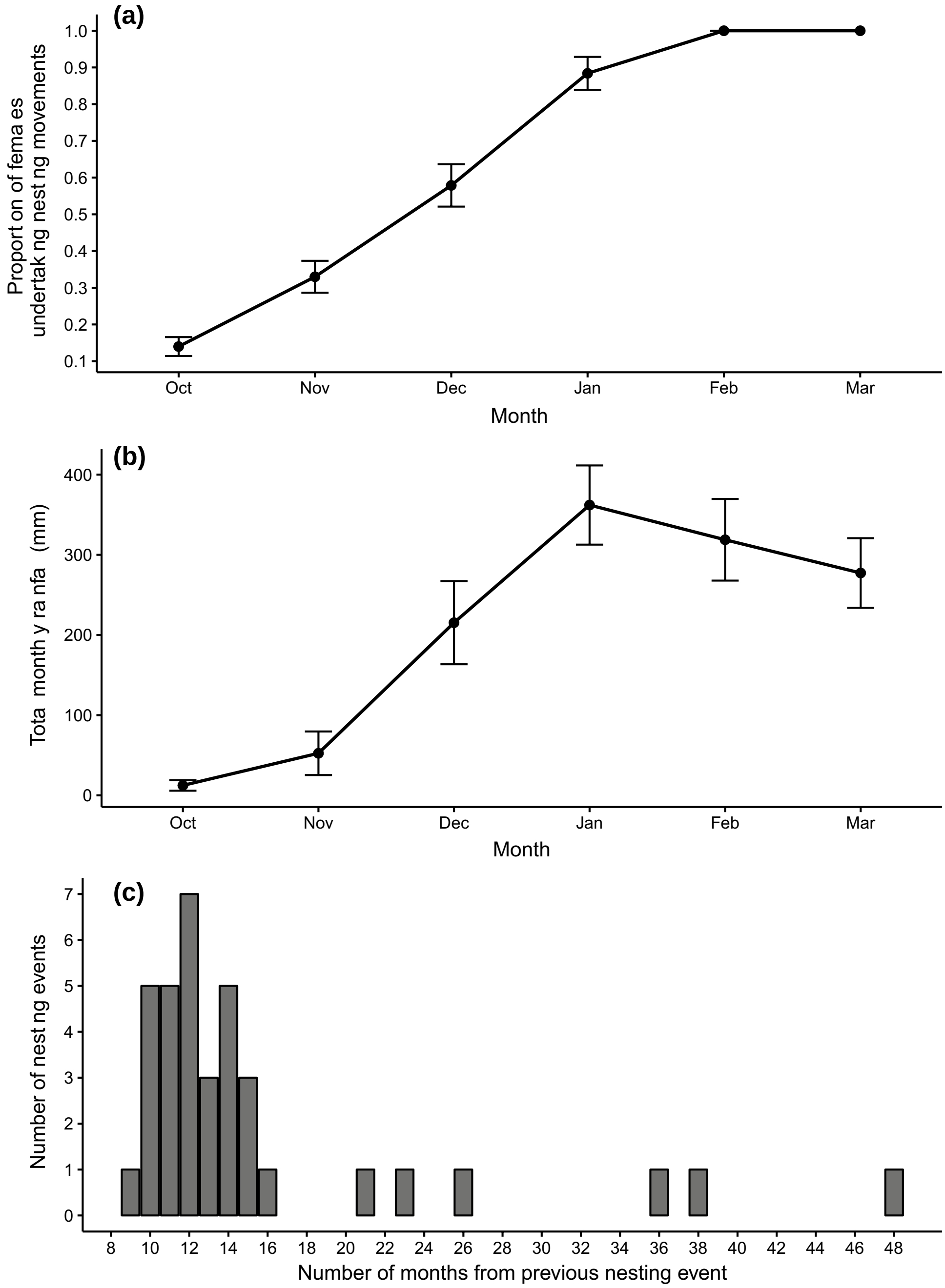

Fig. 3 **a** The mean cumulative proportion of female crocodiles leaving the acoustic array per calendar month between 2008 and 2017. **b** The mean monthly total rainfall for the Wenlock River during the study period. **c** The frequency of reproductive events for females with greater than two nesting events recorded. Error bars display standard error

little as 1 h or as long as 48 days. As the distance migrated increased, so did the duration females spent away from their dry season home range (GLM, $t = 2.694$, $df = 70$, $P = 0.008$; Fig. 4a). The duration females remained away from the dry season home range ranged from 90 to 273 days (157 ± 5 days; $n = 72$; Table 2).

Influence of body size

The timing and frequency of nesting migrations was independent of body size (LME, $t = 0.278$, $df = 35$, $P > 0.5$; LME, $t = 1.415$, $df = 14$, $P = 0.178$, respectively). However, larger females travelled further (LME, $t = 4.519$, $df = 34$, $P < 0.001$; Fig. 4b) and were away from their dry season home ranges for longer (LME, $t = 2.811$, $df = 35$, $P = 0.008$; Fig. 4c) than smaller females. This relationship was not observed within tagged male crocodiles (LME, $t = 0.077$, $df = 32$, $P = 0.938$; LME, $t = 0.304$, $df = 32$, $P = 0.763$, respectively).

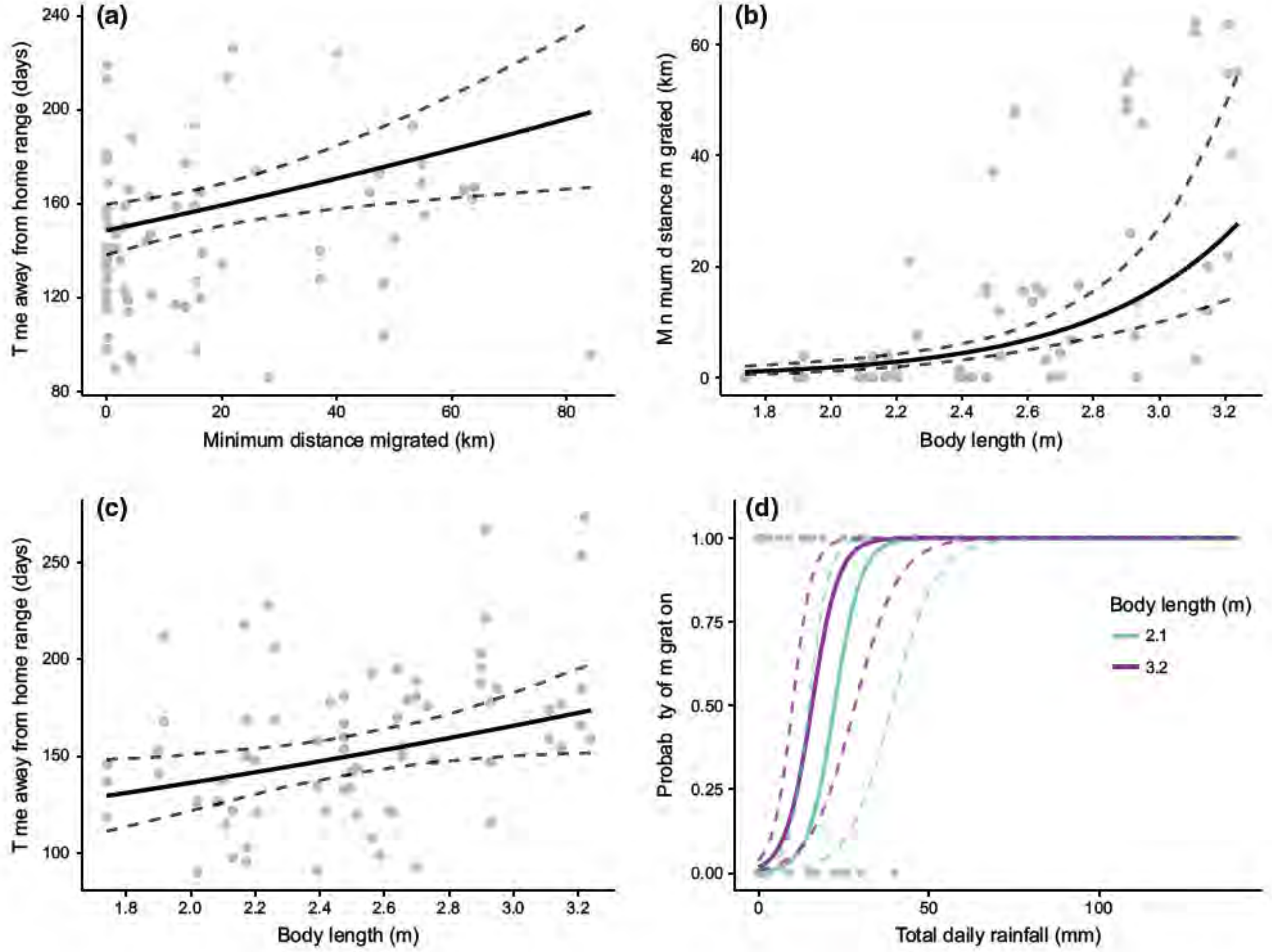

Fig. 4 The relationship between **a** the number of days spent away from the dry season home range and the minimum distance migrated (km) by a female crocodile to a presumed nest sites; **b** the minimum distance migrated (km) and crocodile body length (m); **c** the number of days spent away from the dry season home range (days) and crocodile body length (m). **d** The influence of total daily rainfall (mm) and body size on the probability of a female crocodile initiating a nesting migration. Grey dots represent observed values, solid lines represent model predictions and dashed lines represent the 95% confidence intervals. Colour version available online

Influence of environmental factors

As no model was superior based upon Akaike weights, model averaging was applied across the top model set and the predictor variables were ranked based on their importance (Table 3). In the averaged model, both total daily rainfall ($P < 0.001$) and body size ($P < 0.001$) significantly correlated with the probability of a female initiating a migration (Fig. 4d). A migration began when rainfall ranged between 0 and 59 mm/day, with the majority of migrations (46%) beginning before peaks in rainfall (Chi squared $\chi^2 = 7.875$, $df = 2$, $P = 0.0195$; Online Appendix S5). As body size increased the threshold for initiating a movement decreased, with a 2.1-m female crocodile having a 50% probability of migrating at 22 mm of rainfall, while a 3.2-m female crocodile has a 50% probability of migrating at 16 mm rainfall.

Discussion

By combining fine-scale behaviours acquired using satellite telemetry with long-term behaviours derived from passive acoustic telemetry, we gained new insights into nesting behaviour and maternal investment in a long-lived and highly mobile aquatic reptile. Not only were we able to establish migratory and nesting behaviours in female estuarine crocodiles, we also found the distance females migrated and the duration spent at a nest site increased with body size. Furthermore, rainfall was a major stimulant of nesting migrations with the threshold for initiating movements being significantly lower in larger individuals. To our knowledge, this is the first time that ontogenetic shifts in nesting behaviours have been shown in a taxa outside of birds and mammals.

Table 3 Summary of the 95% confidence interval top model set of the influence of environmental variables on the nesting migrations of female estuarine crocodiles *Crocodylus porosus*

Predictor variable	Model ID											Predictor weight	*P* value
	1	2	3	4	5	6	7	8	9	10	11		
Total daily rainfall	X	X	X	X	X	X	X	X	X	X	X	1	< 0.001
Body length	X	X	X	X	X	X	X	X	X	X	X	1	< 0.001
Minimum daily temperature	X	X	X	X		X	X	X				0.85	0.141
Moon phase	X	X	X		X	X			X	X		0.76	0.178
Daily difference in barometric pressure		X				X	X		X			0.35	> 0.800
Maximum daily river height			X			X		X		X		0.25	> 0.800

Predictor variables considered in each model are indicated with an X

Predictor weights calculated by summing the Akaike weights for all of the models in the best model set that the variable occurred. The larger the predictor weight, the greater the importance of that predictor

Body size is a major factor influencing reproduction

By studying the natural behaviours of 57 female estuarine crocodiles in a tropical river system over a 10-year period, we discovered that while smaller females chose to nest close to dry season territories, larger females would migrate up to 50 km to a preferred nesting site. Furthermore, smaller individuals were absent from their dry season home range for periods of < 150 days, whereas larger females were absent for > 150 days. Given that egg incubation in *C. porosus* typically ranges between 80 and 117 days, with females displaying extended parental care up to 2 months post-hatching (Webb et al. 1977), these results suggest that smaller females are either spending less time selecting nest sites and/or guarding nests or hatchlings. These findings are consistent with previous work where body size was found to be a significant predictor of crocodile behaviour (Brien et al. 2008; Hanson et al. 2015; Thorbjarnarson 1996; Webb and Manolis 1989).

There are several reasons why it may be advantageous for larger females to travel further and spend more time selecting and/or guarding their nests. Across taxa, body size has been shown to be a crucial factor influencing the extent to which a female invests in reproduction; with larger females investing greater levels of resource investment into their offspring (e.g., increased fecundity, greater offspring size, increased postnatal care) than smaller individuals (Barneche et al. 2018; Bekoff et al. 1981; King et al. 2016). Thus, the patterns observed here may simply reflect an increased willingness or capacity of larger animals to invest in reproduction compared to smaller individuals. Alternatively, it is well documented among birds and mammals that parental investment is greatest among older individuals, with shifts in reproductive timing (Robertson and Rendell 2001), nest site selection (Pärt 2001), foraging ability (Hipfner and Gaston 2002) and parental attentiveness (Snyder et al. 2016) often observed as individuals age. While several hypotheses have been put forward to explain these shifts (Forslund and Pårt 1995), experience has been suggested as the main driving factor with individuals increasing reproductive investment with increased experience through successive reproductive events (Curio 1983). In *C. porosus,* flooding and predation are the two major causes for nest and hatchling mortality (Webb and Manolis 1989), and it is possible that smaller females may lack the required experience and skills to effectively detect and mitigate these threats. This is consistent with our finding that larger females initiate nesting migrations at lower rainfall thresholds than smaller individuals, suggesting that previous nesting experience (both successes and failures) may assist individuals to optimize the timing of nesting migrations, improve nest site selection and extend nest guarding to mitigate key threats to nests and hatchlings. Similar patterns have been observed in other ectotherms such as loggerhead turtles *Caretta caretta* (Pfaller et al. 2009) and convict cichlids *Amatitlania siquia* (Santangelo 2015), with previous nesting experience found to increase nesting success through improved nest site selection and care of young for some species. However, fully distinguishing the influence of experience from just body size alone on nesting behaviours and success is difficult due to the correlations between age, experience and body size. Further observational studies examining fine-scale nest site selection, nest attentiveness and reproductive success are required to fully disentangle how body size and experience influence reproductive and nesting behaviours, along with individual fitness in female estuarine crocodiles.

Rainfall cues nesting movements

In tropical environments, rainfall and the tropical monsoon are often the primary trigger of reproductive and nesting behaviours across animal taxa (Bowen et al. 2005; Monadjem and Bamford 2009; Pike 2008; Whitehead and Saalfeld 2000). In northern Australia, the reproductive period for *C.*

porosus runs between late October and March coinciding with the annual monsoonal wet season (Webb and Manolis 1989). As such, rainfall has previously been suggested to be an important factor influencing nesting in *C. porosus* (Webb et al. 1977). By remotely monitoring crocodile behaviour throughout the breeding season via animal-borne telemetry, we were able to confirm that rainfall stimulates the migration of female crocodiles from their dry season home range to their nesting sites, with individuals typically beginning migrations before peak rainfall events (Online Appendix S5). This pattern remained clear even though the movements of our tagged animals spanned 180 km of river and estuary, and the rainfall gauge was located 42 km from the furthest upstream acoustic hydrophone within our array. While body size was not a significant predictor of the timing of nesting movements, it did influence the rainfall threshold for initiating 'nesting' migrations with larger females migrating at a lower rainfall threshold than smaller individuals. A similar pattern has also been observed in magpie geese *Anseranas semipalmata*, another species occupying wetland regions in northern Australia, where older magpie geese required lower levels of rainfall to initiate nesting than younger individuals (Whitehead and Saalfeld 2000). A reason why larger and more experienced females may choose to migrate at a lower rainfall threshold may be to reduce the energetic costs associated with migration, particularly for upstream movements where freshwater inflow during the wet season can be considerable (Campbell et al. 2013; Lyon et al. 2017). There may also be additional advantages of arriving earlier at nesting sites, such as to select areas that have low levels of intraspecific competition, predation rates and a reduced risk of flooding (Webb and Manolis 1989).

Previously, it was assumed that female crocodiles began nesting immediately upon arrival to nesting sites (Campbell et al. 2013; Webb et al. 1977). However, our GPS-derived observations revealed that females exhibit fine-scale exploratory movements over a 10- to 52-day period prior to settling at a nesting site on land. Similar behaviours have been observed in birds (Therrien et al. 2015) and in other reptiles (Angilletta et al. 2009), where such movements represent females searching for appropriate nesting sites. Furthermore, of the 72 potential nesting events observed via acoustic telemetry during our 10-year study, 11 were preceded by an initial exploratory migration of females (2–3.1 m TL) to the locality of their nesting site. This raises the question of why perform such a potentially energy expensive trip so close to nesting? One possibility is that these 'exploratory' movements represent premature nesting migrations, with nine of these 'exploratory' migrations occurring prior to the nesting peak in January and before the onset of the wet season. While increased rainfall appeared to initially stimulate the migration (Online Appendix S5), other features important for successful nesting (e.g., appropriate vegetation for nest construction, flooding) may not have been present so early in the nesting season. As where a female chooses to nest can have major influences on the development and survival of her offspring (Angilletta et al. 2009), further work is required to confirm the purpose of these exploratory migrations and local factors influencing nest site selection.

Nesting migrations are a common occurrence

Large-scale movements have been observed previously among female *C. porosus* (Campbell et al. 2013; Kay 2004); however, due to limited samples of tagged individuals and short study durations these earlier studies were unable to confirm if these movements were part of a nesting migration and if they were a common occurrence. Using long-lived implanted acoustic tags and a network of acoustic receivers, we discovered that migrations to nesting sites occurred annually in female *C. porosus* with individuals commonly exiting the acoustic array at the same river location (i.e., the nesting site) as the previous year. This finding is consistent with accounts of female Nile crocodiles *Crocodylus niloticus* (Combrink et al. 2017) and American alligators *Alligator mississippiensis* (Elsey et al. 2008) returning frequently to nesting areas used in previous years, and visits to crocodile nesting sites identified in this study revealed the presence of multiple nests in various states of decay (R.G. Dwyer, pers obs). However, by examining for periods of transmitter absence from the acoustic array it is possible that behaviours other than nesting may have been misidentified (type I error) or actual nesting events may have been missed (type II error). While we accept that there is potential for type I and type II error, our observations gathered passively via acoustic telemetry support previous observations of nesting female crocodiles and contrast with male behaviours observed in this study. First, the proportion of nesting females and migration distances estimated using acoustic telemetry were comparable to those estimated from our GPS-derived observations and to earlier observations based on radio and satellite telemetry (Campbell et al. 2013; Dwyer et al. 2015b; Kay 2004). Second, no relationship was found between body size and distance migrated or duration out of the acoustic array in males, suggesting that these traits are unique among nesting females. Finally, in contrast to males, female crocodiles typically exited from the middle extent of our array where steep eucalyptus-lined banks were replaced by wetlands dominated by *Nypa fruticans*, Melaleuca swamps and flood plains. The habitats where females exited the array are consistent with the known nesting preferences of *C. porosus* (Webb and Manolis 1989) and evidenced by crocodile nesting surveys conducted previously in the Wenlock River (QDEH 1995).

Conclusions

By tracking the behaviour of 57 female crocodiles over a 10-year period, we were able to provide a rare insight into the influence of body size on the nesting behaviours of a highly mobile long-lived ectothermic vertebrate. We found evidence to suggest that longer periods absent from dry season home ranges, greater migration distances and lower extrinsic migration thresholds seen among larger females was likely influenced by them being more experienced and hence more willing to invest in nesting. While such correlations are well described in relation to age in among birds and mammals, we provide some of the first evidence that such shifts in nesting behaviours in relation to individual body size are also present in crocodylians. We also show how utilising a combination of telemetric technologies, behaviour-classifying state-space models and knowledge of nesting behaviours can help gain insights into the underlying reproductive strategies of long-lived, highly mobile and cryptic species.

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Author contribution statement CB, RD, HC and CF conceived the ideas and designed methodology; All authors 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.

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Data availability Data available from ZoaTrack (https://zoatrack.org/projects) for satellite-telemetry locations and from the IMOS Animal Tracking facility (http://imos.org.au/) for acoustic telemetry data.

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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 $P < 0{\cdot}01$.

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

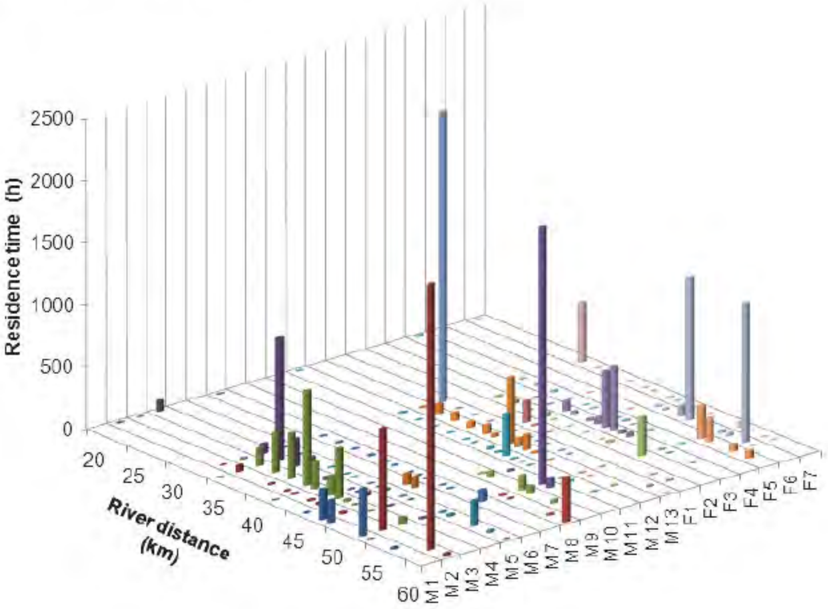

Fig. 1. The amount of time (h) that each acoustically tagged *Crocodylus porosus* (*n* 20) spent at discrete locations along the Kennedy River. River distance is expressed km from the River mouth. Crocodile ID is on the *z* axis (M, male; F, female), Crocodiles M2, M3, M5, M7, M11, F4 & F7 all undertook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

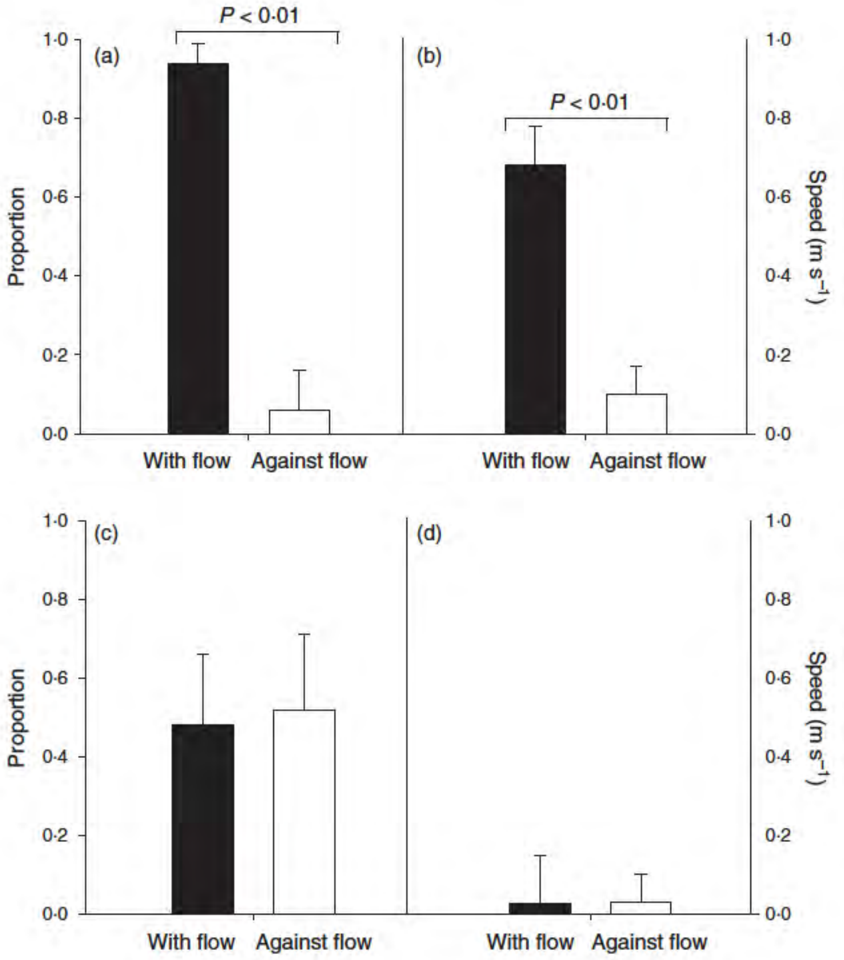

Fig. 2. The effects of current directional flow on movement during long and short distance travel in *Crocodylus porosus* (*n* 8). The black bars show movement when the current was flowing in the same direction as the travelling crocodile and the clear bars demonstrate movement when the current was flowing 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 ($Z > 18·2$, $P < 0$ 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

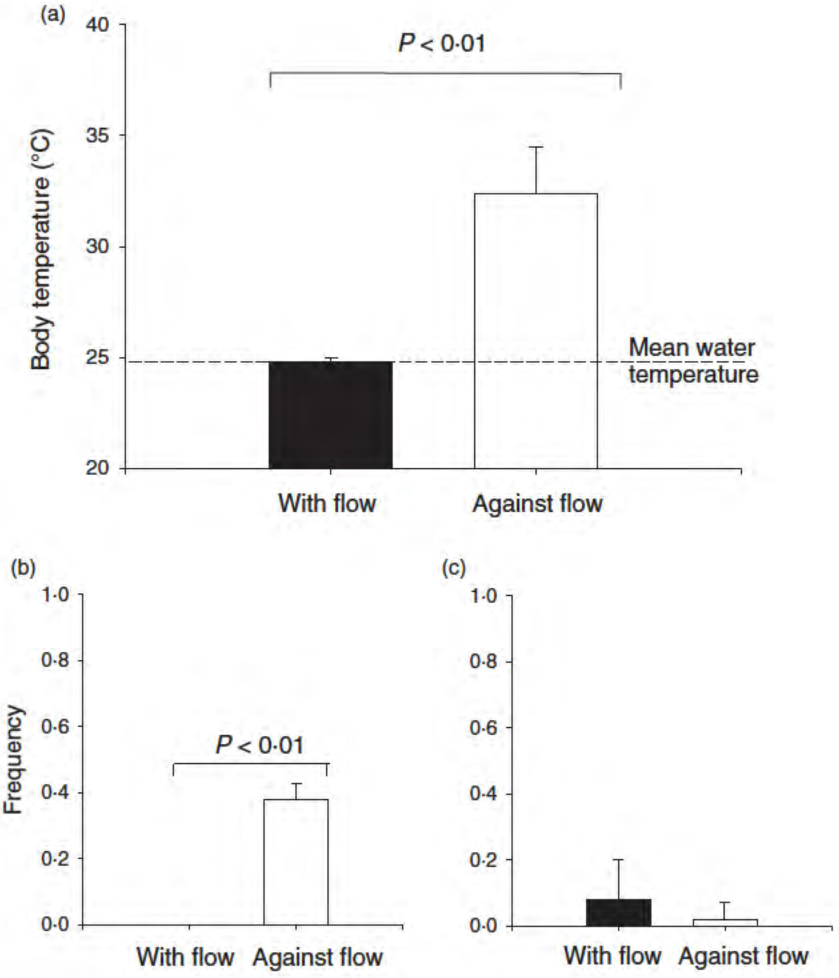

Fig. 3. The effect of current flow direction on river exiting in *Crocodylus porosus*. (a) The maximum body temperature recorded for each hour during long distance journeys (n 42, N 2). (b) The proportion of time spent out of the water when engaged on journeys when the daily distance travelled was > 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

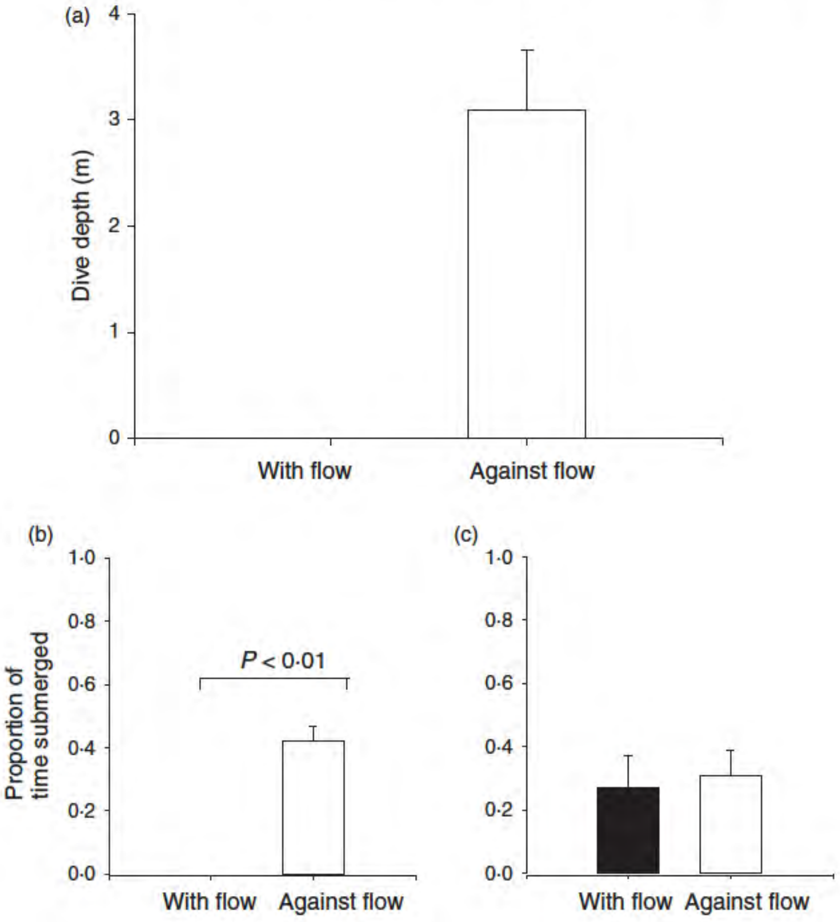

Fig. 4. The effect of current flow direction on diving in *Crocodylus porosus*. (a) The maximum depth dive attained during each hour during long distance travel (n 190, N 6). (b) The amount of time spent submerged when engaged on journeys when the daily distance travelled was >10 km in a constant direction.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

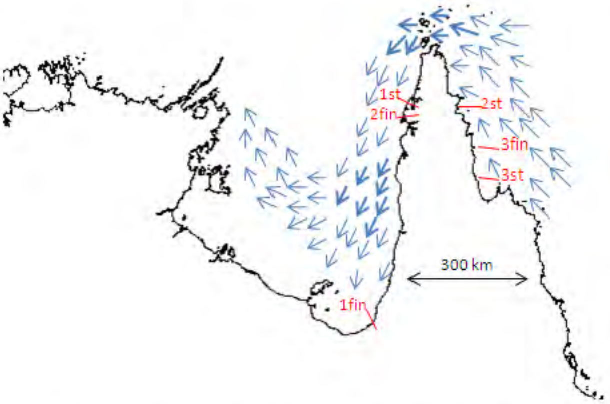

Fig. 5. Schematic diagram showing the coastal travel by three adult *Crocodylus porosus* around Cape York Peninsula, Northern Australia. Start (st) and finish (fin) locations for each journey are shown for crocodile: (1) a 3·84 m male travelled between the 18th December, 2004 to 11th January, 2005; (2)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

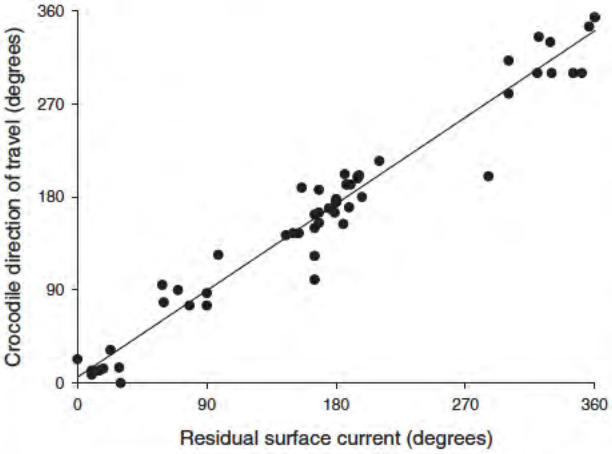

Fig. 6. The relationship between residual surface current direction and the bearing in which *Crocodylus porosus* moved between consecutive satellite fixes (n 56, N 3,). Y 0·91X + 10·4, r^2 0·92.

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 lifestyle 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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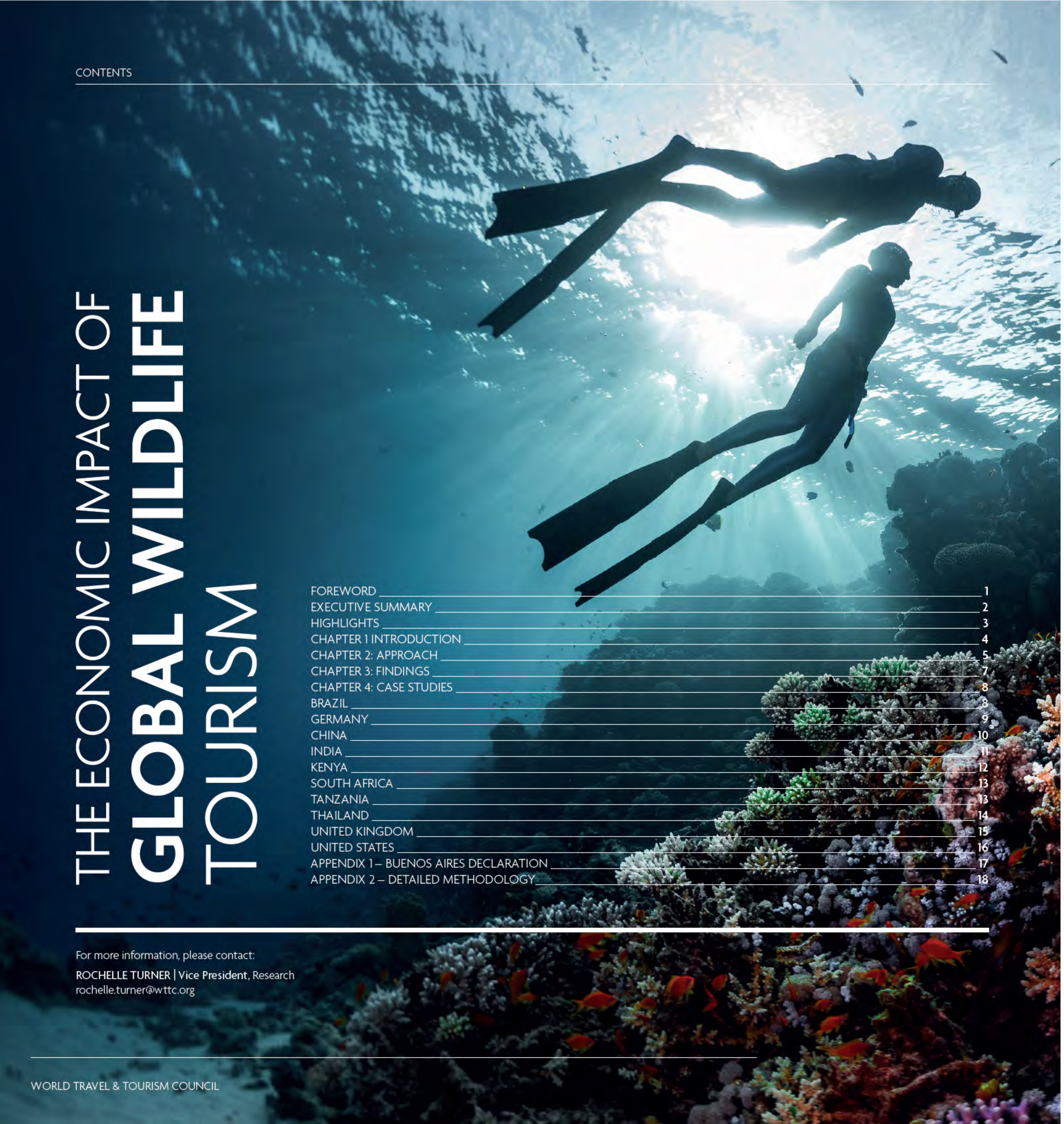
THE ECONOMIC IMPACT OF GLOBAL WILDLIFE TOURISM

TRAVEL & TOURISM AS AN ECONOMIC TOOL FOR THE PROTECTION OF WILDLIFE - AUGUST 2019



THE ECONOMIC IMPACT OF GLOBAL WILDLIFE TOURISM

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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].

02

APPROACH

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 km^2, 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
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6 https://www.weforum.org/agenda/2016/09/fighting-illegal-wildlife-and-forest-trade/
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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.
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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.
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82 The Scottish Government (2010) The Economic Impact of Wildlife Tourism in Scotland. This is slightly higher than 3% of overnight trips accounted for by WT estimated for Great Britain below. A higher figure would be expected for Scotland given that its natural beauty and accompanying wildlife are particularly important attraction for visitors.

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85 VisitEngland (2017) Optimising the Discover England Fund Application through Insight

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87 US Fish and Wildlife Service (2016), National Survey of Fishing, Hunting and Wildlife Associated Recreation. Note these surveys are conducted every five years, with 2016 being the most recent year available.

88 While the same report includes costs of items such as specialist vehicles and land ownership and leasing these are essentially fixed costs and, consistent with the data used elsewhere in this report, were not included in the calculations of WT spend.

89 US domestic person trips are recorded in US Travel Association (2016) US Travel and Tourism Overview. These data include all trips away from home over 50 miles. However, given that the Fish and Wildlife Service data record trips over 1 mile from home, the figures do not consider same geographical scope. The US domestic person trip data would also need to include trips 1 mile from home and over to allow for a true like for like comparison.

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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.

95 UNWTO data for sub-Saharan Africa for example suggest that the vast majority of WT takes place in PAs. The UNWTO surveyed 48 African government institutions and 145 tour operators running wildlife tours in sub-Saharan Africa. When listing the top five wildlife watching destinations, government institutions referred almost exclusively to PAs. Some tour operators referred to wildlife watching on private or communal lands but to a much lesser extent. See World Tourism Organization (UNWTO) (2014) Towards Measuring the Economic Value of Wildlife Watching Tourism in Africa – Briefing Paper.

96 See Newhouse, H. (2017) Which features of protected areas make them attractive to wildlife-based tourists ?: A thesis submitted in candidature for the degree of Masters by Research, Durham University. Newhouse focused on the extent to which WT literature mentions PAs. From this she develops a Likelihood of Selection (LOS) Index for WT in PAs. Statistical analysis indicates that while wildlife is an attractor for such tourists in visiting global PAs. PAs in North America and Europe are significantly less likely to attract wildlife tourists. PAs most likely to attract wildlife tourists were found to be in sub-Saharan Africa, upper Amazonia and Asia.

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.

98 US Fish and Wildlife Service (2016), National Survey of Fishing, Hunting and Wildlife Associated Recreation. Note these surveys are conducted every five years, with 2016 being the most recent year available.

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.

102 Visit Britain (2016) The GB Tourist: Statistics 2015 and Visit Britain (2016) The GB Day Visitor Statistics 2015

103 Visit Britain (2015) Valuing Activities: Final Report

104 Visit England (2017) Optimising the Discover England Fund Application through Insight

105 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 suggest an overestimation. It has been assumed these two effects roughly balance each other out.

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.

108 BTE (2016) op. cit.

109 Karanth, K., Defries, R, Srivathsa, A. Sankaraman, V. (2012) "Wildlife tourists in India's emerging economy: Potential for a conservation constituency?", July 2012, Oryx 46(03)

110 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%).

111 Hausmann,A., Toivonen, T., Slotow, R., Tenkanen, H., Moilanen, A., Heikinheimo, V., Di Minin, E., (2018) "Social Media Data Can Be Used to Understand Tourists' Preferences for Nature Based Experiences in Protected Areas" Conservation Letters, January/February 2018, 11(1)

112 Balmford et al. (2015) op. cit.

113 Based on extracts from the Databank dated 3 February 2019.

114 (Thai National Parks Office website) http://portal.dnp.go.th/p/nationalpark accessed 18 February 2019

115 Karanth,K., Jain, S, Mariyam, D., (2017) "Emerging Trends in Wildlife and Tiger Tourism in India" in Nature Tourism, Chen, J. and Prebensen N. (eds)

116 South African National Parks, Annual Report 2007-08 and South African National Parks, Annual Report 2016-17

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.

118 Souza, T., (2016) Recreation classification, tourism demand and economic impact analyses of the federal protected areas of Brazil. PhD dissertation, University of Florida

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120 The authors report the cost of wildlife boat tour excursions in Manaus as ranging from $48-$112 per day with excursions lasting 1-3 days, though it is again noted this is only a segment of WT and/or WT costs. See 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

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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.

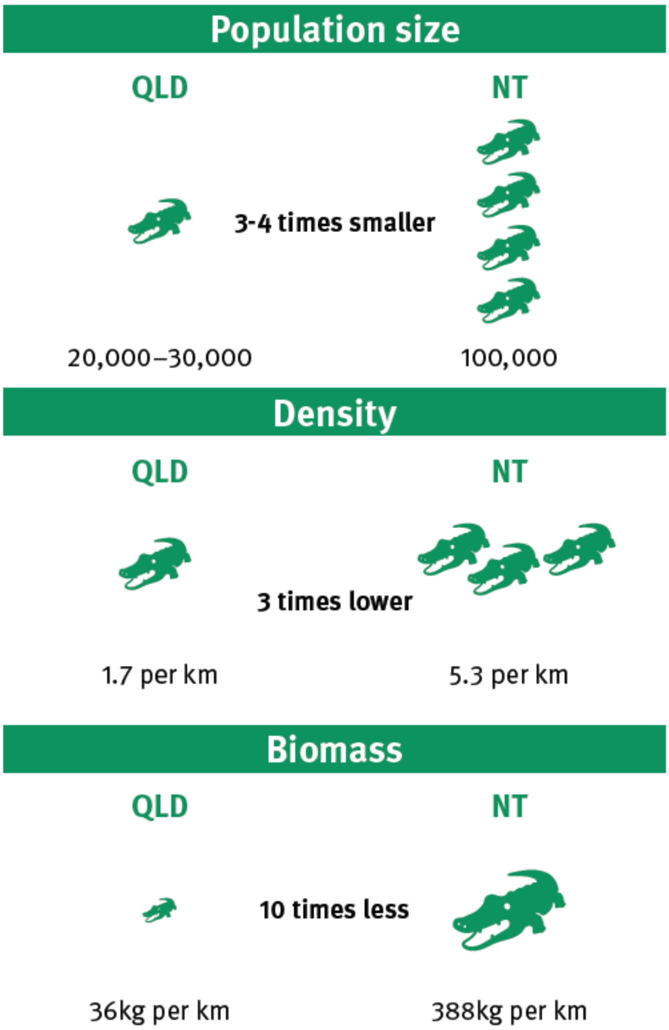

Figure 2. The contemporary population of estuarine crocodiles in the Northern Territory is 3-4 times larger (100,000), 3 times more abundant (5/km), and 10 times heavier/km (388kg) than in Queensland.

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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.

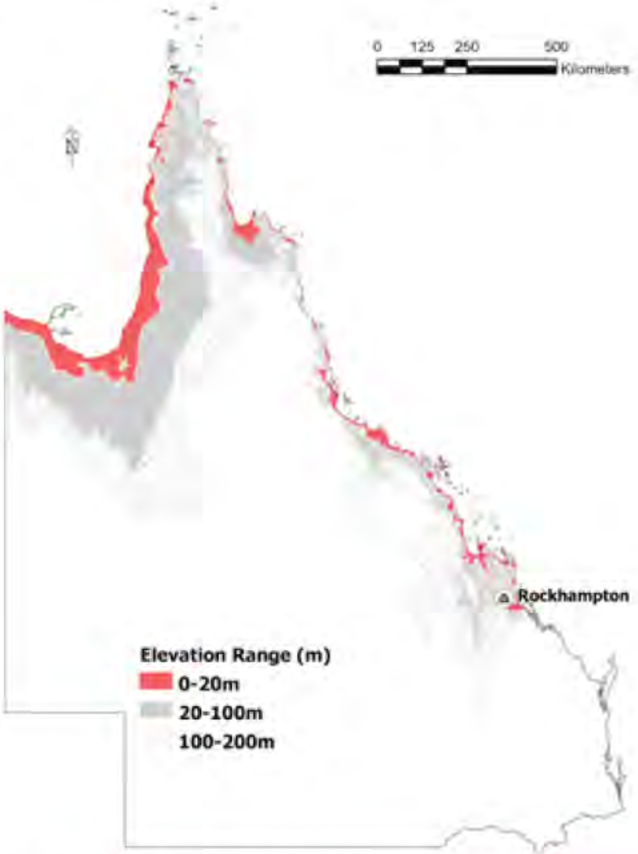

Figure 3. The majority (>90%) of the estuarine crocodile population in Queensland exists below 20m elevation above sea level, with a further ~9% at 20-100m elevation and ~1% at 100-200m elevation.

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.

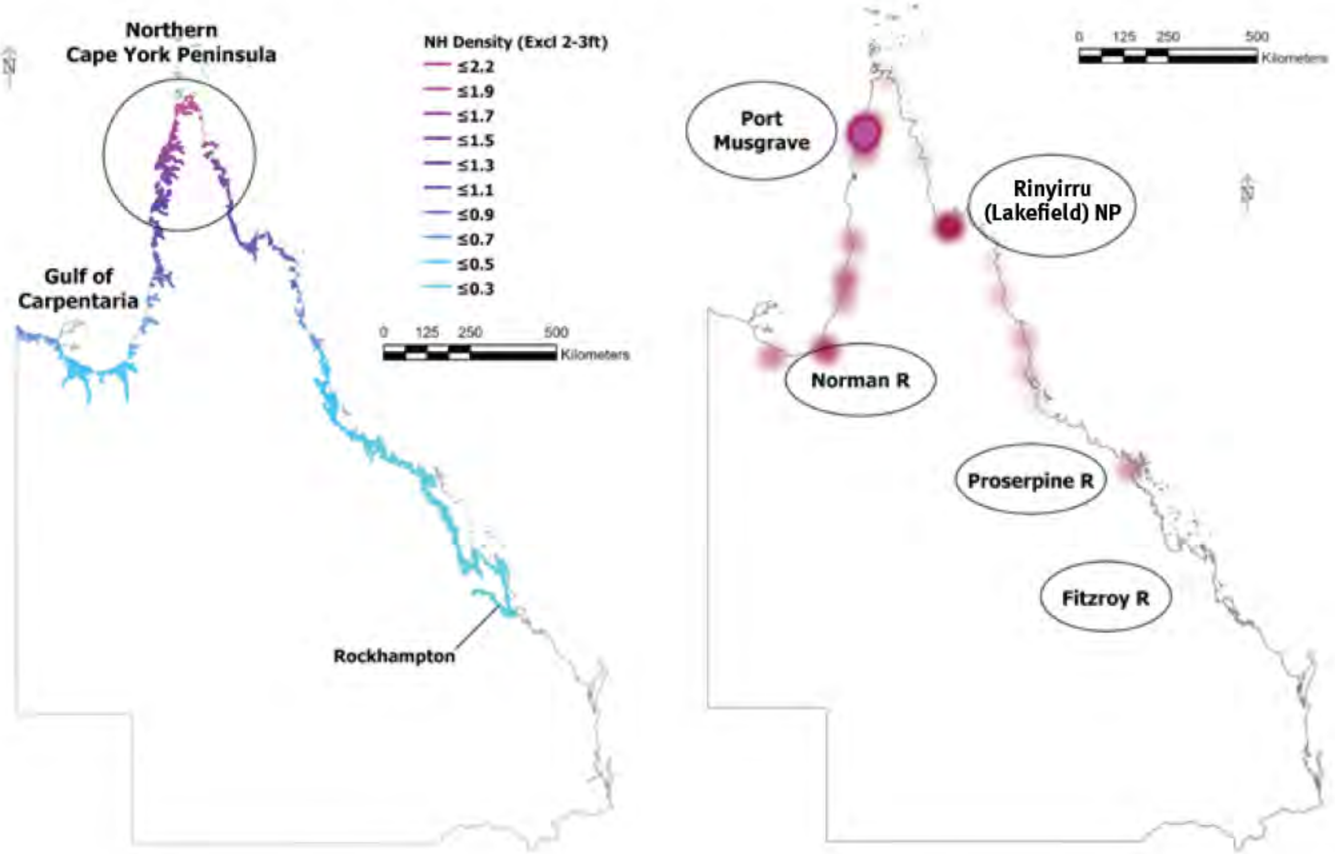

Figure 4. a) Crocodile densities are highest in northern Cape York Peninsula and decline southward; b) The far north-west of CYP contains 40% of the population, while Rinyirru (Lakefield) National Park and the Norman River are also key areas for nesting and recruitment. The Proserpine River has the highest 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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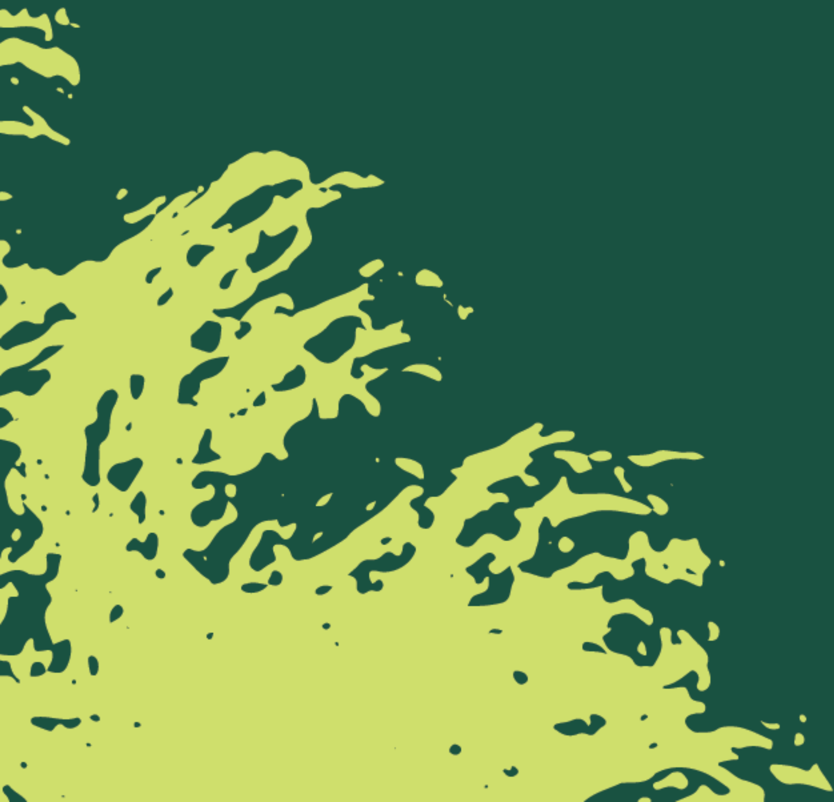

Information sheet

Crocodile attacks on humans in Queensland

This information sheet provides a summary on crocodile attacks on humans in Queensland. The Department of Environment and Science (the department) records and investigates all crocodile reports made by the public and will take appropriate action in accordance with the Queensland Crocodile Management Plan. Unfortunately despite best efforts by the department to ensure the safety of the public, crocodile attacks occur on humans in Queensland

Crocodile attacks on humans in Queensland - 21 December 1985 to 31 July 2023

Year	Date	Location	Comments
1985	21 December	Barratt Creek, Daintree River	Fatal Attack
1986	11 February	Staaten River, Gulf of Carpentaria	Fatal Attack
1987	04 February	Mulgrave River, Gordonvale	Non-fatal Attack
1987	26 June	Mabuiag Island, Torres Strait	Fatal Attack
1993	29 December	Jardine River Ferry Crossing, Cape York Peninsula	Fatal Attack
1996	23 February	Cape Flattery Jetty, Princess Charlotte Bay, Cape York Peninsula	Non-fatal Attack
1997	28 November	Yorkeys Knob, Cairns	Non-fatal Attack
1998	6 February	Chinamans Creek, Cairns	Non-fatal Attack
1999	18 August	MacArthur Island, Shelburne Bay, Cape York Peninsula	Non-fatal Attack
1999	20 September	Russell River, near Babinda	Non-fatal Attack
2000	21 August	Pine River, Weipa, Cape York Peninsula	Non-fatal Attack
2001	02 July	Hann Crossing, Rinyirru (Lakefield) National Park, Cape York Peninsula	Non-fatal Attack
2001	29 September	Four-Mile Beach, Port Douglas	Non-fatal Attack
2004	05 April	Margaret Bay, Eastern Cape York Peninsula	Non-fatal Attack
2004	11 October	Bathurst Bay, east of Rinyirru (Lakefield) National Park	Non-fatal Attack
2004	10 December	Barron River, Cairns	Non-fatal Attack
2005	16 August	Midway Waterhole, Rinyirru (Lakefield) National Park	Fatal Attack
2006	11 October	Mt Adolphus Island, Torres Strait	Unconfirmed Non-fatal Attack
2006	08 November	Mason's Creek, Cape Tribulation	Non-fatal Attack
2007	08 January	Mt Adolphus Island, Torres Strait	Non-fatal Attack

Year	Date	Location	Comments
2007	16 October	Cow Bay, north of Daintree River	Non-fatal Attack
2008	30 September	Endeavour River, Cooktown Cape York Peninsula	Fatal Attack
2008	18 December	False Pera Heads, Weipa, Cape York Peninsula	Non-fatal Attack
2009	08 February	Daintree River, near Daintree Township	Fatal Attack
2011	05 February	Beening Creek, Weipa, Cape York Peninsula	Non-fatal Attack
2011	09 March	Trunding Creek, Weipa, Cape York Peninsula,	Non-fatal Attack
2011	07 December	Bushy Island, Shelbourne Bay, Cape York Peninsula	Fatal Attack
2015	13 April	Port Douglas Golf Course	Non-fatal Attack
2015	03 December	Lizard Island	Non-fatal Attack
2016	29 May	Thornton Beach, near Cape Tribulation	Fatal Attack
2017	18 March	Palmer Point, north of Innisfail	Fatal Attack
2017	19 March	Johnstone River, Innisfail	Non-fatal Attack
2017	12 October	Craiglie Creek, Port Douglas	Fatal Attack
2017	27 November	Mason Creek, Cape Tribulation	Non-fatal Attack
2018	15 January	Nagi (Mt Ernest Island), Torres Strait	Non-fatal Attack
2019	10 November	Captain Billy's Landing, Heathlands, Cape York Peninsula	Non-fatal Attack
2020	23 September	Lizard Island	Non-fatal Attack
2020	28 November	Lizard Island	Non-fatal Attack
2021	28 January	Lake Placid, Cairns	Non-fatal Attack
2021	31 January	Vyce's Crossing, Weipa, Cape York Peninsula	Non-fatal Attack
2021	11 February	Hinchinbrook Island	Fatal Attack
2021	6 August	Portland Roads, Cape York Peninsula	Non-fatal Attack
2021	3 November	McIvor River, near Hopevale, Cape York Peninsula	Non-fatal Attack
2023	22 February	Bloomfield River Boat Ramp, Cape York Peninsula	Non-fatal Attack
2023	08 April	Archer Point, Cape York Peninsula	Non-fatal Attack
2023	29 April	Kennedy River, Rinyirru National Park, Cape York Peninsula	Fatal Attack
2023	27 May	Charles Hardy Islands	Non-fatal Attack

Further information

For further information, contact Wildlife Operations on 1300 130 372 or by email at wildlife.operations@des.qld.gov.au.

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