

RESEARCH ARTICLE



Natal origin and dispersal of problem saltwater crocodiles in the Darwin Harbor, Australia

Yusuke Fukuda^{1,2} | Craig Moritz² | Nancy N. FitzSimmons³ |
 Namchul Jang⁴ | Grahame Webb⁵ | Garry Lindner⁶ |
 Hamish Campbell⁷ | Keith Christian⁷ | Steven Leeder⁸ |
 Sam Banks⁷

¹Department of Environment, Parks and Water Security Government, Darwin, Northern Territory 0828, Australia

²Research School of Biology and Center for Biodiversity Analysis, the Australian National University, Canberra, Australian Capital Territory 2601, Australia

³Australian Rivers Institute, Griffith University, Nathan, Queensland 4111, Australia

⁴Namchul Photography, Noonamah, Northern Territory 0837, Australia

⁵Wildlife Management International Pty Ltd, Darwin, Northern Territory 0812, Australia

⁶Parks Australia, Australian Government, Jabiru, Northern Territory 0886, Australia

⁷Research Institute for the Environment and Livelihoods, Faculty of Science and Technology, Charles Darwin University, Darwin, Northern Territory 0909, Australia

⁸Department of Biodiversity, Conservation and Attractions, Government of Western Australia, Kununurra, Western Australia 6743, Australia

Correspondence

Sam Banks, Research Institute for the Environment and Livelihoods, Faculty of Science and Technology, Charles Darwin University, Darwin, Northern Territory 0909, Australia.
 Email: sam.banks@cdu.edu.au

Abstract

Management programs that successfully recovered wild saltwater crocodile (*Crocodylus porosus*) populations in the Northern Territory of Australia did so with an expanding commitment to maintaining public safety. One aspect of the program is the ongoing removal of resident and immigrant crocodiles within Darwin Harbor (since 1979), the main urban center. We determined the likely sources of crocodiles caught as problem animals between 2015–2017 by comparing recently developed methods for population assignment. Depending on the assignment model used, we estimated that between 30% and 50% of crocodiles in Darwin Harbor originated from the Adelaide and Mary rivers, and the Kakadu region east of Darwin, and between 20% and 30% of crocodiles originated from the Finniss, Reynolds, and Daly rivers southwest of Darwin. Saltwater crocodiles occur at particularly high densities in these catchments. The remainder came from a mixture of different sources across the Northern Territory. The most common animals captured were immature (150–180 cm) males that have traveled 100–200 km. We did not identify any relationships between the distance from the inferred origin to Darwin Harbor and the size and sex of the

This is an open access article under the terms of the [Creative Commons Attribution-NonCommercial-NoDerivs](https://creativecommons.org/licenses/by-nc-nd/4.0/) License, which permits use and distribution in any medium, provided the original work is properly cited, the use is non-commercial and no modifications or adaptations are made.

© 2023 The Authors. *The Journal of Wildlife Management* published by Wiley Periodicals LLC on behalf of The Wildlife Society.

Funding information

Australian National University; Charles Darwin University; National Geographic Society, Grant/Award Number: 51-16; IUCN-SSC Crocodile Specialist Group Student Research Assistance Scheme, Grant/Award Number: 15/5; Holsworth Wildlife Research Endowment, Grant/Award Number: HWRE2016R2027NEW; Wildlife Management International; Northern Territory Government; ACT Herpetological Association

crocodiles, or the year of capture. The targeted removal of crocodiles from specific sites such as Darwin Harbor, near where most people live, improves public safety in the highest risk areas, without compromising abundant source populations in most areas.

KEYWORDS

Crocodylus porosus, dispersal, estuarine crocodile, genetics, human–crocodile conflict, natal origin, population assignment, SNP

Many large predator populations, including a number of crocodilian species (Groombridge 1987), were depleted historically by direct hunting but were subsequently rebuilt by conservation action, potentially compromising public safety in various ways (Ferretti et al. 2015, Wallach et al. 2015, Marshall et al. 2016, Pooley et al. 2021). In the Northern Territory (NT) of Australia, the depletion and recovery of saltwater crocodiles (*Crocodylus porosus*), one of the largest and most aggressive of extant crocodilian species, exemplifies this conundrum. The NT now contains the largest population of saltwater crocodiles throughout its range (Webb et al. 2010, Fukuda et al. 2011). While valued highly by some stakeholders for aesthetic, cultural, ecological, and economic reasons (Lanhupuy 1987, Ryan 1998, Saalfeld et al. 2015, Campbell et al. 2022), widespread public and political support to sustain large wild populations depends on minimizing crocodile attacks on people (Webb 2012, Fukuda et al. 2014).

The management protocols that evolved after protection in 1971 for saltwater crocodiles were initially focused on preserving a small remnant population (Webb et al. 1984, 1994). But by the end of the 1970s, with crocodile abundance increasing across coastal wetlands, direct action regarding public safety became increasingly important (Webb 2014, 2021). This was the basis of the decision to remove crocodiles from Darwin Harbor in 1979, where the highest human population of the NT occurs in residential and industrial areas that are expanding (Australian Bureau of Statistics 2022). Current government programs manage approximately 32 traps across Darwin Harbor to maintain crocodile density at minimal levels for public safety (Fukuda et al. 2014, Saalfeld et al. 2016, Department of Environment, Parks and Water Security [DEPWS] 2021). Roughly 250–300 crocodiles are removed annually (Fukuda et al. 2014, Saalfeld et al. 2016, DEPWS 2021). The removed crocodiles are predominantly sexually immature males (150–200 cm total length), thought to be excluded by dominant males from core habitats and searching for a potential home territory in marginal habitats along the coastlines (Nichols and Letnic 2008, Fukuda et al. 2014, 2022b). Although saltwater crocodiles are highly adapted for saline environments, and they may travel along coastlines or take long sea voyages (Read et al. 2004, Campbell et al. 2010, Fukuda et al. 2019, Spennemann 2021), they need access to lower salinity waters if remaining in a marine environment for long periods (Grigg et al. 1980, Taplin and Grigg 1981, Taplin 1985). Their breeding areas are largely confined to freshwater or low salinity parts of rivers and associated wetlands (Webb et al. 1977, Magnusson 1980, Webb 1991, Fukuda and Cuff 2013, Fukuda et al. 2022a). To build nests, females use a reasonably narrow range of vegetation types such as tall, closed tussock grasslands with rice (*Oryza* spp.) and open forests of eucalyptus (*Eucalyptus* spp.), paperbark (*Melaleuca* spp.), and screw pine (*Pandanus* spp.) with tussock sedgeland ground layers (Magnusson 1980, Fukuda et al. 2007, Fukuda and Cuff 2013). Extensive vegetation mapping across the NT indicates that such suitable nesting habitat is extremely limited in the Darwin Harbor catchment (Fukuda et al. 2007, 2022a; Fukuda and Cuff 2013). Subsequently, very few hatchlings have ever been encountered in Darwin Harbor (Messel et al. 1981, Nichols and Letnic 2008, Fukuda et al. 2014). All these suggest that most crocodiles caught in the harbor are not locally recruited but are migrants from other populations within variable proximities. In addition, recent molecular analyses suggested fairly high gene flow among crocodile populations in the NT, with approximately 42% of 515 crocodiles sampled across the NT being identified as originating from areas outside where they were sampled (Fukuda et al. 2022b).

If the source populations and more detailed movement patterns of crocodiles caught in Darwin Harbor can be identified, safety programs can be more strategic and effective at mitigating potential conflicts between crocodiles and people. For example, if a certain population is the source of most crocodiles in the harbor, management efforts that often have limited resources, can be focused on that population as a priority. Alternatively, if crocodiles are a mixture from different origins, they may be managed more efficiently within the harbor.

In this study, we tested a hypothesis that crocodiles found in Darwin Harbor, where local recruitment is considered minimal, are sourced from other populations by applying various, recently developed genetic population assignment methods. After we determined the likely sources of crocodiles in the harbor, we also examined whether crocodiles from different origins varied in their length, sex, and time of capture.

STUDY AREA

The study focused on Darwin Harbor, with reference samples collected from a focused region around the Top End of NT and East Kimberley of Western Australia (WA; Figure 1A) and lower density sampling from a broader area across northern Australia and Southeast Asia (Figure 1B). The Top End of the NT (~400,000 km², elevation 0–300 m) and East Kimberley (117,5100 km², elevation 0–1,200 m) contain numerous coastal rivers and creeks, lined with mangroves and under tidal influence, and extending upstream from the sea to a diversity of freshwater, non-tidal floodplain wetlands and sand and rock-lined water courses (Webb 1991). All are occupied by saltwater crocodiles at different densities, as indicated by spotlight surveys, ranging from 0.1 to 15 crocodiles sighted per kilometer of river (Fukuda et al. 2007, 2011; Saalfeld et al. 2016). The species also occurs along the coastline between rivers and occupies near coastal islands (Webb and Manolis 1989, Webb 1991). The climate in the study region is monsoonal, with a distinct wet season with heavy rains from November to April, and a dry season from May until October with little rain. Available wetlands expand during the wet season when crocodiles nest, and contract during the dry season (Webb 1991, Fukuda and Cuff 2013), when many temporary waterbodies dry completely if early rains are delayed. Crocodiles tend to remain in permanent waterbodies during the dry season, but are sometimes forced to aestivate in drying mud (Webb and Manolis 1989, Lindner 2004). In the NT, there is limited intensive agriculture and most coastal and riparian vegetation communities remain intact (Fukuda et al. 2007). Outside Australia, the species is distributed in many Indo-Pacific countries ranging from the eastern coasts of India in the west, to Vanuatu in the east, and from the Philippines in the north to around 23°S latitude in Australia in the south.

METHODS

Sample collection and genotyping

We collected 939 geo-referenced saltwater crocodile tissue samples from across northern Australia and the nearby countries of Cambodia, Indonesia, Malaysia, New Caledonia, Papua New Guinea (PNG), Singapore, Timor-Leste, and Vietnam (Figure 1). The tissue samples were pieces of skin collected randomly from 1) free-ranging crocodiles using a biopsy pole (Barrow and Halford 2019) or by hand capture in 2016–2021, 2) crocodiles captured as part of the public safety programs in 2015–2017 (Fukuda et al. 2014, Saalfeld et al. 2016), 3) embryos that failed to develop to term during incubation in 2015–2020, or 4) museum samples that had been collected for previous studies in 1997–2000 (FitzSimmons et al. 2001, 2002). The embryos came from eggs collected from wild populations as part of the NT's commercial egg ranching program (Leach et al. 2009, Saalfeld et al. 2016), and we used one egg per clutch collected from a geo-referenced nest location. The free-ranging crocodiles sampled ranged from 0.3 m to 5.1 m long.

Technicians conducted DNA extraction and genotyping at Diversity Arrays Technology (Canberra, Australia) using the DArTseq approach (Kilian et al. 2012). This method uses genome complexity reduction and next

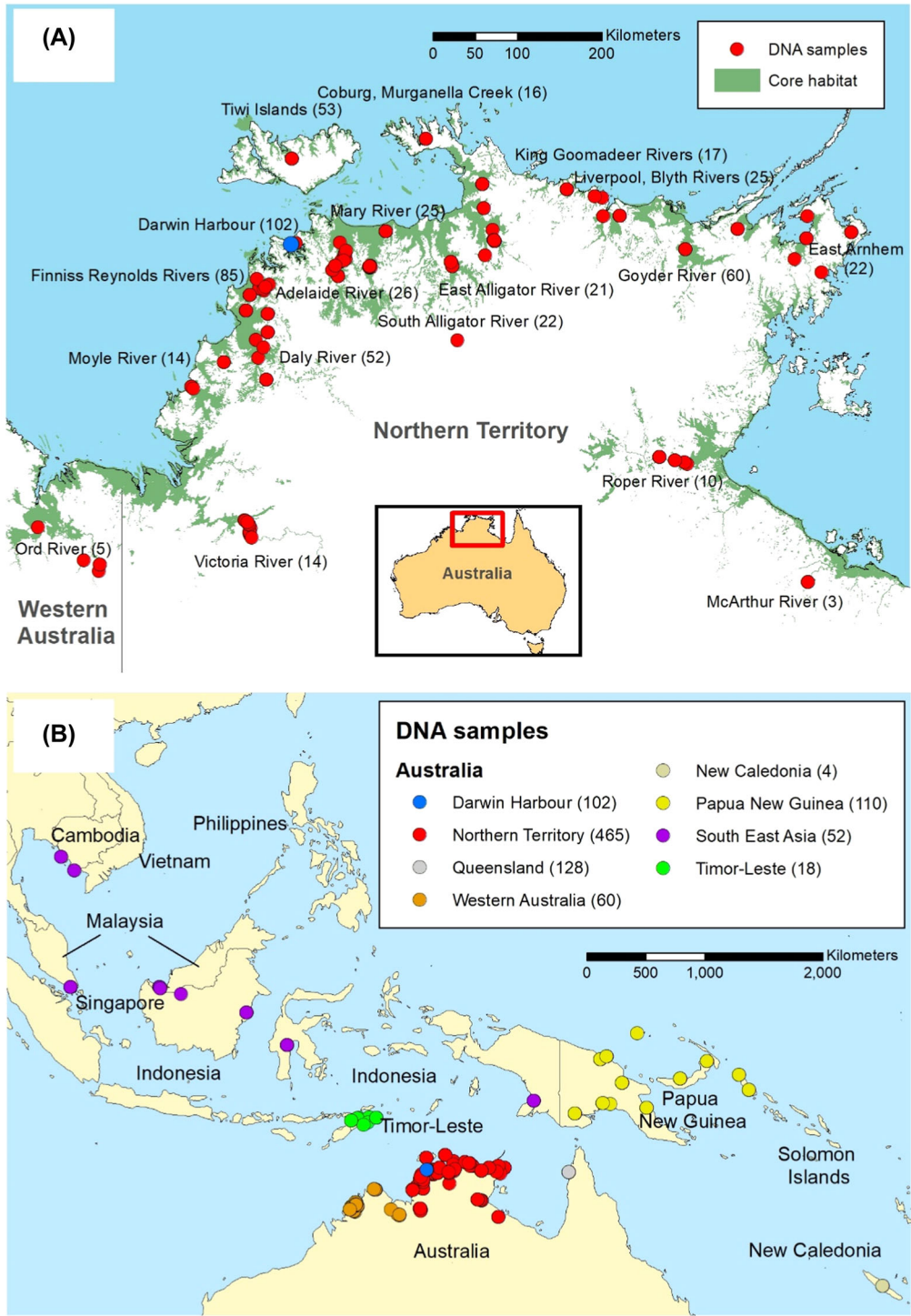


FIGURE 1 Locations of genetic samples of saltwater crocodiles collected in A) the Northern Territory and Western Australia, Australia and B) the neighboring countries between 1997 and 2022. The number in parentheses is the number of the samples collected for each location.

generation sequencing conceptually similar to RADseq, in this case based around an SphI enzyme digestion of genomic DNA and Illumina HiSeq. 2500 sequencing. We ran 30% of samples twice as technical replicates to assess the repeatability of single nucleotide polymorphism (SNP) calls. Initial sequence processing and SNP calling by DART yielded 22,227 SNP loci across 16,637 contigs. The reference genome assemblies were CroPor_comp1 (Mississippi State University 2016) and Cpor_3.0 (The International Crocodilian Genomes Working Group [ICGWG] 2020). We retained 19,630 SNPs that mapped to either of these assemblies. As an initial data exploration step, we plotted basic SNP metrics on sequence depth and other quality metrics and explored relationships between these metrics and basic population genetics statistics, including observed and expected heterozygosity. We used the graphical analysis to evaluate whether genotype properties (e.g., observed heterozygosity) were associated with SNP quality metrics such as mean sequencing depth.

Population assignment–broad scale

Before assigning crocodiles samples (with unknown, mixed origins) from Darwin Harbor to broad geographic sources, we filtered the SNPs, using the dartR package in R 4.2.2 (Gruber et al. 2017), according to call rate (>0.80), repeatability (>0.95), mean total depth (10–200), and mean ratio of sequence depth (0.5–2). We set the allele depth ratio criterion to remove loci in which one allele was preferentially detected, indicating potential susceptibility to null alleles through polymerase chain reaction bias. We also dropped 1) SNPs (ranked by polymorphic information content) within sequences with >1 SNP present, 2) SNPs that did not align to the reference genomes (Mississippi State University 2016, ICGWG 2020) with an e-value threshold of -10 or lower, and 3) SNPs that mapped to >1 location on the reference genome. We dropped genotypes of individuals for which $>10\%$ of SNPs were not genotyped. Following these filtering steps, we retained 1,270 SNPs in 912 of the 939 sampled individuals with a minor allele frequency of >0.02 , corresponding to ≥ 20 allele copies for analysis. We graphed the distribution of the genetic diversity statistics to visualize any unexpected patterns with regard to Hardy-Weinberg expectations within populations but did not filter any further based on this graphical analysis (Figure S1, available in Supporting Information).

Depending on the location of the 912 filtered samples, we broadly grouped the Australian samples ($n = 732$) as being from Darwin Harbor ($n = 95$), non-Darwin Harbor NT ($n = 463$), Queensland (QLD; $n = 126$), and WA ($n = 55$), and other samples as PNG ($n = 100$), Southeast Asia ($n = 49$; Cambodia, Indonesia, Malaysia, Singapore, Vietnam), and Timor-Leste ($n = 18$; Figure 1B). We excluded New Caledonia from this analysis because of its geographic isolation and small sample size ($n = 4$). We kept PNG and Timor-Leste samples separate because of their close proximity to Darwin Harbor. We calculated the observed heterozygosity (H_O), expected heterozygosity (H_E), inbreeding coefficient (F_{IS}) within populations, and genetic differentiation among populations (F_{ST}) to assess the genetic differentiation differences between these broad groups, using GenAlEx (Peakall and Smouse 2006, 2012).

For the broad genetic assignment, we used the R package assignPOP (Chen et al. 2018) and program Structure (Pritchard et al. 2000, Wang 2017). The assignPOP package estimates membership probabilities of each individual with unknown origins in a supervised machine-learning framework (Chen et al. 2018). We used the support vector machines (SVM) option with linear kernel and parameter cost = 1 to build the predictive models for estimating probabilities, as it generally gives higher accuracies than other models in mixed-stock analyses (Chen et al. 2018, Euclidean et al. 2021). In Structure, we set 20,000 for the length of burn-in period and 80,000 for the number of Markov chain Monte Carlo (MCMC) repetitions after burn-in with 2 iterations. We used the admixture model with GENSBACK = 2, MIGPRIOR = 0.05, and ALPHA = 0.03 and the correlated allele frequency model with 0.01 prior mean, 0.05 prior standard deviation, and 1.0 lambda. We also considered other population assign methods (BONE [Kuismin et al. 2020] and rubias [Moran and Anderson 2018]), but found these more sensitive to differences in the sample size than assignPOP and Structure (Figure S2, available in Supporting Information).

Population assignment—fine scale

As all broad genetic assignments indicated that the crocodiles sampled in Darwin Harbor were most likely related to the NT group (Figure 2), we conducted further analyses at a finer scale within the Northern Territory (Figure 1A). We used the same criteria for the SNP filtering but only used the NT samples and Ord River ($n = 565$). Prior to filtering, we excluded the McArthur River ($n = 3$) and Roper River ($n = 10$) from the analysis because of their distance from Darwin Harbor ($>2,000$ km along the coast) and small sample sizes. Analyzed sample locations from west to east included Ord River ($n = 5$), Victoria River ($n = 14$), Moyle River ($n = 14$), Daly River ($n = 52$), Finniss and Reynolds rivers ($n = 85$), Adelaide River ($n = 26$), Mary River ($n = 25$), Tiwi Islands ($n = 52$), Kakadu ($n = 55$), Cobourg Peninsula and Murganella Creek with $n = 16$, East Alligator River with $n = 18$, South Alligator River with $n = 21$, West Arnhem Land ($n = 40$), Blyth River with $n = 23$, King Goomadeer River with $n = 17$, Goyder River ($n = 60$), and East Arnhem Land ($n = 22$; Figure 1A).

We estimated H_O , H_E , F_{IS} , and F_{ST} within the NT as the smallest unit of the collected samples. Because of the generally low genetic differentiation among the catchments (Figure S3, available in Supporting Information) and some sample sizes being so low (Table 1), we combined the catchments into distinct genetic clusters for the population assignments within the NT. For this, we conducted discriminant analysis of principal components (DAPC) using the R package adegenet (Jombart 2008, Jombart et al. 2010). We selected the optimized number of clusters with the lowest value of Bayesian Information Criterion (BIC) estimated by DAPC (Figure 3A). Based on the a-score analysis (Jombart 2008; Figure 3B), we set the number of retained principal components at 52 and the number of retained discriminant functions at 4. Based on the results of DAPC (Figure 3C–F), we separated the NT and Ord River samples into 6 groups of Darwin Harbor ($n = 95$), Daly River–Finniss and Reynolds rivers ($n = 137$), Adelaide River–Mary River–Kakadu ($n = 106$), West and East Arnhem Land ($n = 62$), Goyder River ($n = 60$), Moyle River–Victoria River–Ord River ($n = 33$), and Tiwi Islands ($n = 52$). Although DAPC grouped Tiwi Islands with Adelaide–Mary–Kakadu when the number of clusters was set at 5 (Figure 3), we separated it as an independent cluster because of its geographic isolation as islands and specific management interest as one of the major sources

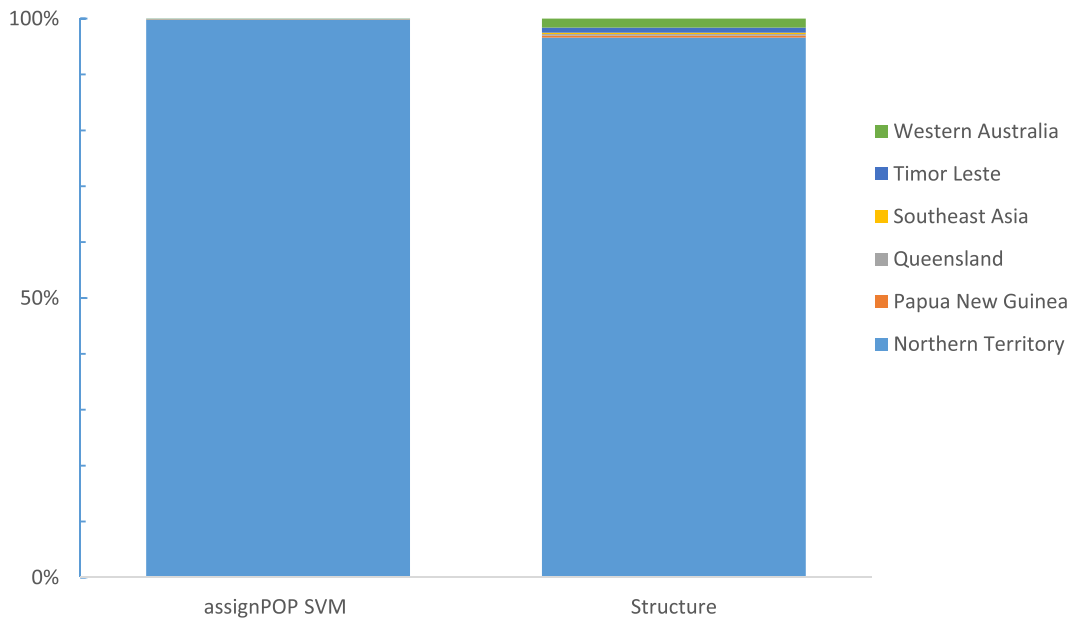


FIGURE 2 Probability of saltwater crocodiles sampled in Darwin Harbor ($n = 95$) being assigned by the different methods (assignPOP with support vector machines [SVM] or Structure) to broad state-wide populations in Australia and neighboring countries between the 1997 and 2022.

TABLE 1 Number of genetic samples of saltwater crocodiles collected from individual catchments in the Northern Territory (NT) and Ord River (Western Australia), Australia, 1997–2022, before and after data filtering and their genetic diversity statistics: H_E = expected heterozygosity, H_O = observed heterozygosity, and F_{IS} = inbreeding coefficient estimated as $(\text{mean } H_E - \text{mean } H_O)/\text{mean } H_E$. Cluster includes a combination of the individual catchments used for the NT population assignments.

Cluster	Catchment	Before filter	After filter	H_E	H_O	F_{IS}
Adelaide River, Mary River, Kakadu	Adelaide River	26	26	0.20	0.19	0.02
	Coburg, Murganella Creek	16	16	0.19	0.19	0.00
	East Alligator River	21	18	0.20	0.20	0.00
	Mary River	25	25	0.20	0.19	0.04
	South Alligator River	22	21	0.20	0.20	0.02
East and West Arnhem Land	Blyth River	23	23	0.21	0.21	0.00
	East Arnhem Land	22	22	0.21	0.21	0.00
	King, Goomadeer rivers	17	17	0.20	0.20	0.01
Daly River, Finniss River, Reynolds River	Daly River	52	52	0.19	0.19	0.00
	Finniss, Reynolds rivers	85	85	0.19	0.19	0.04
Goyder River	Goyder River	60	60	0.21	0.20	0.06
Moyle River, Ord River, Victoria River	Moyle River	14	14	0.20	0.18	0.10
	Ord River	5	5	0.17	0.19	−0.11
	Victoria River	14	14	0.19	0.18	0.02
Tiwi Islands	Tiwi Islands	53	52	0.21	0.20	0.02

of eggs for commercial ranching; we thus used 6 clusters in total. As above, we used assignPOP (SVM) and Structure to assign the Darwin Harbor crocodiles to the populations.

With the possible sources of the individual samples from Darwin Harbor inferred by the different methods (with >0.8 probability), we examined whether there was any particular trend between the inferred origins and their biological attributes including total length (TL), sex, and year of capture (2015–2017). We examined these relationships using generalized liner modeling (GLM) and set the distance from the inferred origin to Darwin Harbor as the response variable and TL, sex, and capture year as the explanatory variables. Because saltwater crocodiles rarely move long distances over land (Baker et al. 2019, Fukuda et al. 2019), we measured the distance to the harbor along the coastlines rather than overland, using the path distance function in ArcGIS 10.6.1 (Esri, Redlands, CA, USA) with a land cover surface derived from Fukuda et al. (2022) being set as the input cost raster. Because the plot of the response variable against the explanatory variable TL showed a somewhat quadratic relationship, we made the variable a quadratic term in the models (and a linear term to compare). We used the Gaussian link function in both the linear and quadratic models. We ran the models on the results given by each of the population assignment methods. We also used G-test to determine whether the proportions of these variables (TL, sex, travel distance, and inferred source) varied significantly.

RESULTS

We filtered SNPs using stringent criteria to retain a set of SNPs consistently genotyped across a large sample size across all populations. From the obtained 19,630 SNPs in 939 individuals, we filtered the dataset to 1,270 SNPs (6.47%) in 912 individuals (97.12%) for the broad-scale analysis. The filtering resulted in a change in total expected

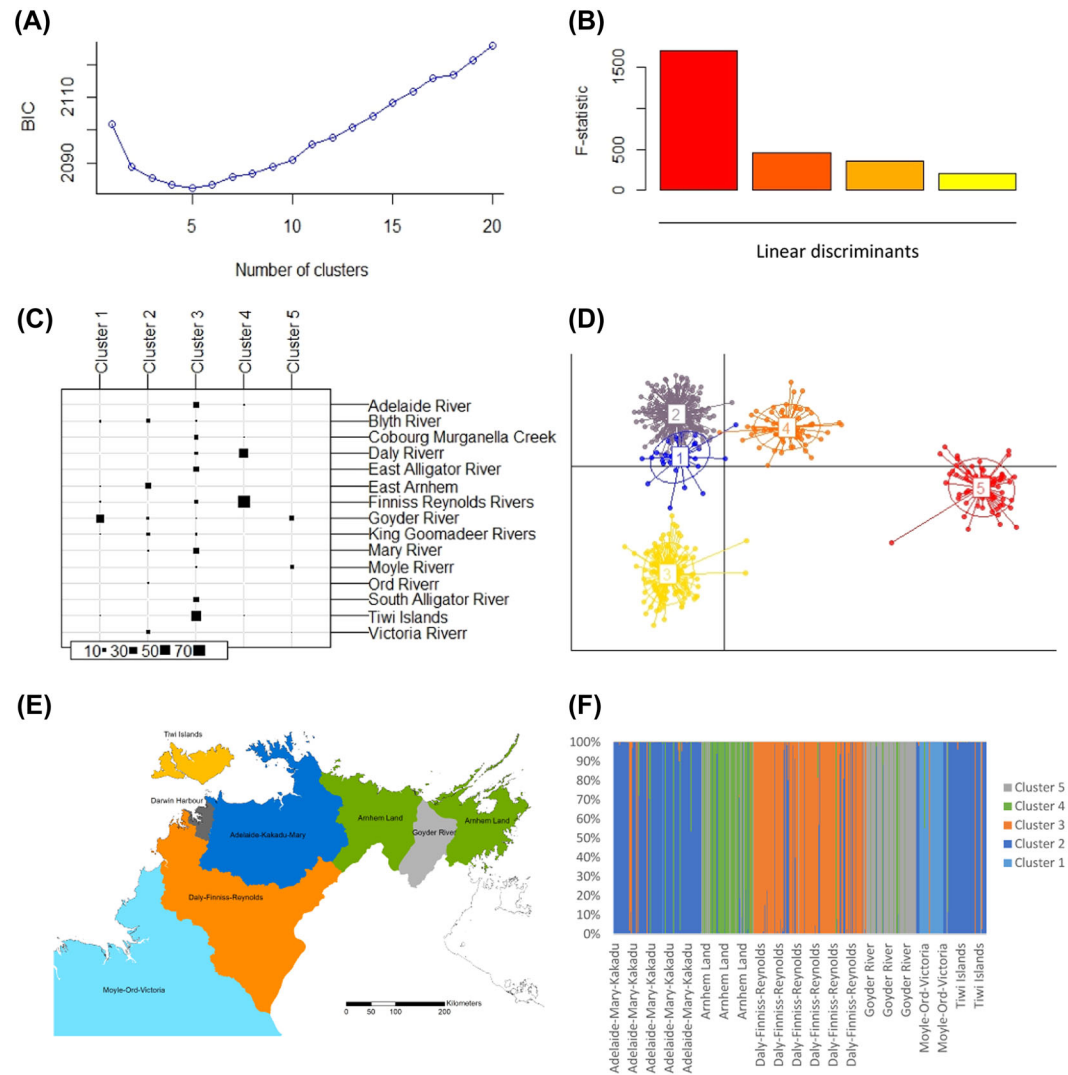


FIGURE 3 Discriminant analysis of principal components (DAPC) of genetic samples of saltwater crocodiles collected in the Northern Territory and Western Australia, Australia, 1997–2021, with A) Bayesian Information Criterion (BIC) estimated for increasing number of clusters, B) eigenvalues estimated by discriminant analysis, and C) cross-validation, D) scatterplot, E) geographic map, and F) bar chart of the genetic clusters separated by DAPC.

heterozygosity (H_T) from 0.19 to 0.20, mean subpopulation heterozygosity (H_S) from 0.13 to 0.15, observed heterozygosity (H_O) from 0.12 to 0.16, and F_{IS} from 0.12 to -0.02 . For the fine-scale analysis, we retained 1,259 SNPs (6.41%) in 545 individuals (58.04%) from the NT and north-eastern WA populations.

The broad-scale analyses showed a high overall level of genetic differentiation ($F_{ST} = 0.144$, $SE = 0.004$). As expected, animals within the Australian regions showed less genetic differentiation relative to more distant locations ($F_{ST} = 0.035$ between the NT and WA, 0.042 between the NT and QLD, 0.102 between the NT and Southeast Asia, 0.089 between the NT and Timor-Leste, and 0.074 between the NT and PNG). The broad genetic assignment of the Darwin Harbor samples by the different methods consistently showed the highest mean probability for the NT among the above 6 regions and countries (Figure 2). Using assignPOP, we estimated the membership probability as 99.9% for the NT, whereas Structure estimated it at 96.6%. Structure estimated a 1.60%

TABLE 2 Genetic diversity statistics for the regional clusters of saltwater crocodiles sampled in the Northern Territory (NT) and Ord River (Western Australia), Australia, 1997–2022, including sample size (n), expected heterozygosity (H_E), observed heterozygosity (H_O), and inbreeding coefficient (F_{IS}) estimated as $(\text{mean } H_E - \text{mean } H_O) / \text{mean } H_E$.

Cluster	n	H_E	H_O	F_{IS}
Adelaide River, Mary River, Kakadu	106	0.20	0.19	0.05
Arnhem Land	62	0.21	0.21	0.03
Daly River, Finniss River, Reynolds River	136	0.19	0.19	0.03
Goyder River	60	0.21	0.20	0.06
Moyle River, Ord River, Victoria River	33	0.20	0.18	0.10
Tiwi Islands	52	0.21	0.20	0.02

probability for WA ($<0.01\%$ for PNG, QLD, Southeast Asia, and Timor Leste). Structure assigned one individual to WA, but assignPOP assigned no individuals to any of the interstate or international groups.

In the fine-scale analyses of the NT and WA, the overall F_{ST} for the individual catchments was 0.065 (SE = 0.003). The highest value of pairwise F_{ST} was 0.062 between the Goyder River (NT) and Ord River (WA). The lowest F_{ST} value was 0.004 between Daly River and the nearby Finniss-Reynolds rivers (NT). The DAPC suggested 5 clusters based on the lowest BIC when testing with 1–20 clusters (Figure 3A). We retained 4 discriminant functions (Figure 3B). Cross validation (Figure 3C), principal components analysis (Figure 3D), and probability of assignment to clusters (Figure 3F) showed distinct genetic separation among the clusters. The genetic diversity statistics (H_E , H_O , and F_{IS}) estimated for the clusters defined by DAPC showed similar values to the catchments (H_O and H_E = 0.18–0.21, F_{IS} = 0.02–0.10; Table 2). The overall genetic differentiation (F_{ST}) for the 5 clusters was 0.045 (SE = 0.003). The highest value of pairwise F_{ST} was 0.083 between the Goyder River and Moyle-Ord-Victoria rivers. The lowest F_{ST} was 0.014 between Adelaide River-Mary River-Kakadu and Tiwi Islands (Figure S4, available in Supporting Information).

The probability estimates from the finer-scale genetic assignment of the Darwin Harbor samples varied across the different methods for the 6 clusters in the NT (Figure 4). In all cases, the proportions of the clusters as a possible origin varied ($P < 0.1$). The combined Adelaide-Mary-Kakadu reference population was the largest source of Darwin Harbor animals and the Goyder River and Moyle-Ord-Victoria the smallest. The combined Finniss-Reynolds-Daly rivers reference group was identified as the second largest source of Darwin crocodiles. Both assignPOP and Structure showed competing probabilities for most individuals between the clusters (Figure 5).

The proportion of the sex of the Darwin Harbor crocodiles was skewed toward males (75.5% male, $P < 0.1$) and the population assignments indicated that the distance most commonly traveled to Darwin Harbor was 100–200 km for both females and males ($P < 0.1$; Figure 6A). The TL of these crocodiles ranged from 119–400 cm for males and from 118–276 cm for females, with the most common size class between 150–180 cm for both sexes ($P < 0.1$; Figure 6B).

The population assignment methods, both the linear and quadratic models, did not provide evidence of relationships between the response variable (distance from the inferred origin to Darwin Harbor) and explanatory variables of TL, sex, or year ($P > 0.1$ in all cases). Similarly, we did not find a relationship between these variables when we analyzed females and males separately ($P > 0.1$ for both female and male; Figure 7).

DISCUSSION

Our results indicate that the region encompassing the Adelaide River, Mary River and Kakadu, to the east of Darwin, is the source of about 50% of the animals found in Darwin Harbor, with the remainder originating from a mixture of the different sources across the NT. The combined Adelaide River, Mary River, and Kakadu National Park

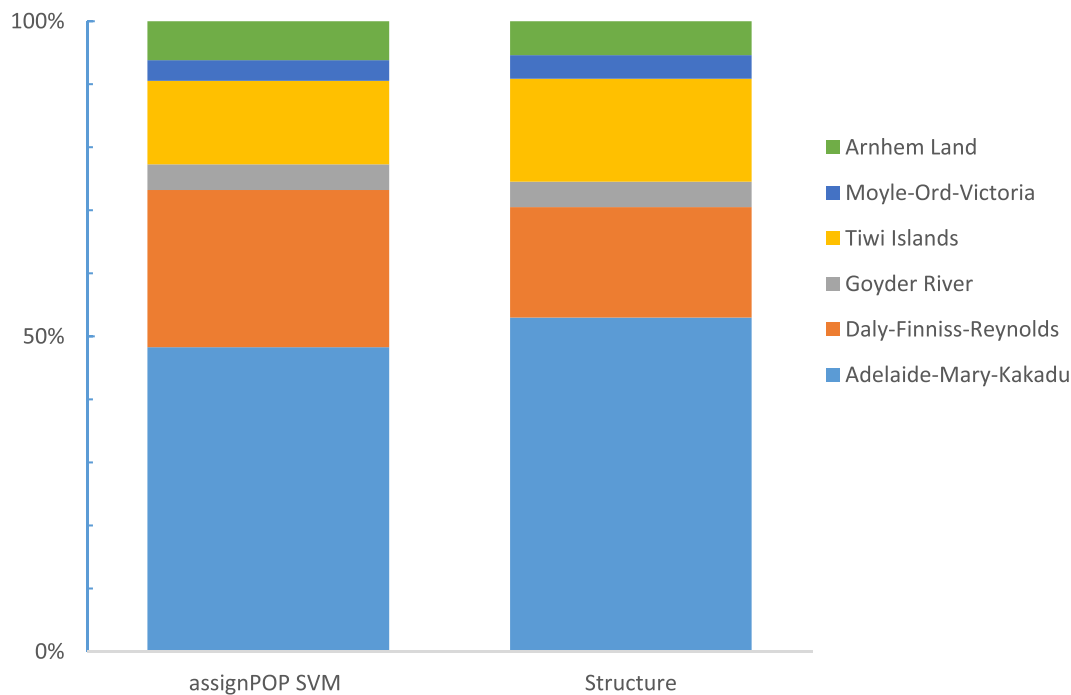


FIGURE 4 Probability of saltwater crocodiles sampled in Darwin Harbor ($n = 95$) being assigned by assignPOP (with support vector machines [SVM]) and Structure to the 6 clusters identified by discriminant analysis of principal components that grouped rivers in the Northern Territory and Ord River in Australia sampled between 1997 and 2022.

region has a very high density of the species and individuals in Kakadu National Park are not subject to any commercial egg collection, harvest, or culling (Fukuda et al. 2011, Saalfeld et al. 2016). The second largest source region (about 20–25%) as estimated in both models for Darwin Harbor encompasses the Daly, Finiss, and Reynolds rivers. These have extensive freshwater floodplains that are highly productive breeding habitats (Fukuda and Cuff 2013) subject to intensive but regulated egg harvesting for the ranching program (Saalfeld et al. 2015, 2016). The Tiwi Islands were the third largest source region for Darwin Harbor (about 15–20%), which is also subject to large egg harvesting (Saalfeld et al. 2015). The other regions were located farther away (>200 km) from Darwin Harbor and inferred as possible sources of crocodiles in much lower numbers.

These results are consistent with a previous finding that environmental resistance, which is a combination of geographic distance and land cover types, affects the species' dispersal patterns (Fukuda et al. 2022b). For example, the Cobourg Peninsula functions as a geographic barrier to east-west and west-east movement (Fukuda et al. 2019), and the relatively small proportion of the Darwin Harbor crocodiles assigned to the sources beyond the Peninsula (<10% for Arnhem Land and Goyder River combined) reflects this. The Goyder River is associated with the Arafura Swamp, one of the largest breeding sites in the Northern Territory (Fukuda and Cuff 2013, Saalfeld et al. 2016), but contributes little to Darwin Harbor. One of the crocodiles assigned to the Goyder River by all 4 methods was confirmed to be an escapee from a commercial farm near Darwin. This crocodile was harvested as an egg from the Arafura Swamp and brought to Darwin, hatched in an incubator, and escaped from the facility to Darwin Harbor but was able to be identified when caught as a problem crocodile. It is possible that the others from the Goyder had a similar history.

Based on the population assignment results, the distance most commonly traveled by crocodiles in Darwin Harbor was 100–200 km for both females and males of all sizes. This is consistent with the previous study, where

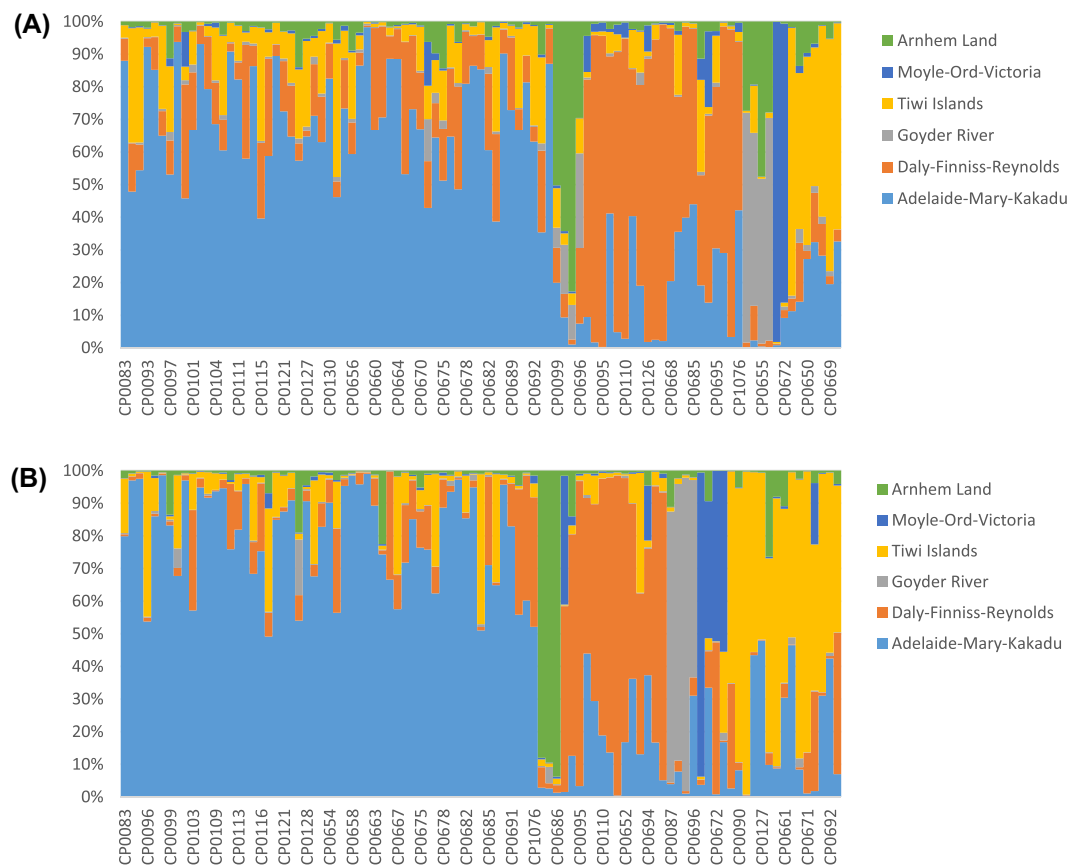


FIGURE 5 Probability of individual saltwater crocodiles sampled in Darwin Harbor ($n = 95$) being assigned by A) assignPOP and B) Structure to the 6 clusters identified by discriminant analysis of principal components in the Northern Territory and Ord River in Australia between 1997 and 2022.

the most commonly traveled distance by crocodiles outside the harbor was 150–200 km in the NT (Fukuda et al. 2022b). Both studies identified a few individuals that traveled long distances (>400 km), and in our study, the long-distance travelers were medium-sized crocodiles (200–250 cm TL). This size range includes males, not sexually mature, and females at or near maturity. They may well be dispersing from core habitats in search of new resources or territories (Campbell et al. 2013; Baker et al. 2019, 2022; Fukuda et al. 2022b). This contrasts situations in QLD where densities are much lower than the NT (Read et al. 2004, Brien et al. 2017, Taplin et al. 2020) and crocodiles display greater site fidelity with their dispersal generally limited to <50 km from the site of origin (Lloyd-Jones et al. 2023). These differences in carrying capacity (and gene flow) are largely influenced by the availability of breeding sites in freshwater floodplains that are much more limited in QLD (Fukuda et al. 2007, Taplin et al. 2020).

Two crocodiles captured in Darwin Harbor (268 and 293 cm long) had individual barnacles (*Chelonibia testudinaria*) on the tail and dorsal osteoderms. The population assignments suggested that both originated from the Daly, Finniss, and Reynolds rivers region that is approximately 200 km west of Darwin Harbor. These marine barnacles are commonly found on sea turtles but cannot survive in low salinity water (505 cyprid survival at 10 psu; Yasuyuki et al. 2011). Given the size of the largest barnacles (~25 mm in diameter) on the larger crocodile and their growth rates (Sloan et al. 2014, Ewers-Saucedo et al. 2015, Doell et al. 2017), this crocodile is likely to have spent at least 90 days in seawater before it was caught in Darwin Harbor.

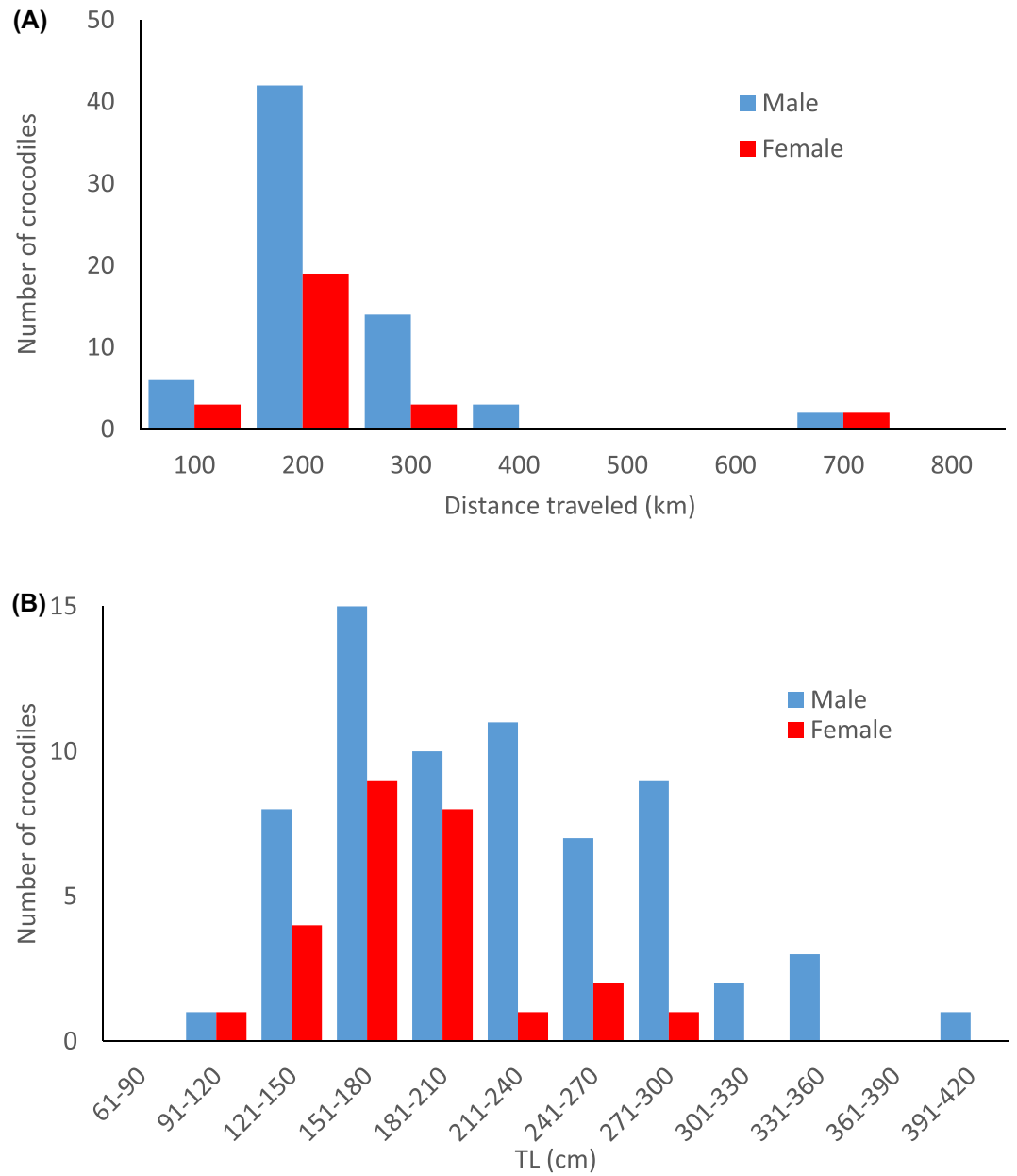


FIGURE 6 Frequencies of saltwater crocodiles caught as problem crocodiles in Darwin Harbor (n = 95) in the Northern Territory, Australia, 2015–2017, by A) distance traveled from their inferred origins and B) their measured total length (TL).

With regard to public safety, crocodiles over 3 m long arriving in Darwin Harbor represent an immediate threat to swimmers (Fukuda et al. 2014, 2015), and their interception is a management priority. Smaller crocodiles, if not removed, may become established in the various tributaries feeding into Darwin Harbor, some of which are popular swimming sites (e.g., Berry Springs and Howard Springs). All the larger crocodiles (>3 m) sampled in Darwin Harbor appeared to originate from the nearby sites (100–200 km), not from long distances away (>400 km).

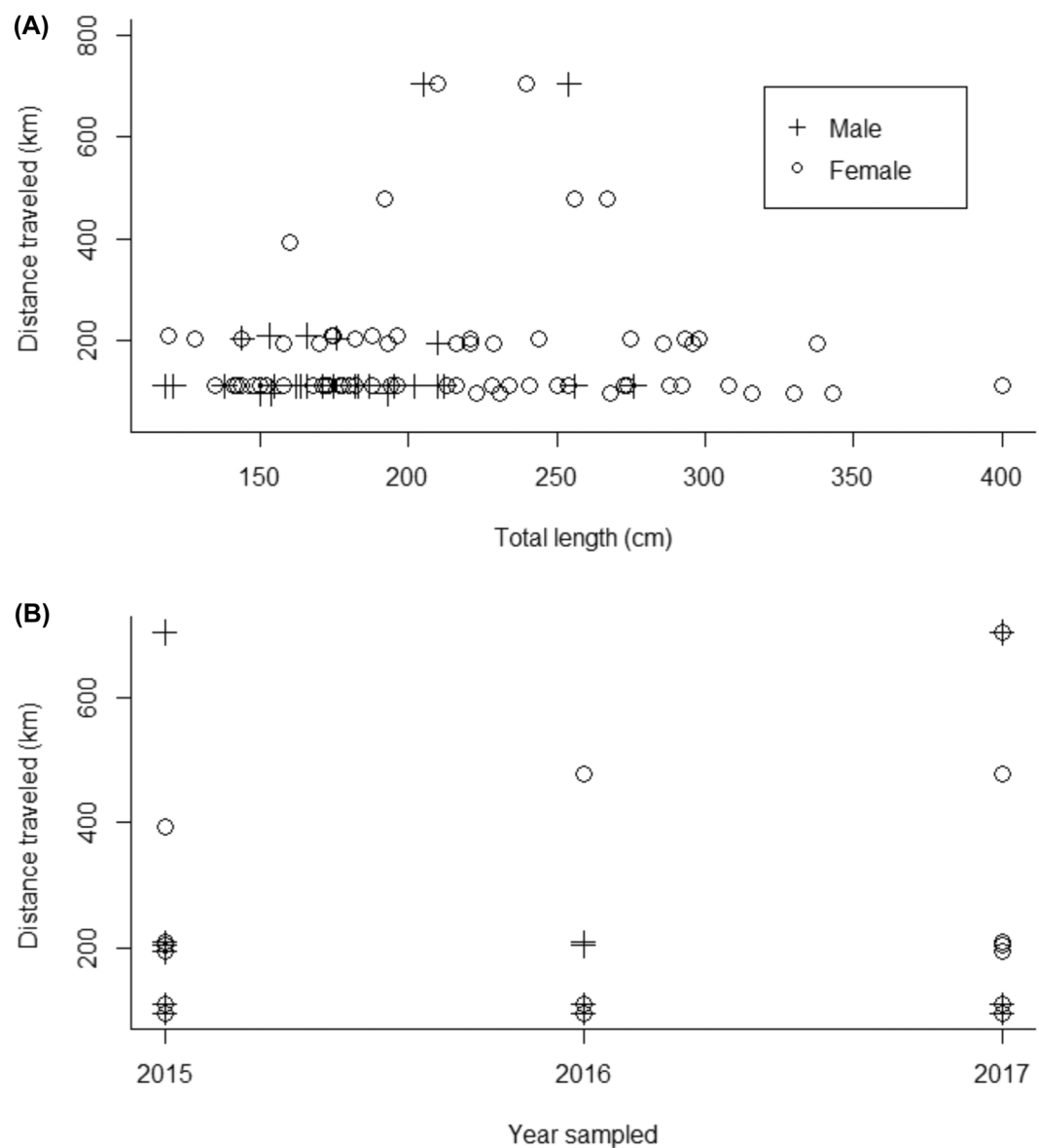


FIGURE 7 Relationships between A) the distance traveled from the identified source population and total length of saltwater crocodiles caught as problem crocodiles ($n = 95$) in Darwin Harbor, Northern Territory, Australia, 2015–2017 and B) the distance traveled and year when the crocodiles were caught.

We were not able to assign the Darwin Harbor samples to the individual catchments with enough confidence (61.8% of the samples had an assignment probability $< 80\%$); thus, we combined catchments into statistically determined clusters. There is a clear trade-off between the geographic precision and the confidence of the genetic assignment. This study did not collect genetic samples from all the major river systems in the NT. The Wildman and West Alligator rivers in Kakadu are major gaps, as are many of the creeks, rivers, and swamps in the Gulf region of the NT. Given more samples, more detailed population assignment with greater confidence may be possible in the future. Full genome sequencing that can generate many more SNPs may also help (Pérez-Reche et al. 2020). Tracking tools in telemetry such as acoustic, radio, and satellite transmitters may complement the genetic methods

(Balaguera-Reina et al. 2016, Combrink et al. 2017, Fukuda et al. 2019, Baker et al. 2022, Mascarenhas-Junior et al. 2023).

MANAGEMENT IMPLICATIONS

Our analyses consistently suggested that crocodiles found in Darwin Harbor are migrants from multiple sources. Emigration from a known source may be able to be reduced by strategic harvesting (pre-migration), but individuals from other sources would still arrive. Thus, targeting a source population may not be effective in reducing management effort required to reduce the risk of crocodile attacks in the harbor. Management should focus on continuing to remove crocodiles within the harbor (post-migration). In addition, given that approximately 50% crocodiles caught in Darwin Harbor come from the rivers to the immediate east, intercepting them closer to the eastern mouth of the harbor may be a strategy worth testing.

ACKNOWLEDGMENTS

The findings and views expressed are those of the authors and do not necessarily represent the views of Parks Australia, the Director of National Parks, the Australian Government, the Northern Territory Government, Queensland Government, or Western Australia Government. E. Anderson, R. Ani, V. de Araujo, L. Baroro, D. Barrow, D. Best, D. Bickford, J. Binaday, I. Buvanoka, T. Clancy, J. Cliff, G. Dally, B. Douma, S. Dwyer, G. Edwards, L. Engkamat, A. Fisher, C. Giru, M. Gorea, J. Gratten, G. Grigg, J. Gus, M. Gusmao, A. Halford, K. Hay, S. Heaton, S. Horner, C. B. How, I. Hunt, F. Hunter, A. Inus Surubai, F. Isi, D. Jacobson, J. Joe, R. Josh, D. Kenesi, R. Kerr, S. Kessner, A. Kipma, Y. Kok Yen, V. Kula, H. Kurniati, E. Lading, G. Laku, E. Langelet, D. Low Choy, R. Manalo, C. Manolis, J. McLachlan, C. Moore, S. Meti, J. Munro, M. Nagta, T. Nichols, Northern Territory Crocodile Farmer Association, H. Onuki, C. Palmer, G. Peckham, L. K. Peng, T. Pine, J. Pridham, O. Pugh, B. Rae, M. Read, A. Ruswan, K. Saalfeld, G. Saputra, H. Saul Suriwa, B. Seah, N. Sua, T. Sugiarto, Sumarmo, C. V. Sumber Murni, C. V. Surya Raya, N. Thuok, A. Underhill, P. Van Muoi, D. Wade, J. Weedon, J. Wilson, D. William, S. Woerle, J. Worthington Wilmer, F. Xavier, S. Yang, and K. Yesinduma provided field support or provided the genetic samples for the study. This study was funded by the Australian National University, Northern Territory Government, National Geographic Society (grant number 51-16), Holsworth Wildlife Research Endowment (grant number HWRE2016R2027NEW), International Union for Conservation of Nature-Species Survival Commission Crocodile Specialist Group Student Research Assistance Scheme (grant number 15/5), and ACT Herpetological Association. Open access publishing facilitated by Charles Darwin University, as part of the Wiley - Charles Darwin University agreement via the Council of Australian University Librarians.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

ETHICS STATEMENT

This study was conducted in accordance with the Code of Practice on the Humane Treatment of Wild and Farmed Australian Crocodiles (Department of the Environment 2013). The protocol was approved by the Animal Ethics Committee of the Australian National University (animal ethics protocol numbers A2017/11 and A2020/09), Parks and Wildlife Commission of the Northern Territory (research permit numbers 57902 and 69126), Department of Parks and Wildlife of the Western Australian Government (permit numbers 08-002527-1 and 08-002527-2), and Parks Australia of the Australian Government (permit number AU-COM2017-361).

DATA AVAILABILITY STATEMENT

The data and analysis codes that support the findings of this study are available from the corresponding author upon reasonable request.

ORCID

Yusuke Fukuda  <http://orcid.org/0000-0002-8675-318X>

REFERENCES

- Australian Bureau of Statistics. 2022. Regional population. 2021. Australian Bureau of Statistics. <<https://www.abs.gov.au/statistics/people/population/regional-population/latest-release>>. Accessed 3 Feb 2023.
- Baker, C. J., C. E. Franklin, H. A. Campbell, T. R. Irwin, and R. G. Dwyer. 2019. Ontogenetic shifts in the nesting behaviour of female crocodiles. *Oecologia* 189:891–904.
- Baker, C. J., C. H. Frère, C. E. Franklin, H. A. Campbell, T. R. Irwin, and R. G. Dwyer. 2022. Crocodile social environments dictated by male philopatry. *Behavioral Ecology* 33:156–166.
- Balaguera-Reina, S. A., M. Venegas-Anaya, A. Sánchez, I. Arbelaez, H. A. Lessios, and L. D. Densmore III. 2016. Spatial ecology of the American crocodile in a tropical Pacific island in Central America. *PLoS ONE* 11:e0157152.
- Barrow, D., and A. R. Halford. 2019. A modified biopsy needle with pole for repeatable tissue extraction from free-ranging crocodiles. *Wildlife Society Bulletin* 43:308–312.
- Brien, M. L., C. M. Gienger, C. A. Browne, M. A. Read, M. J. Joyce, and S. Sullivan. 2017. Patterns of human–crocodile conflict in Queensland: a review of historical estuarine crocodile (*Crocodylus porosus*) management. *Wildlife Research* 44:281–290.
- Campbell, H. A., R. G. Dwyer, T. R. Irwin, and C. E. Franklin. 2013. Home range utilisation and long-range movement of estuarine crocodiles during the breeding and nesting season. *PLoS ONE* 8:e62127.
- Campbell, H. A., M. E. Watts, S. Sullivan, M. A. Read, S. Choukroun, S. R. Irwin, and C. E. Franklin. 2010. Estuarine crocodiles ride surface currents to facilitate long-distance travel. *Journal of Animal Ecology* 79:955–964.
- Campbell, M. A., V. Udyawer, T. D. Jardine, Y. Fukuda, R. K. Kopf, S. E. Bunn, and H. A. Campbell. 2022. Dietary shifts may underpin the recovery of a large carnivore population. *Biology Letters* 18:20210676.
- Chen, K.-Y., E. A. Marschall, M. G. Sovic, A. C. Fries, H. L. Gibbs, and S. A. Ludsin. 2018. assignPOP: an R package for population assignment using genetic, non-genetic, or integrated data in a machine-learning framework. *Methods in Ecology and Evolution* 9:439–446.
- Combrink, X., J. K. Warner, and C. T. Downs. 2017. Nest-site selection, nesting behaviour and spatial ecology of female Nile crocodiles (*Crocodylus niloticus*) in South Africa. *Behavioural Processes* 135:101–112.
- Department of the Environment. 2013. Code of practice for the humane treatment of wild and farmed Australian crocodiles. Text. <<http://www.environment.gov.au/resource/code-practice-humane-treatment-wild-and-farmed-australian-crocodiles>>. Accessed 28 Feb 2014.
- Department of Environment, Parks and Water Security [DEPWS]. 2021. Northern Territory saltwater crocodile (*Crocodylus porosus*) risk management framework 2021–2026. Northern Territory Government, Darwin, Australia.
- Doell, S. A., R. M. Connolly, C. J. Limpus, R. M. Pearson, and J. P. van de Merwe. 2017. Using growth rates to estimate age of the sea turtle barnacle *Chelonibia testudinaria*. *Marine Biology* 164:222.
- Euclidean, P. T., T. MacDougall, J. M. Robinson, M. D. Faust, C. C. Wilson, K.-Y. Chen, E. A. Marschall, W. Larson, and S. Ludsin. 2021. Mixed-stock analysis using Rapture genotyping to evaluate stock-specific exploitation of a walleye population despite weak genetic structure. *Evolutionary Applications* 14:1403–1420.
- Ewers-Saucedo, C., M. D. Arendt, J. P. Wares, and D. Rittschof. 2015. Growth, mortality, and mating group size of an androdioecious barnacle: implications for the evolution of dwarf males. *Journal of Crustacean Biology* 35: 166–176.
- Ferretti, F., S. Jorgensen, T. K. Chapple, G. De Leo, and F. Micheli. 2015. Reconciling predator conservation with public safety. *Frontiers in Ecology and the Environment* 13:412–417.
- FitzSimmons, N. N., J. C. Buchan, P. V. Lam, G. Polet, T. T. Hung, N. Q. Thang, and J. Gratten. 2002. Identification of purebred *Crocodylus siamensis* for reintroduction in Vietnam. *Journal of Experimental Zoology* 294:373–381.
- FitzSimmons, N. N., S. Tanksley, M. R. Forstner, E. E. Louis, R. Daglish, J. Gratten, and S. Davis. 2001. Microsatellite markers for *Crocodylus*: new genetic tools for population genetics, mating system studies and forensics. Pages 51–57 in G. C. Grigg, F. Seebacher, and C. E. Franklin, editors. *Crocodylian biology and evolution* Surrey Beatty, Chipping Norton, New South Wales, Australia.
- Fukuda, Y., and N. Cuff. 2013. Vegetation communities as nesting habitat for the saltwater crocodiles in the Northern Territory of Australia. *Herpetological Conservation and Biology* 8:641–651.
- Fukuda, Y., C. Manolis, and K. Appel. 2014. Management of human–crocodile conflict in the Northern Territory, Australia: review of crocodile attacks and removal of problem crocodiles. *Journal of Wildlife Management* 78: 1239–1249.
- Fukuda, Y., C. Manolis, K. Saalfeld, and A. Zuur. 2015. Dead or alive? Factors affecting the survival of victims during attacks by saltwater crocodiles (*Crocodylus porosus*) in Australia. *PLoS ONE* 10:e0126778.

- Fukuda, Y., P. J. McDonald, and B. Crase. 2022a. Lost to the sea: predicted climate change threats to saltwater crocodile nesting habitat. *Frontiers in Ecology and Evolution* 10: 839423.
- Fukuda, Y., C. Moritz, N. Jang, G. Webb, H. Campbell, K. Christian, G. Lindner, and S. Banks. 2022b. Environmental resistance and habitat quality influence dispersal of the saltwater crocodile. *Molecular Ecology* 31:1076–1092.
- Fukuda, Y., G. Webb, C. Manolis, R. Delaney, M. Letnic, G. Lindner, and P. Whitehead. 2011. Recovery of saltwater crocodiles following unregulated hunting in tidal rivers of the Northern Territory, Australia. *Journal of Wildlife Management* 75:1253–1266.
- Fukuda, Y., G. Webb, C. Manolis, G. Lindner, and S. Banks. 2019. Translocation, genetic structure and homing ability confirm geographic barriers disrupt saltwater crocodile movement and dispersal. *PLoS ONE* 14:e0205862.
- Fukuda, Y., P. Whitehead, and G. Boggs. 2007. Broad-scale environmental influences on the abundance of saltwater crocodiles (*Crocodylus porosus*) in Australia. *Wildlife Research* 34:167–176.
- Grigg, G. C., L. E. Taplin, P. Harlow, and J. Wright. 1980. Survival and growth of hatchling *Crocodylus porosus* in saltwater without access to fresh drinking water. *Oecologia* 47:264–266.
- Groombridge, B. 1987. The distribution and status of world crocodilians. Pages 9–21 in G. J. W. Webb, S. C. Manolis, and P. J. Whitehead, editors. *Wildlife management: crocodiles and alligators*. Surrey Beatty & Sons, Sydney, the Conservation Commission of the Northern Territory, Darwin, Australia.
- Gruber, B., A. Georges, P. J. Unmack, and O. Berry. 2017. dartR: importing and analysing SNP and Silicodart data generated by genome-wide restriction fragment analysis. <<https://cran.r-project.org/web/packages/dartR/>>.
- The International Crocodilian Genomes Working Group [ICGWG]. 2020. Cpor_3.0 GCA_000768395.2—Genome - Assembly—NCBI *Crocodylus porosus* (Australian saltwater crocodile). <https://www.ncbi.nlm.nih.gov/assembly/GCA_000768395.2/>. Accessed 12 Nov 2021.
- Jombart, T. 2008. adegenet: a R package for the multivariate analysis of genetic markers. *Bioinformatics* 24:1403–1405.
- Jombart, T., S. Devillard, and F. Balloux. 2010. Discriminant analysis of principal components: a new method for the analysis of genetically structured populations. *BMC Genetics* 11:94.
- Kilian, A., P. Wenzl, E. Huttner, J. Carling, L. Xia, H. Blois, V. Caig, K. Heller-Uszynska, D. Jaccoud, C. Hopper, et al. 2012. Diversity arrays technology: a generic genome profiling technology on open platforms. Pages 67–89 in F. Pompanon, and A. Bonin, editors. *Data production and analysis in population genomics*. Methods in Molecular Biology. Humana Press, Totowa, New Jersey, USA.
- Kuismis, M., D. Saatoglu, A. K. Niskanen, H. Jensen, and M. J. Sillanpää. 2020. Genetic assignment of individuals to source populations using network estimation tools. *Methods in Ecology and Evolution* 11:333–344.
- Lanhupuy, W. 1987. Australian aboriginal attitude to crocodile management. Pages 145–147 in G. J. W. Webb, S. C. Manolis, and P. J. Whitehead, editors. *Wildlife management: crocodiles and alligators*. Surrey Beatty & Sons, Sydney, the Conservation Commission of the Northern Territory, Darwin, Australia.
- Leach, G., R. Delaney, and Y. Fukuda. 2009. Management program for the saltwater crocodile in the Northern Territory of Australia, 2009–2014. Northern Territory Department of Natural Resources, Environment, the Arts and Sport, Darwin, Australia.
- Lindner, G. 2004. Crocodile management - Kakadu National Park. Pages 41–51 in. *Crocodiles*. Proceedings of the 17th Working Meeting of the IUCN-SSC Crocodile Specialist Group. IUCN, Gland, Switzerland.
- Lloyd-Jones, L. R., M. L. Brien, P. Feutry, E. Lawrence, P. Beri, S. Booth, S. Coulson, S. M. Baylis, K. Villiers, L. E. Taplin, and D. A. Westcott. 2023. Implications of past and present genetic connectivity for management of the saltwater crocodile (*Crocodylus porosus*). *Evolutionary Applications* 16:911–935.
- Magnusson, W. E. 1980. Habitat required for nesting by *Crocodylus porosus* (Reptilia: Crocodylidae). *Wildlife Research* 7: 149–156.
- Marshall, K. N., A. C. Stier, J. F. Samhouri, R. P. Kelly, and E. J. Ward. 2016. Conservation challenges of predator recovery. *Conservation Letters* 9:70–78.
- Mascarenhas-Junior, P. B., J. M. Sousa Correia, and P. I. Simões. 2023. Tracking crocodylia: a review of telemetry studies on movements and spatial use. *Animal Biotelemetry* 11:21.
- Messel, H., G. V. Vorlicek, G. A. Wells, and W. J. Green. 1981. Surveys of the tidal systems in the Northern Territory of Australia and their crocodile populations. The Blyth-Cadell River systems study and the status of *Crocodylus porosus* populations in the tidal waterways of northern Australia. Pergamon Press, Sydney, Australia.
- Mississippi State University. 2016. CroPor_comp1 GCA_001723895.1 - Genome - Assembly - NCBI *Crocodylus porosus* (Australian saltwater crocodile). <https://www.ncbi.nlm.nih.gov/assembly/GCF_001723895.1/>. Accessed 12 Nov 2021.
- Moran, B. M., and E. C. Anderson. 2018. Bayesian inference from the conditional genetic stock identification model. *Canadian Journal of Fisheries and Aquatic Sciences* 76:551–560.
- Nichols, T., and M. Letnic. 2008. Problem crocodiles: reducing the risk of attacks by *Crocodylus porosus* in Darwin Harbour, Northern Territory, Australia. Pages 503–511 in J. C. Mitchell, R. E. Jung Brown, and B. Bartholomew, editors. *Urban*

- herpetology. Herpetological Conservation 3. Society for the Study of Amphibians and Reptiles, Salt Lake City, Utah, USA.
- Peakall, R., and P. E. Smouse. 2006. genalex 6: genetic analysis in Excel. Population genetic software for teaching and research. *Molecular Ecology Notes* 6:288–295.
- Peakall, R., and P. E. Smouse. 2012. GenAlEx 6.5: genetic analysis in Excel. Population genetic software for teaching and research—an update. *Bioinformatics* 28:2537–2539.
- Pérez-Reche, F. J., O. Rotariu, B. S. Lopes, K. J. Forbes, and N. J. C. Strachan. 2020. Mining whole genome sequence data to efficiently attribute individuals to source populations. *Scientific Reports* 10:12124.
- Pooley, S., S. Bhatia, and A. Vasava. 2021. Rethinking the study of human–wildlife coexistence. *Conservation Biology* 35: 784–793.
- Pritchard, J. K., M. Stephens, and P. Donnelly. 2000. Inference of population structure using multilocus genotype data. *Genetics* 155:945–959.
- Read, M. A., J. D. Miller, I. P. Bell, A. Felton, M. A. Read, J. D. Miller, I. P. Bell, and A. Felton. 2004. The distribution and abundance of the estuarine crocodile, *Crocodylus porosus*, in Queensland. *Wildlife Research* 31:527–534.
- Ryan, C. 1998. Saltwater crocodiles as tourist attractions. *Journal of Sustainable Tourism* 6:314–327.
- Saalfeld, K., Y. Fukuda, T. Duldig, and A. Fisher. 2015. Wildlife trade management plan for the saltwater crocodile (*Crocodylus porosus*) in the Northern Territory of Australia, 2016–2020. Northern Territory Department of Land Resource Management, Darwin, Australia.
- Saalfeld, K., Y. Fukuda, T. Duldig, and A. Fisher. 2016. Management program for the saltwater crocodile in the Northern Territory of Australia, 2016–2020. Northern Territory Department of Environment and Natural Resources, Darwin, Australia.
- Sloan, K., M. Jones, and J. Zardus. 2014. Substratum fidelity and early growth in *Chelonibia testudinaria*, a turtle barnacle especially common on debilitated loggerhead (*Caretta caretta*) sea turtles. *Bulletin of Marine Science* 90:581–597.
- Spennemann, D. H. R. 2021. Cruising the currents: observations of extra-limital saltwater crocodiles (*Crocodylus porosus* Schneider, 1801) in the Pacific Region. *Pacific Science* 74:211–227.
- Taplin, L., M. Brien, P. Beri, S. Booth, S. Mastromonaco, C. Browne, and M. Joyce. 2020. Estuarine crocodile population monitoring in Queensland (1979–2019) Technical Report. Queensland Department of Environment and Science, Brisbane, Australia.
- Taplin, L. E. 1985. Sodium and water budgets of the fasted estuarine crocodile, *Crocodylus porosus*, in sea water. *Journal of Comparative Physiology B* 155:501–513.
- Taplin, L. E., and G. C. Grigg. 1981. Salt glands in the tongue of the estuarine crocodile *Crocodylus porosus*. *Science* 212: 1045–1047.
- Wallach, A. D., M. Bekoff, M. P. Nelson, and D. Ramp. 2015. Promoting predators and compassionate conservation. *Conservation Biology* 29:1481–1484.
- Wang, J. 2017. The computer program Structure for assigning individuals to populations: easy to use but easier to misuse. *Molecular Ecology Resources* 17:981–990.
- Webb, G. 2012. Crocodile culls won't solve crocodile attacks. *The Conversation*. <<http://theconversation.com/crocodile-culls-wont-solve-crocodile-attacks-11203>>. Accessed 13 Feb 2014.
- Webb, G. 2014. *Wildlife conservation: in the belly of the beast*. Charles Darwin University Press, Darwin, Northern Territory, Australia.
- Webb, G., and S. C. Manolis. 1989. *Crocodiles of Australia*. Reed Books, Sydney, Australia.
- Webb, G., S. Manolis, P. Whitehead, and G. Letts. 1984. A proposal for the transfer of the Australian population of *Crocodylus porosus* Schneider (1801), from Appendix I to Appendix II of C.I.T.E.S. Conservation Commission of the Northern Territory, Darwin, Australia.
- Webb, G. J. W. 1991. The influence of season on Australian crocodiles. Pages 125–131 in M. G. Ridpath, C. D. Haynes, and M. J. D. Williams, editors. *Monsoonal Australia - landscape, ecology and man in the northern lowlands*. A.A. Balkema, Rotterdam, Netherlands.
- Webb, G. J. W. 2021. History of crocodile management in the Northern Territory: past present and future. *Wildlife Management International*, Darwin, Australia.
- Webb, G. J. W., S. C. Manolis, and M. L. Brien. 2010. Saltwater crocodile *Crocodylus porosus*. Pages 99–113 in S. C. Manolis and C. Stevenson, editors. *Crocodiles status survey and conservation action plan*. Third edition. Crocodile Specialist Group, Darwin, Australia.
- Webb, G. J. W., S. C. Manolis, and B. Ottley. 1994. Crocodile management and research in the Northern Territory: 1992–94. Pages 167–180 in *Crocodiles. Proceedings of the 12th Working Meeting of the IUCN-SSC Crocodile Specialist Group*. IUCN, Gland, Switzerland.
- Webb, G. J. W., H. Messel, and W. E. Magnusson. 1977. The nesting biology of *Crocodylus porosus* in Arnhem Land, northern Australia. *Copeia* 1977:238–249.

Yasuyuki, N., T. Namiko, Y. Erina, S. Kana, E. Noriyuki, M. Kiyotaka, and S. Haruo. 2011. Salinity limitations on larval settlement of four barnacle species. *Sessile Organisms* 28:47–54.

Associate Editor: Sarah Baker.

SUPPORTING INFORMATION

Additional supporting material may be found in the online version of this article at the publisher's website.

How to cite this article: Fukuda, Y., C. Moritz, N. N. FitzSimmons, N. Jang, G. Webb, G. Lindner, H. Campbell, K. Christian, S. Leeder, and S. Banks. 2024. Natal origin and dispersal of problem saltwater crocodiles in the Darwin Harbor, Australia. *Journal of Wildlife Management* 88:e22525.
<https://doi.org/10.1002/jwmg.22525>