




ORIGINAL ARTICLE

Environmental resistance and habitat quality influence dispersal of the saltwater crocodile

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Abstract

Landscape genetics commonly focuses on the effects of environmental resistance on animal dispersal patterns, but there is an emerging focus on testing environmental effects on emigration and settlement choices. In this study, we used landscape genetics approaches to quantify dispersal patterns in the world's largest crocodilian, the saltwater crocodile (*Crocodylus porosus*), and demonstrated environmental influences on three processes that comprise dispersal: emigration, movement and settlement. We found that both environmental resistance and properties of the source and destination catchments (proportion of breeding habitat) were important factors influencing observed dispersal events. Our habitat quality variables related to hypotheses about resource competition and represented the ratio of breeding habitat (which limits carrying capacity), suggesting that competition for habitat influences emigration and settlement choices, together with the strong effect of environmental resistance to movement (where high-quality habitat was associated with greatest environmental permeability). Approximately 42% of crocodiles were migrants from populations other than their sampling locations and some outstandingly productive populations had a much higher proportion of emigration rather than immigration. The distance most commonly travelled between source and destination was 150–200 km although a few travelled much longer distances, up to 600–700 km. Given the extensive dispersal range, individual catchments or hydrographic regions that combine two or three adjacent catchments are an appropriate scale for population management.

KEYWORDS

Crocodylus porosus, dispersal, genetics, habitat, movement, population, resistance

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1 | INTRODUCTION

Animal dispersal influences the dynamics and distribution of populations, and an understanding of dispersal patterns has direct application to population management for some species (Banks & Lindenmayer, 2014; Bowler & Benton, 2005; Morales et al., 2010; Nathan, 2001). Genetic data can identify dispersal events and estimate rates of effective migration, thereby enabling researchers to model the effects of environmental conditions on dispersal within and among populations. Landscape genetics has provided a wealth of tools to explore associations between environmental variation and population connectivity, yet the focus of research in this field has been predominantly on environmental influences on the “movement” phase of dispersal (such as land cover variables that cause resistance to movement). However, dispersal is the outcome of several interacting factors (Saastamoinen et al., 2018). Bowler and Benton (2005) considered that animal dispersal is not a single process but comprises three interdependent phases: emigration (decision to leave), interpatch movement and finally immigration (decision to settle). Emigration and immigration may be influenced by a number of factors such as competition, habitat saturation, breeding opportunity and inbreeding risk while movement may be influenced by factors that include the existence of geographical barriers, landscape “permeability” to movement and the mobility of an individual (Banks & Lindenmayer, 2014; Fraser et al., 2015; Robertson et al., 2019). Different environmental or demographic conditions may influence these phases of dispersal individually (Pflüger & Balkenhol, 2014; Travis et al., 2012) and understanding these relationships will improve our capacity to model dispersal and population connectivity for wildlife population management.

When managing wildlife, understanding the role of dispersal in population growth is particularly important (Pease et al., 1989; Pulliam, 1988). Quantifying the dependence of recruitment on local reproduction vs. immigration, and mapping the locations and environmental properties of net sources and sinks of dispersers across population networks can help to understand population dynamics and prioritize actions to achieve management goals (Fletcher & Westcott, 2013; Hampton et al., 2004; Hörnell-Willebrand et al., 2014). Landscape genetics studies can map dispersal across the landscape and model the properties of dispersal sources and sinks. To do this, such studies need to focus not only on landscape resistance to movement (i.e., matrix quality among populations) but also on the local environmental properties of dispersal sources and destinations that influence dispersal events (Fraser et al., 2015; Parsley et al., 2020; Pflüger & Balkenhol, 2014). Here, we apply landscape genetics approaches to provide dispersal data to model movement by a large, top-order predator, the saltwater crocodile (*Crocodylus porosus*). The motivation of the study is to provide biological data to inform population management and to investigate the relative importance of landscape resistance (i.e., intersite environmental characteristics) and site-level environmental characteristics on dispersal patterns.

The saltwater crocodile is an iconic species subject to intensive management in northern Australia because they are of conservation importance and represent a sustainable natural resource yet are dangerous predators of people and domestic animals (Leach et al., 2009; Saalfeld et al., 2016). Populations were seriously depleted between 1946 and 1971, and subsequently received protection (Webb et al., 1984), which was followed by the introduction of sustainable use programmes aimed at increasing the value of these dangerous predators to landowners and the public (Hutton et al., 2002; Webb & Manolis, 1993). Wild populations have been closely monitored since protection in the 1970s (Fukuda et al., 2011; Messel et al., 1981; Webb et al., 1984). Their ability to travel a long distance to occupy habitat in the sea, rivers, lakes, floodplains and swamps has been well established (Campbell et al., 2010, 2013; Read et al., 2007). However, dispersal rates among populations and the environmental influences on dispersal are not understood.

In this study, we used landscape genetics to investigate genetic structure, movement patterns and the spatial scale of dispersal by saltwater crocodiles in northern Australia. We also investigate the role of environmental variables (habitat quality in terms of suitability for breeding (Fukuda & Cuff, 2013; Fukuda et al., 2007) in influencing dispersal. We focus on three phases of dispersal to test two major hypotheses about environmental processes driving dispersal patterns:

1. Resistance to movement hypothesis: Dispersal will be influenced by environmental resistance to movement between source and destination, with resistance inversely correlated with habitat quality. A common assumption is that habitat quality is correlated with habitat permeability, yet this is rarely tested empirically (Spear et al., 2010). We estimated environmental resistance to movement via landscape genetics approaches (Peterman, 2018).
2. Habitat availability hypothesis: The availability of habitat in dispersal sources and destinations will influence both emigration and settlement phases of dispersal. We predicted that emigration will be more likely from river systems with high proportion of breeding habitat relative to total habitat as mapped by previous studies (Fukuda & Cuff, 2013; Fukuda et al., 2007), corresponding to predicted high resource competition for habitat (Pflüger & Balkenhol, 2014). Immigration rates will be higher in river systems with a low proportion of breeding habitat relative to total habitat. This relates to the priority effects hypothesis, where high population density and local reproduction precludes settlement by dispersing individuals (Fraser et al., 2015).

Using landscape genetic information collected from contemporary populations of saltwater crocodiles, we quantify the relative importance of environmental influences on the emigration, resistance and settlement phases of dispersal by large and highly mobile predators. This information can potentially advance the application of landscape genetics to wildlife population management through informing spatial population dynamics.

2 | MATERIALS AND METHODS

2.1 | Study area and context

The Top End of Northern Territory (NT) (~400,000 km²) and East Kimberley (1,175,100 km², Figure 1) contain many coastal rivers and creeks, lined with mangroves and under tidal influence near the sea, extending to a diversity of freshwater, nontidal floodplain wetlands and sand and rock-lined water courses upstream. All are occupied by *Crocodylus porosus* at different densities, as indicated by sighting densities ranging from 0.1 to 15 crocodiles sighted per kilometre of river (Fukuda et al., 2007, 2011; Webb, 1991). The species also occurs along the coastline between rivers, and occupies near-coastal islands (Webb, 1991; Webb & Manolis, 1989).

The climate in the study region is monsoonal, with a distinct wet season (November to April) and dry season (May to October).

Available wetlands expand during the wet season, during which crocodiles nest, and contract during the dry season (Fukuda & Cuff, 2013; Webb, 1991), when many temporary water bodies dry out if early rains are delayed. Crocodiles tend to move back into permanent water areas during the dry season, but are sometimes forced to aestivate in drying mud (Webb & Manolis, 1989). In the NT, there is limited intensive agriculture and most coastal and riparian habitats remain intact (Fukuda et al., 2007).

2.2 | Single-nucleotide polymorphism genotyping and filtering

From a sample of 714 georeferenced *C. porosus* tissue samples collected across northern Australia and nearby countries, we analysed 515 samples from across the focal area for this study in northern

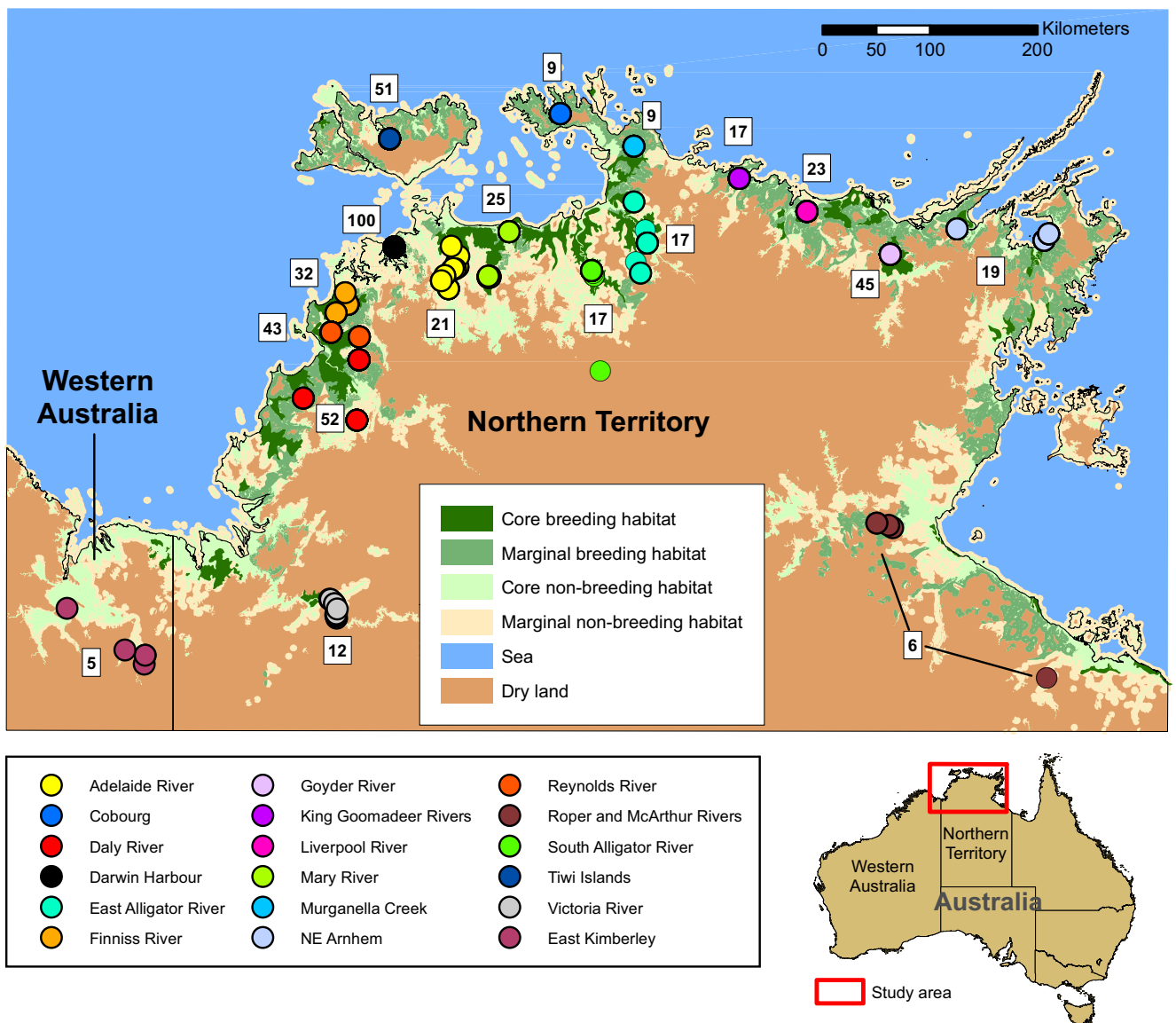


FIGURE 1 Catchment-based populations of *Crocodylus porosus* sampled within the study area in the Northern Territory and Western Australia. The number of samples collected for each population is shown on the map

Australia (Figure 1). The remaining 199 samples outside the study area were included in the single-nucleotide polymorphism (SNP) filtering process but the samples were excluded from population analyses. For analyses where population allele frequencies were required, we grouped individuals according to the 18 river systems in which sampling was conducted. The tissue samples were pieces of skin collected randomly from either (i) free-ranging crocodiles, using a biopsy pole (Barrow & Halford, 2019) or by hands ($N = 60$), (ii) crocodiles captured as part of the public safety programme (Fukuda et al., 2014; Saalfeld et al., 2016; $N = 117$), or (iii) embryos that failed to develop to term during incubation ($N = 338$). These embryos came from eggs collected from wild populations as part of the NT's commercial crocodile farming programme and we used one egg per clutch collected from a georeferenced nest location (Leach et al., 2009; Saalfeld et al., 2016). The length of the sampled (free-ranging) crocodiles ranged from 0.3 to 5.1 m. We assumed that it was unlikely that these sampled crocodiles were related to each other because only a fractional number of samples (e.g., minimum of two at the Adelaide River and maximum of 21 at the East Alligator River) were collected along long transects (135.7 km at the Adelaide River and 49.0 km at the East Alligator River) set as a part of population monitoring programmes (Fukuda et al., 2013; Fukuda et al., 2011). These sampled numbers represented only 0.3%–6.0% of the relative abundance (number of crocodiles sighted per kilometre of river) estimated from these surveys (see Table 1; Saalfeld et al., 2016). The tissue samples used for the analyses were all collected between 2015 and 2019.

DNA extraction and genotyping were conducted at Diversity Arrays Technology using the DArTseq approach (Kilian et al., 2012). DArTseq uses genome complexity reduction and next-generation sequencing (NGS) approaches 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 SNP calls. Initial sequence processing and SNP calling by DArT yielded 17,791 SNP loci across 16,637 contigs. 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 (Appendix S1: S1–3). The graphical analysis was used to evaluate whether genotype properties (e.g., observed heterozygosity) were associated with SNP quality metrics such as mean sequencing depth.

We used the *dartR* package in R 3.5.3 (Gruber et al., 2017) to filter SNPs according to call rate (CallRate > 0.90) and repeatability (RepAvg > 0.98) and added custom filtering criteria to drop SNPs with a mean sequence depth of less than 8 and a mean ratio of sequence depth between alleles of greater than 2 (to remove loci in which one allele was preferentially detected, indicating potential susceptibility to null alleles through PCR [polymerase chain reaction] bias). We also dropped SNPs (ranked by polymorphic information content) within sequences with more than one SNP

present, SNPs that did not align to a reference genome (ICGWG, 2014) with e-value threshold of -20 or lower, and SNPs that mapped to more than one location on the reference genome. We dropped genotypes of individuals for which greater than 10% of SNPs were not genotyped. Following these filtering steps, we retained 4703 SNPs in 515 individuals with a minor allele frequency of greater than 0.02, corresponding to 20 or more allele copies for analysis. We graphed the distribution of the inbreeding coefficient (F_{IS}), observed heterozygosity (H_O), expected heterozygosity within populations (H_S), expected heterozygosity overall (H_T) and genetic differentiation among populations (F_{ST}) to visualize any unexpected patterns in regard to Hardy–Weinberg expectations within populations but did not filter any further based on this graphical analysis.

2.3 | Genetic diversity and population structure

We calculated the basic genetic diversity statistics, including H_S , H_O , H_T and F_{IS} of the data set before and after filtering. We then estimated Smouse and Peakall's (1999) genetic distance metric among individuals and performed a principal coordinates analysis (PCoA) on the genetic distances to visualize patterns of genetic similarity among individuals and populations.

To quantify fine-scale patterns of genetic structure among individuals, we calculated a multilocus spatial correlogram from genetic and geographical distances among individuals, following Smouse and Peakall (1999) in GENALEX 6.503 (Peakall & Smouse, 2012, 2017). We used distance intervals with upper bounds of 10, 50, 100, 200, 400, 600, 800 and 1000 km for the analysis and calculated multilocus spatial autocorrelation r values with 1000 bootstraps and 1000 permutations of the data to evaluate significance. We did not include populations with a small number of samples (WA East Kimberley with $N = 5$, and Roper and NT MacArthur Rivers with $N = 6$) in the population-level PCoA and the genetic–geographical distance analysis.

2.4 | Landscape resistance analysis

We used the ResistanceGA R package (Peterman, 2018) to evaluate models of environmental resistance to between-population movement, represented by individual pairwise genetic distances among individuals. ResistanceGA models pairwise genetic distances in response to pairwise “ecological distances” using linear mixed effects models with a maximum-likelihood population effects (MLPE) random effects structure (Clarke et al., 2002), represented by individual ID in our models. We used Smouse and Peakall's (1999) pairwise genetic distance as the response variable for this purpose. We constructed landscape layers representing the major habitat-related environmental categories that we predicted would be relevant to crocodile movement.

TABLE 1 Basic genetic diversity for the individual populations (individuals grouped by river system) and areas of quality habitats

Population	Centroid latitude	Centroid longitude	<i>n</i>	<i>N_e</i>	<i>H_O</i>	<i>H_E</i>	<i>F_{IS}</i>	Core breeding (km ²)	Core nonbreeding (km ²)	Marginal breeding (km ²)	Marginal nonbreeding (km ²)	Density (sighting km ⁻¹)	Years surveyed
Adelaide River	-12.66	131.34	21	1.370 (0.005)	0.223 (0.003)	0.226 (0.003)	0.018 (0.003)	1039	2830	1051	1957	4.98	2016, 2017, 2018
Cobourg	-11.34	132.24	9	1.363 (0.005)	0.212 (0.003)	0.219 (0.003)	0.024 (0.005)	29	737	1326	1512		
Daly River	-13.48	130.55	52	1.365 (0.005)	0.207 (0.002)	0.223 (0.003)	0.069 (0.003)	1818	4378	4584	5670	7.13	2013, 2016, 2018
Darwin Harbour	-12.46	130.85	100	1.38 (0.005)	0.215 (0.002)	0.235 (0.002)	0.085 (0.002)	<10	813	<10	1275		
East Alligator River	-12.43	132.97	17	1.36 (0.005)	0.216 (0.003)	0.22 (0.003)	0.017 (0.004)	1029	1579	1009	1945	7.17	2014, 2016, 2017
Finniss River	-12.96	130.43	32	1.354 (0.005)	0.205 (0.003)	0.216 (0.003)	0.042 (0.003)	709	1581	1152	1479		
Goyder River	-12.52	135.00	45	1.376 (0.005)	0.204 (0.002)	0.228 (0.003)	0.098 (0.003)	634	1251	934	1072	5.63	2012, 2016
King and Goomadeer Rivers	-11.88	133.74	17	1.39 (0.005)	0.226 (0.003)	0.238 (0.003)	0.04 (0.004)	13	718	1264	2131		
Liverpool River	-12.16	134.30	23	1.396 (0.005)	0.228 (0.003)	0.242 (0.003)	0.05 (0.003)	817	2190	2652	3210	3.4	2012, 2016, 2018
Mary River	-12.33	131.81	25	1.372 (0.005)	0.209 (0.003)	0.228 (0.003)	0.075 (0.004)	915	2179	683	1156	9.81	2013, 2015, 2017
Roper and McArthur Rivers	-14.78	134.95	6	1.38 (0.005)	0.234 (0.003)	0.228 (0.003)	-0.037 (0.005)	39	3618	1578	6014	2.77	2017
Murganella Creek	-11.62	132.85	9	1.344 (0.005)	0.202 (0.003)	0.206 (0.003)	0.01 (0.006)	415	997	1705	1548		
North East Arnhem	-12.38	136.31	19	1.393 (0.005)	0.227 (0.003)	0.24 (0.003)	0.047 (0.004)	244	2096	3473	4259		
Reynolds River	-13.18	130.36	43	1.362 (0.005)	0.207 (0.002)	0.222 (0.003)	0.059 (0.003)	682	929	745	661		
South Alligator River	-12.663	132.507	17	1.37 (0.005)	0.228 (0.003)	0.225 (0.003)	-0.01 (0.003)	949	1916	373	3068	5.28	2015, 2016, 2017
Tiwi Islands	-11.5599	130.8163	51	1.39 (0.005)	0.22 (0.002)	0.241 (0.002)	0.082 (0.003)	49	1863	3214	3321		
Victoria River	-15.487	130.3555	12	1.354 (0.005)	0.207 (0.003)	0.212 (0.003)	0.015 (0.004)	421	1593	169	2298	1.92	2017
East Kimberley	-12.3533	136.3312	5	1.346 (0.005)	0.215 (0.003)	0.208 (0.003)	-0.049 (0.006)	<10	1299	<10	1129		

Abbreviations: *F_{IS}*, inbreeding coefficient; *H_E*, expected heterozygosity; *H_O*, observed heterozygosity; *n*, number of samples analysed; *N_e*, number of effective alleles. Numbers in parentheses are standard errors.

We created a categorical resistance surface layer using a 3×3 -km cell size raster (with 325×202 cells) with cells classified as sea, dry land and the different types of habitats (Figure 1). We classified habitats into “core breeding habitat,” “marginal breeding habitat,” “core nonbreeding habitat” or “marginal nonbreeding habitat,” based on the previous habitat suitability models (Fukuda & Cuff, 2013; Fukuda et al., 2007; Webb, 1991). Breeding of *C. porosus* is highly seasonal during the wet season (November–April) and constrained to temporarily flooded, freshwater waterbodies which are not necessarily the most suitable habitat for saltwater crocodiles outside the breeding period (Campbell et al., 2013; Fukuda & Cuff, 2013; Fukuda et al., 2007; Webb, 1991). The core breeding habitats are the most favourable nesting areas represented by particular vegetation types such as *Melaleuca*, *Eucalyptus* and *Pandanus* open forests in perennial, freshwater wetland and swamp with mixed grasses and sedges (*Chrysopogon*, *Xerochloa*, *Oryza* and *Eleocharis* species) derived from the Vegetation Communities of the Tropical Savanna (CRC, 2004) as described by Fukuda et al. (2007), while the marginal breeding habitats were identified by broader vegetation communities occasionally used for nesting, derived from National Vegetation Information System (NVIS) version 4.1 (DSEWPC, 2012; Fukuda & Cuff, 2013). The core nonbreeding habitats are the permanent waterbodies as defined being suitable for residence (Fukuda & Cuff, 2013), but persisting outside the breeding areas defined above. These GIS data were derived from Geoscience Australia (2006). We defined the marginal nonbreeding habitats by buffering the core nonbreeding habitats by 3 km so that these habitats would include temporary waterbodies that may dry up during the dry season (May–October) or coastal areas with salinity levels similar to seawater (typically 35 parts per thousand). Although *C. porosus* is highly adapted to the saline environment (Cramp et al., 2008; Grigg et al., 1980; Taplin, 1985), the species occurs in much higher density in brackish or freshwater (Fukuda et al., 2011; Webb & Manolis, 1989) and nesting females and embryos require access to freshwater (Webb et al., 1977, 1983). Although some individuals access the sea, especially when moving between the rivers (Campbell et al., 2010; Fukuda et al., 2019), it is considered less favoured than brackish or freshwater habitats, and dry land is almost inaccessible to crocodiles as suggested by the previous tracking by satellites (Fukuda et al., 2019). Because these habitats for *C. porosus* have largely remained intact over years (Grahame Webb & Manolis, 1989), we assumed that bias from asynchronicity in the time frame between the parameterization of the environmental variables and the collection of the genetic samples was unlikely.

We used ResistanceGA to estimate resistance surfaces that optimized random-walk commute distances (Etten, 2018) among the locations of sampled individuals as an explanatory variable in models of pairwise genetic distances among individuals. We ran a single surface optimization in ResistanceGA (Peterman, 2018) to estimate resistance values for the six environmental cover categories

and stopped each model after 25 consecutive generations of no improvement in log-likelihood (see S5 for R script).

We visualized predicted flow using the optimized resistance surface layer in OMNISCAPE (Landau et al., 2021), with source strength set to a value of 2 for core breeding habitat and 1 for marginal breeding habitat, with a maximum radius corresponding to 900 km, which was the largest individual crocodile movement inferred from assignment tests (see below).

2.5 | Population assignment to identify movement events

We used a genetic assignment test approach to estimate the origin of each individual in the sampled river systems across the study, using the R package *rubias* (Moran & Anderson, 2018). We excluded the Darwin Harbour region as a candidate source population for assignment because there is no breeding population in Darwin Harbour (Fukuda & Cuff, 2013). As above, we did not include WA East Kimberley or NT Roper and MacArthur Rivers in the assignment. We used the *self_assign* function of the *rubias* package that implements Bayesian inference to estimate the posterior probability of assigning each individual to the geographical “reference populations” given equal priority on every population in the reference (Moran & Anderson, 2018).

2.6 | Modelling environmental effects on crocodile population connectivity

We used the individual movements (dispersal destinations) identified in the genetic population assignment analysis as a response variable in a multinomial logit model (Croissant, 2020a, 2020b) to identify the influence of site-level habitat properties and between-site landscape permeability (within- vs. between-site variables) on dispersal patterns by saltwater crocodiles. The data set comprised all free-ranging crocodiles over 1 m in total length (i.e., free-living crocodiles sampled in the field) assigned to a single population with greater than 90% probability. An exploratory analysis found that all crocodiles under 1 m in length had not yet dispersed (all assigned to the “home” population) so we did not include such individuals in the analysis of dispersal patterns. We did not include the size of crocodiles as an explanatory variable because there was not a significant difference in the mean between the individuals that migrated (249.27 cm) and those did not (244.70 cm; $F(1,51) = 0.036, p = .85$).

We used the multinomial (discrete choice) modelling function (R package *mlogit* version 1.1-1; Croissant, 2020b) to model environmental influences on crocodile movement. The (true or false) response variable was a matrix for each possible dispersal destination and natal population (river system). The data for each crocodile were represented as a “True” for the dispersal choice and “False” for all the other populations.

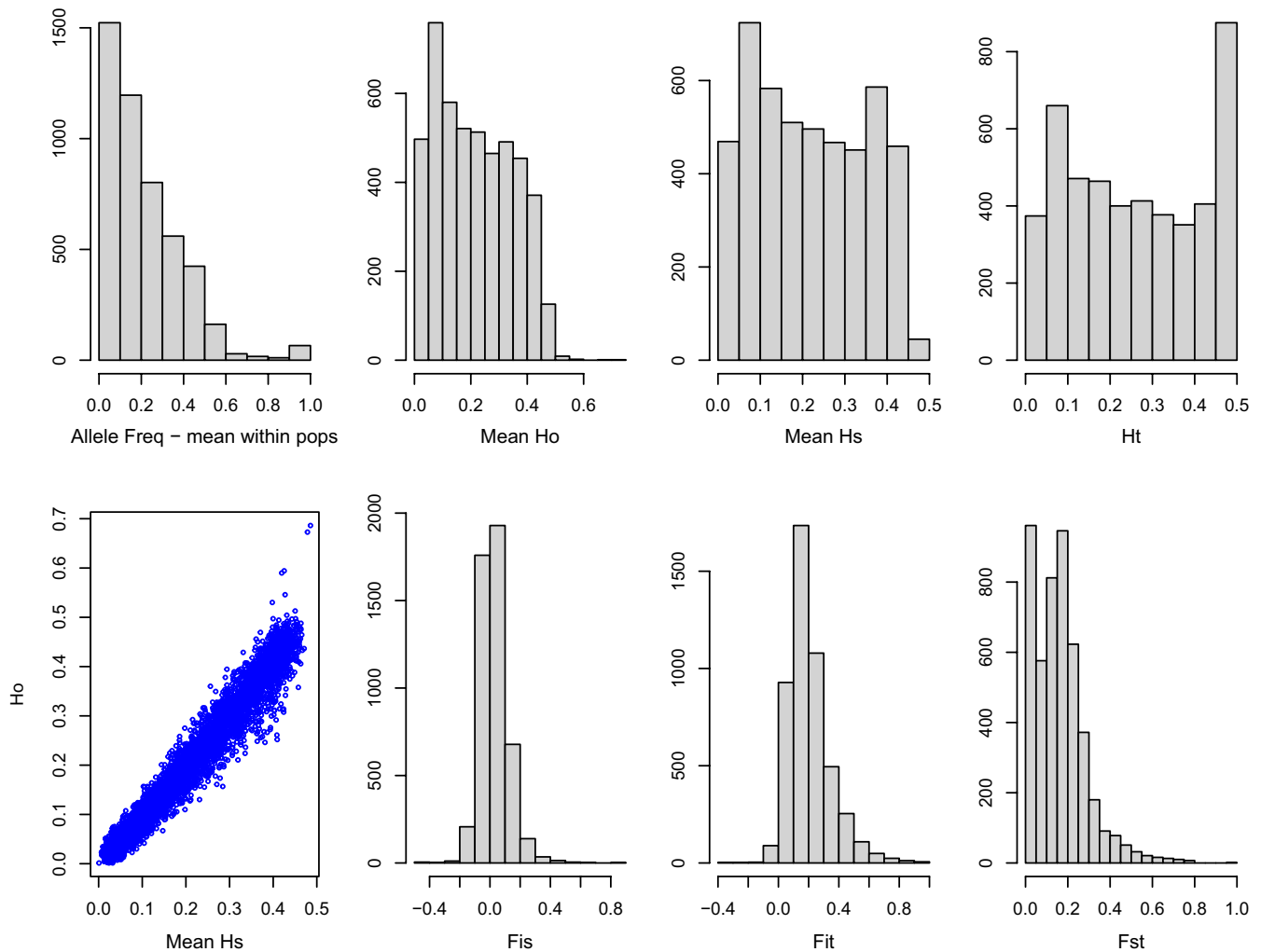


FIGURE 2 Histograms of the population genetics statistics after filtering (see S2 for those before filtering). The y-axis is the number of SNPs unless labelled differently

For each dispersal choice from the assigned natal location to the sampled destination, we modelled the influences of the estimated resistance distance (from the best ResistanceGA model) between the source and the destination (relating to the movement phase of dispersal) and the environmental properties of the “destination” population where the crocodile was sampled (relating to the immigration or settlement stage of dispersal). The candidate explanatory variables were: (i) resistance calculated as the pairwise commute distance calculated in *gdistance* (Peterman, 2018) from a resistance landscape parameterized to match the best ResistanceGA model; (ii) ratio of area suitable for breeding to total habitat area at the destination as described by Fukuda and Cuff (2013) and Fukuda et al. (2007); and (iii) interaction between these two variables. For this analysis, we combined the “core” and “marginal” breeding habitat categories to represent estimated total breeding area available in each catchment. Likewise, to examine the influence of the environmental properties of the assigned “source” population (relating to the emigration stage of dispersal), we ran another set of models for each natal assignment (response variables) with resistances, ratios of

breeding area to total habitat at source and the interaction between these two (explanatory variables).

We ranked the models using Akaike's Information Criteria (AIC) and examined visually the effects of the environmental variables on the dispersal probability, generating heatmaps using the *levelplot* function in the *lattice* R package (Sarkar et al., 2021).

3 | RESULTS

3.1 | Genetic diversity and population structure

From an initial 17,791 SNPs in 679 individuals (11 were excluded from the filtering process due to SNP coverage) with mean H_T , H_S , H_O and F_{IS} of 0.19, 0.15, 0.15 and 0.01, respectively, we filtered the data set to 4807 SNPs in 503 individuals (Figure 4), with mean H_T , H_S , H_O and F_{IS} of 0.29, 0.23, 0.25 and -0.08 , respectively (Figures 2 and 4). Population-specific genetic diversity metrics for the 18 sampling locations are shown in Table 1.

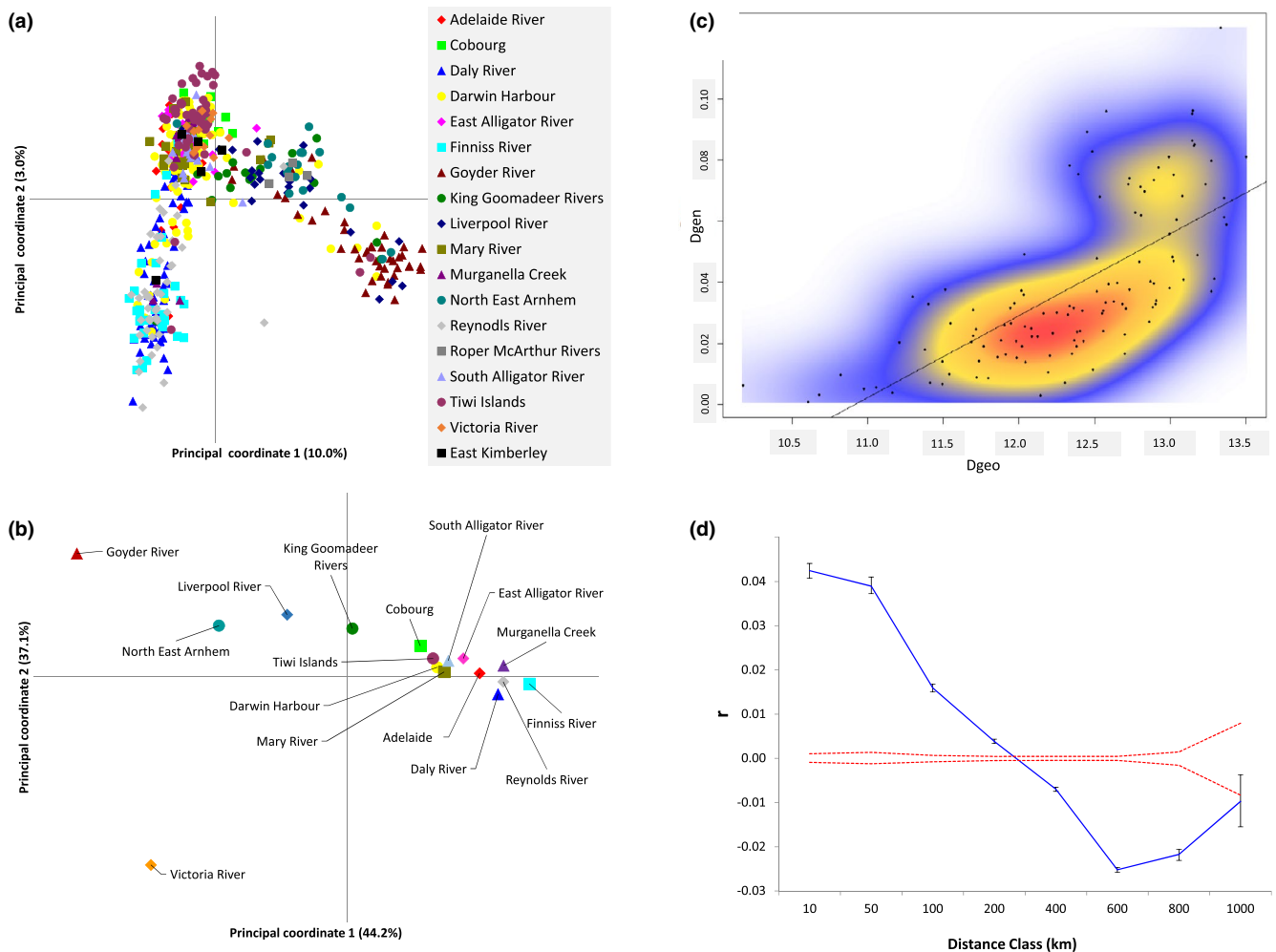


FIGURE 3 (a) PCoA of the individual crocodiles based on the genetic distances (F_{ST}) (Smouse & Peakall, 1999), (b) PCoA for the populations based on a nonstandardized distance metric among the populations, (c) isolation by distance (IBD) plot between the genetic and geographical distances (Dgen and Dgeo, respectively), and (d) spatial autocorrelation at the distance of 10, 50, 100, 200, 400, 600, 800 and 1000 km with r = autocorrelation coefficient. The density of data points is indicated by colours (red = high, medium = yellow, and blue = low) in (c) [Correction added on 16 March 2022, after first online publication: Labels for Figure 3b and Figure 3c have been correctly transposed.]

Overall F_{ST} among populations was 0.032 with mean pairwise F_{ST} of 0.034. Pairwise genetic F_{ST} among the 18 populations ranged from 0.001 (between the Reynolds River and Daly River) to 0.110 (between the Victoria River and Goyder River) as shown in S6.

The first three PCoA axes explained 7.0%, 3.0% and 2.1% of the variation in genetic distances among individuals and loosely clustered individuals into geographical groupings corresponding to spatial proximity of sampling locations (Figure 3a). The population-level PCoA (based on pairwise F_{ST}) grouped populations broadly according to geographical proximity (Figure 3b). Genetic differentiation among populations was consistent with geographical distances, as indicated by the isolation by distance plot (Figure 3c). The spatial autocorrelation analysis showed significant positive spatial correlation in distance classes up to 200 km (Figure 3d).

3.2 | Landscape resistance analysis

ResistanceGA fitted using individual-level pairwise genetic distance data showed that the model fitted with resistance distances received much greater support ($\Delta AIC = 0$, $R^2m = 0.297$, $R^2C = 0.725$) than the null model ($\Delta AIC = 31,819$, $R^2m = 0.0$, $R^2C = 0.603$) or the unmodified geographical distance model ($\Delta AIC = 11,646$, $R^2m = 0.090$, $R^2C = 0.653$). Scatterplots of pairwise geographical and fitted resistance distances (random walk commute distance) for the individual-level distance data set are shown in S4.

The selected model identified core breeding habitat as having the lowest resistance (fitted cell value = 1), with increasing resistance attributed to core nonbreeding habitat (21.2). Marginal habitats whether breeding (125.7) or nonbreeding (122.7) had similar resistances to each other (Figure 4b). Fitted resistance values for

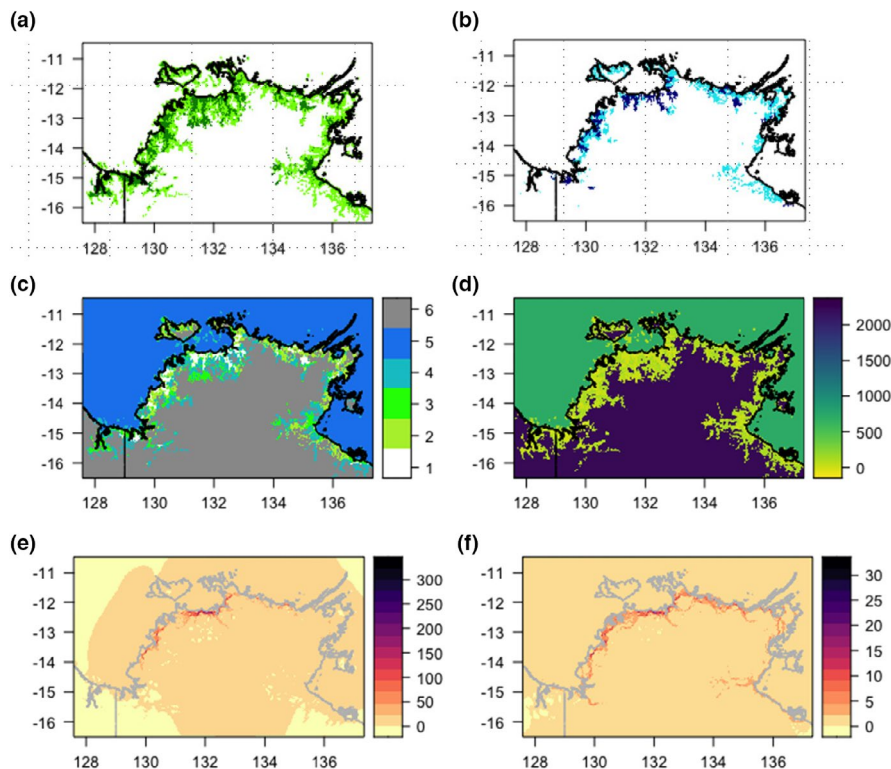


FIGURE 4 Spatial analyses of the crocodile habitats and movement resistances. (a) Core (dark green) and marginal (light green) habitats, (b) breeding habitats in the core (dark blue) and marginal (light blue) habitats, (c) categorical (1 = breeding areas in core habitats, 2 = breeding areas in marginal habitats, 3 = core habitats, 4 = marginal habitats, 5 = sea, and 6 = land), environmental surfaces used for the resistance modelling, (d) optimized resistance surface, (e) cumulative current flow mapped by OMNISCAPE and (f) normalized current flow mapped by OMNISCAPE

open sea (707.0) and dry land (2216.9) were much greater than the other environmental cover categories.

Cumulative and normalized current flow maps we created in OMNISCAPE as an exploratory analysis, using the optimized resistance surface from ResistanceGA are shown in Figure 4(e,f), respectively.

3.3 | Population assignment to identify movement events

Population assignment testing suggested that 41.67% of free-ranging crocodiles sampled were most likely to come from a different river to where they were sampled, based on an assignment threshold probability of 0.9 for $N = 60$ crocodiles (Figure 5). Among the assigned individuals that moved between the populations, the most common distance travelled between populations, typically between river mouths along coasts, was 150–200 km ($N = 48$), with fewer than 20% of assigned nonembryo crocodiles moving over 200 km between rivers, but some dispersal events over 500 km were detected (Figure 6).

3.4 | Modelling environmental effects on crocodile population connectivity

The best-supported model of dispersal choice from natal locations to destination included negative effects of landscape resistance and the ratio of breeding area to total habitat in the destination river

catchment (Figure 7, Tables 2 and 3). The best-supported model of natal assignment from sampled locations included negative effects of landscape resistance and the ratio of breeding area to total habitat in the source river catchment, as well as positive effect of the interaction of these variables. The negative effect of landscape resistance was weaker in cases where source populations have a high ratio of breeding habitat area to total habitat area. Overall, both landscape resistance and habitat characteristics (proportion of breeding habitat) were important in both sets of models, receiving a variable importance of over 0.99 when we summed the Akaike weights of all models containing either variable (Table 2).

4 | DISCUSSION

Our analyses supported both the resistance to movement hypothesis and the habitat availability hypothesis as influencing dispersal by *Crocodylus porosus*. Landscape resistance had slightly higher support than habitat characteristics (proportion of breeding habitat) in our models of assigned movement but the difference was minor and we conclude that these are both important and interacting drivers of dispersal behaviour. Further, we found that there was an interaction between these variables in their effect on assigned dispersal events, suggesting that populations in catchments with a high proportion of breeding habitat to total habitat can contribute to recruitment via dispersal to populations separated by large resistance distances. This information enabled us to quantify and compare the roles of the environmental influences on *C. porosus* dispersal that has been little known previously.

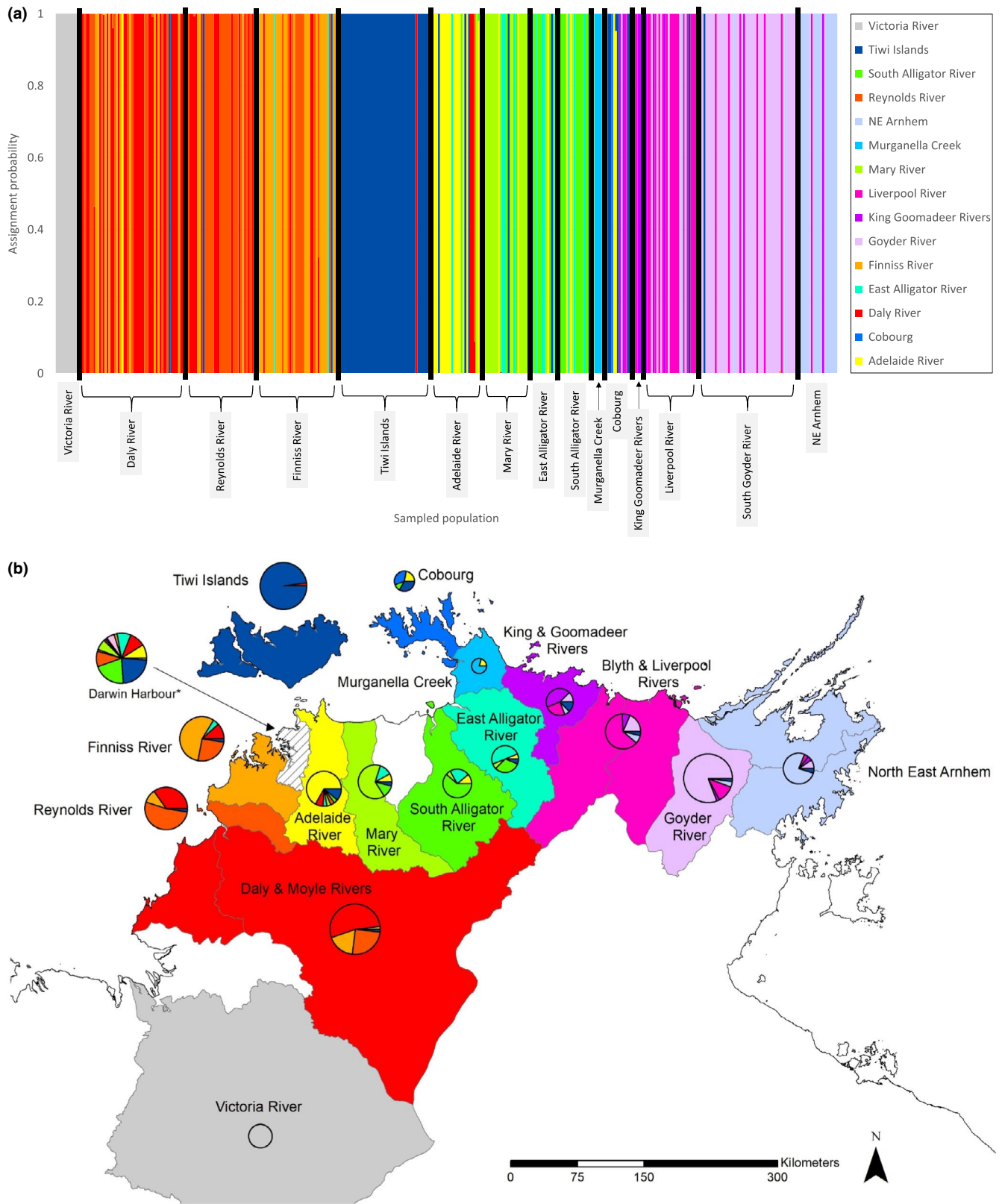


FIGURE 5 Population assignment of sampled crocodiles across the study area. (a) The colour of the bars signifies the source locations of each crocodile sampled and (b) the colour of the catchments shows the source locations. The size of the pie charts is proportional to the sample size (see Table 1) and the pie chart in each location shows the proportion of the crocodiles assigned to different sources indicated by the colour coding. Catchments without a colour indicate that no sample was collected

4.1 | The resistance to movement hypothesis

We found that the environmental resistance surface, the environmental variable most relevant to the movement phase of dispersal, was the most important variable in our multinomial models of dispersal choices. The optimized resistance surface was inversely correlated with habitat quality, which is commonly assumed to influence connectivity (Spear et al., 2010). Similar approaches that incorporate genetic connectivity in parameterizing resistance surfaces have been used for many predatory species at different spatial scales (Cushman & Lewis, 2010; Garroway et al., 2011; Ruiz-González et al., 2014; Warren et al., 2016). While we detected effects of source and destination habitat on dispersal, our results are in concordance with recent research suggesting that landscape permeability can be more important than local habitat characteristics in shaping functional connectivity in semi-aquatic species (Parsley et al., 2020). The broad environmental variables relating to habitat quality could be used to map likely patterns of population connectivity. However, we note that the effects of resistance were mediated by habitat characteristics in each catchment. Essentially, the negative effect of increasing resistance distance on assigned dispersal events (crocodiles were less likely to be assigned to source populations separated by greater resistance distances to their sampled location) was moderated by the proportion of breeding habitat in the source population.

The large variation in the resistance estimated for *C. porosus*, ranging from 1.0 for core breeding habitat to 2216.9 for dry land, is consistent with empirical data that the availability of breeding habitat is the primary influence on population abundance (Fukuda et al., 2007; Webb, 1991) and the species rarely moves over land. While overland movement is more frequently reported for other crocodylian species such as *Alligator mississippiensis* (Woolard et al., 2004) and *Crocodylus niloticus* (Combrink, 2015), such movement is rare for *C. porosus* as shown by tracking of over 100 crocodiles in Australia (Baker et al., 2019; Fukuda et al., 2019). It should be noted that the open sea had a relatively high resistance (707.0) compared to the other estuarine or freshwater habitat types (marginal habitats whether breeding 125.7 or nonbreeding 122.7). This suggests that, despite their physiological adaptation to the fully saline environment (Grigg, 1981; Grigg et al., 1980; Taplin, 1984; Taplin & Grigg, 1981), brackish or freshwater environments, generally more preferred habitats (Fukuda & Cuff, 2013; Fukuda et al., 2007), are also better for population connectivity.

4.2 | The habitat availability hypothesis

As well as the importance of landscape resistance to movement, we identified effects of breeding habitat at the dispersal sources and destinations in our modelling and model selection process. This highlights the importance of addressing immigration and emigration as well as movement in considering the dispersal process (Banks & Lindenmayer, 2014; Bowler & Benton, 2005; Travis et al., 2012). Density and resource competition within a population

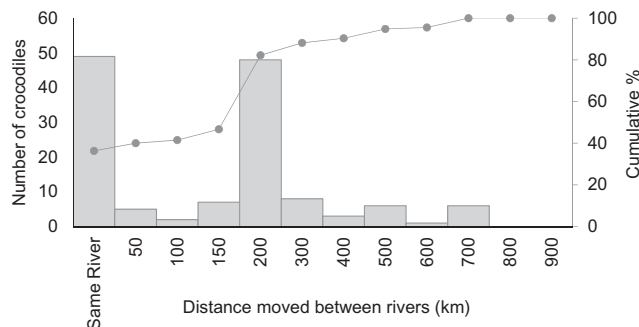


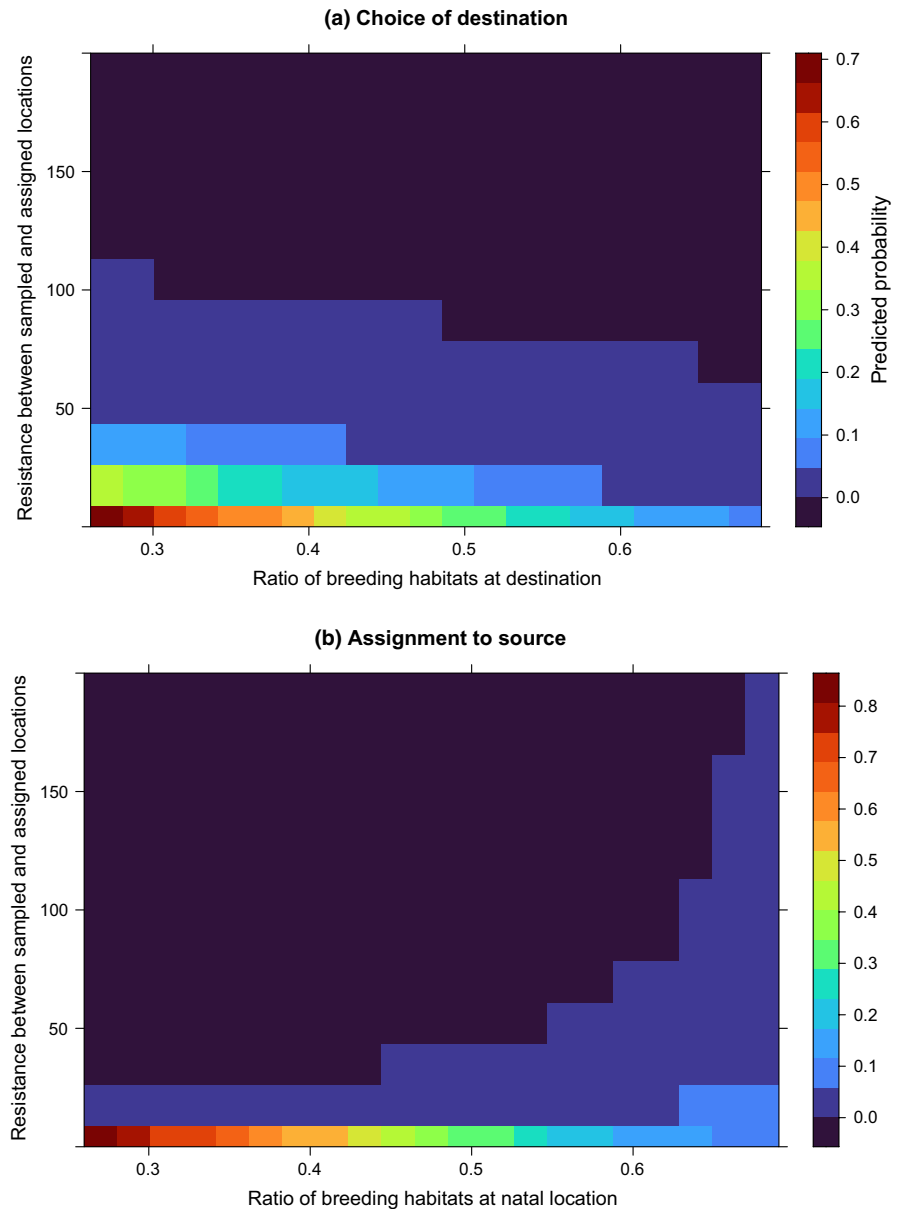
FIGURE 6 The number (bars) and cumulative percentage (line) of nonembryo crocodiles travelling over different distances among river systems as identified by genetic assignment testing. Only crocodiles assigned to a population with a probability greater than 0.9 are included

are hypothesized to be important drivers of emigration and settlement choices in animals (Bowler & Benton, 2005; Gadgil, 1971; Travis et al., 2012). A number of studies have shown that dispersal is related to population density at the source location (Amarasekare, 2004; Matthysen, 2005; Poethke et al., 2011) and that population density and resource competition can be negatively correlated with settlement opportunities (Fraser et al., 2015; Wauters et al., 2010).

Our hypothesis regarding the ratio of mapped breeding to total habitat is that a high ratio is likely to correspond to high competition from locally born individuals, leading to fewer opportunities for settlement by immigrants. In our case, the relative availability of breeding habitats at destination sites was included in the best supported model for dispersal choice. The negative coefficient for breeding habitat at the destination site as an important component of settlement is consistent with the suggestion that habitats become occupied with a net flow of individuals from higher to lower suitability when density is increasing (Carr et al., 2007). Given that crocodile density in most rivers in the NT have been increasing towards an asymptote (Fukuda et al., 2011; Saalfeld et al., 2016), it is likely that individuals are forced out of favourable, and thus saturated sources to habitats less suitable for breeding as indicated by our destination choice models. The interaction between breeding habitat to total habitat ratio and landscape resistance supports this, suggesting that populations with a high proportion of breeding habitat can contribute long-distance dispersers that recruit to distant populations. This may explain increasing sighting of crocodiles in places where they were previously scarce such as distant waterholes and extreme upstream of rivers far inland (Fukuda et al., 2014; Letnic & Connors, 2006; Webb, 2012).

Contrary to our expectation, our models on the assignment to natal sources showed a negative effect of the ratio of breeding habitats on emigration, suggesting that migrants were more likely to come from habitats where less breeding areas were available. As shown by Carr et al. (2007) that habitats are filled in order of suitability in an increasing population, if breeding areas are available at a higher proportion, crocodiles may remain within quality habitat. This is not surprising given that our assignment analysis showed that

FIGURE 7 Heatmaps of the effects of (a) landscape resistance and ratio of breeding area to total habitat in sampled destination and (b) landscape resistance and ratio of breeding area to total habitat in assigned source on the probability of movement predicted by the best supported models (see Table 2)



more than 58% of the sampled crocodiles did not leave the natal sources. Crocodiles that did not disperse may be mature individuals, dominating limited breeding opportunities while many of the crocodiles leaving their natal rivers could be subordinate, actively looking for new territories, although we did not find a significant difference in the mean total length between these two groups ($p = .85$).

As in many other species (Cano et al., 2008; Liebgold et al., 2011; Prugnolle & de Meeus, 2002), *C. porosus* males are more actively dispersing while females are philopatric (Campbell et al., 2013). Although we were not able to identify the sex of each sampled individual in the noninvasive biopsy method (Barrow & Halford, 2019), the empirical data suggested that nomad individuals captured as problem crocodiles in the NT were most commonly immature males (Fukuda et al., 2014; Nichols & Letnic, 2008). Moreover, nonenvironmental factors that were not considered in this study, such as individual, genetic variation in dispersal-linked traits (DiLeo et al., 2018), can also influence population connectivity and dispersal.

4.3 | Wildlife management applications

How we apply movement data, whether generated through landscape genetics or other approaches, to wildlife population management is determined by the management context. In the case of the saltwater crocodile, sustainable harvest and safety of humans and livestock are major issues around which population management is framed, with conservation as an underlying goal (Saalfeld et al., 2015, 2016; Webb et al., 1984). Currently, the major hydrographic catchments or regions that group two or three adjacent catchments are treated as population units for population monitoring (Fukuda et al., 2011) and egg harvest allocation for the crocodile farming industry (Saalfeld et al., 2016). Our data support this strategy of classifying these catchments or regions as “management units” (Moritz, 1994, 2002; Waples, 1998) as the intervening land or saline environments limit movement among river systems. In addition, coastal geographical features or regions of high or complex ocean current flow may

Model set	Model	df	AIC	Δ AIC	wAIC
A	Resistance + Breeding habitat	3	257.45	0	>0.99
	Resistance	2	275.24	17.79	<0.01
	Breeding habitat	2	377.43	119.98	<0.01
	Resistance * Breeding habitat	4	1005.38	747.93	<0.01
B	Resistance * Breeding habitat	7	251.45	0	>0.99
	Resistance + Breeding habitat	3	266.11	14.66	<0.01
	Resistance	2	279.16	27.71	<0.01
	Breeding habitat	2	381.89	130.44	<0.01

TABLE 2 The models ranked by AIC to examine the environmental effects on the dispersal choice (A) and natal assignment (B) of free-ranging crocodiles in the study area

Model	Variable	Coefficient	SE
A. Resistance + Breeding habitat	Intercept	2.67	0.82
	Resistance	-0.07	0.02
	Breeding habitat	-7.37	1.88
B. Resistance * Breeding habitat	Intercept	3.96	0.88
	Resistance	-0.54	0.12
	Breeding habitat	-9.34	1.83
	Resistance * Breeding habitat	0.77	0.18

TABLE 3 The models most supported by AIC to examine the environmental effects on the dispersal choice (A) and natal assignment (B) of free-ranging crocodiles in the study area

exacerbate difficulties in moving among river systems (Fukuda et al., 2019). However, our data show that populations are linked by extensive dispersal, with ~42% of individuals having been born in a different catchment to where they were sampled. The data also show that some river systems are disproportionately important for providing recruits to other populations. For instance, the Goyder River (Arafura Swamp) population can be seen in Figure 5 as contributing recruits to many other river systems in either direction along the coast from this productive breeding population. In contrast, the Tiwi Islands population appears to draw recruits predominantly from the local population and is the source of immigrants to few areas other than the nearby Cobourg Peninsula (Figure 5), presumably due to the high resistance of the marine environment surrounding the islands.

Our approach can help manage populations by identifying recruitment patterns, including the location of dispersal sources and sinks. As previous studies have suggested (Carr et al., 2007), dynamic population connectivity and habitat quality, which is difficult to map due to some uncertainty in interannual variation in environmental conditions (e.g., rainfall known to influence the abundance of hatchlings in the following year; Fukuda & Saalfeld, 2014), can be inferred from the genetic structure. Different levels of carrying capacity in recovering populations shown by the extensive monitoring (Fukuda et al., 2011; Messel et al., 1981; Saalfeld et al., 2016) suggest that dispersal of individuals is density-dependent and such movement patterns are predictable.

Managing large predator populations for human safety can also benefit from the kind of dispersal data generated through landscape genetics. Saltwater crocodiles (and other large predators) are often removed from locations with high usage by humans such as major population centres (Brien et al., 2017; Fukuda et al., 2014; Saalfeld et al., 2016). Understanding the population sources and dispersal

distances of problem animals can help identify and evaluate management options (such as increased intervention or harvest at source locations, or identification of probable dispersal destinations). From our data, 200 km appears to be the most common range of *C. porosus* movement between the river mouths along the coast (Figure 6), but a few dispersed much long distances (up to 600–700 km). Campbell et al. (2010) showed that such long-distance movement could be assisted by ocean currents and that individuals of the species are likely to be able to move much farther from its natal location than other crocodylian species that are predominantly constrained to freshwater, for which much shorter movement events have been reported (Campos et al., 2006; Combrink, 2015; Lance et al., 2011; Woolard et al., 2004).

In summary, resistance or environmental permeability was most important in the environmental models of the observed dispersal events, but properties of the source and sink catchments also influenced patterns of emigration and immigration. Our habitat quality variables representing the availability of wet season breeding habitat suggested that competition for habitat influences both emigration and settlement choices, together with the strong effect of environmental resistance to movement.

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CONFLICT OF INTEREST

The authors have no conflict of interest.

AUTHOR CONTRIBUTIONS

Research was designed by Fukuda, Moritz and Banks. Research was performed and data were analysed by Fukuda, Moritz, Jang, Lindner and Banks. The paper was written by Fukuda, Moritz, Webb, Campbell, Christian and Banks.

OPEN RESEARCH BADGES



This article has earned an Open Data Badge for making publicly available the digitally-shareable data necessary to reproduce the reported results. The data are available on Dryad at <https://doi.org/10.5061/dryad.bcc2fqz94>, <https://doi.org/10.5061/dryad.q2b-vq83gb>, and <https://doi.org/10.5061/dryad.2z34tmpj1>.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in dryad at the following doi reference numbers: (Fukuda & Banks, 2020a, 2020b, 2020c).

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