



RESEARCH ARTICLE

# Modelling dispersal in a large parrot: a comparison of landscape resistance models with population genetics and vocal dialect patterns

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## Abstract

**Context** Identifying the range, core areas and dispersal pathways or barriers in heterogeneous landscapes is important for managing threatened species. Studies of variation in learned vocalisations are a promising complementary tool to traditional landscape genetics studies for identifying potential dispersal barriers. Here we use multiple data sources to inform the conservation of a parrot species.

**Objectives** We tested for correlations between landscape resistance models, population genetic structure and vocal variation of parrots to investigate the effects of natural barriers on genetic and behavioural population structure including narrow habitat corridors and a mountain range.

**Methods** We studied palm cockatoos (*Probosciger aterrimus*) within their Australian distribution. We constructed landscape resistance surfaces restricted to

areas of high climatic suitability from a maximum entropy (MAXENT) distribution model. We verified three landscape resistance predictions from CIRCUITS-CAPE (isolation by elevation, habitat and distance) using four data sets (individual genetic divergence, acoustic divergence in repertoire and two call types).

**Results** Landscape resistance models revealed strong effects of isolation by elevation on genetic, repertoire and structural call differentiation. Neither isolation by habitat nor isolation by distance were well supported by differentiation in the data.

**Conclusions** Our landscape resistance analysis validated by four datasets supports the Great Dividing Range as the main limitation on dispersal and connectivity among palm cockatoo populations. Combined genetic and behavioural approaches can determine landscape-level connectivity of individuals and demonstrate how dispersal barriers influence genetic and behavioural patterns in a large parrot.

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## Introduction

Small populations are generally at higher risk of extinction than larger populations due to stochastic genetic and demographic factors (Frankham 2005).

However local population declines may not affect overall meta-population viability if numbers are replenished by dispersal from other populations. This allows geographically separate populations to function as one interconnected population increasing the effective population size (Frankham 2005; Sunnucks 2011). Predicting connectivity between apparent populations in heterogeneous landscapes requires detailed assessment beyond dispersal distance alone because it depends on species specific landscape permeability (e.g. Robertson and Radford 2009). Typically, assessing landscape permeability for a species involves capture and subsequent tracking of individuals, which can prove to be logistically infeasible for some species.

Electrical circuit theory (McRae 2006) is an example of a non-invasive technique for predicting dispersal through landscapes with heterogeneous resistance to movement. This effectively models population connectivity by integrating multiple movement paths between populations through hypothetical resistance-to-flow (resistance) surfaces. Hypothetical resistance estimates between pairs of locations can be validated through correlation with other kinds of interaction data on the population or individual scale such as landscape genetics, or vocal variation (McRae et al. 2008).

The ability to distinguish explicitly between connectivity hypotheses in heterogeneous landscapes can be greatly improved using alternative data sets, such as vocal dialects (Pavlova et al. 2012; Goretkaia et al. 2018). Vocal behaviour is inherited by learning (hereafter ‘culturally’) in some birds and mammals (reviewed in Janik and Slater 2000). Cultural inheritance allows rapid transmission and evolution of behaviour within generations, and cultural variation can evolve between groups within years to decades (Laiolo 2010; Robin et al. 2011). Variation is expected to be greatest between animals that are more distant from each other in their communication networks (McGregor 2005). In this way, fine-scale acoustic structure of avian vocalisations can reflect landscape-scale patterns of social interaction (e.g. Irwin 2000; Ribot et al. 2012), and may complement landscape genetics (Balkenhol et al. 2009) with information about meta-population processes on more recent time scales (Janik and Slater 2000; Laiolo and Tella 2005, 2006, 2007).

Vocal learning is common in parrots (Psittaciformes) and many species can adjust their calls to converge with their territorial neighbours or social partners in support of the social adaptation hypothesis (Farabaugh et al. 1994; Hile et al. 2000; Walløe et al. 2015). However, vocal variation at the landscape scale manifests differently across species depending on a range of factors (reviewed in Wright and Dahlin 2017). For example, distinct boundaries (dialects) may occur and be maintained through time in sedentary species (e.g. Kleeman and Gilardi 2005), if the vocally divergent populations have little contact (Irwin 2000) or if local vocalizations are learned especially quickly and accurately by immigrant birds (e.g. Salinas-Melgoza and Wright 2012). On one hand, with rapid learning, dialect boundaries can persist regardless of genetic admixture among vocally distinct populations (e.g. western Australian ring-necked parrot *Platycercus zonarius*, Baker 2008). On the other hand, vocal differences can also impede ongoing gene flow (e.g. crimson rosella *Platycercus elegans* species complex in south-eastern Australia, Ribot et al. 2012). An alternative hypothesis known as acoustic environmental adaptation has not been well-documented in parrots (Wright and Dahlin 2017).

In this study, we assessed whether interpopulation variation in vocal repertoire, fine-scaled acoustic structure and genetic population structure are affected by landscape features in a threatened parrot species, the palm cockatoo (*Probosciger aterrimus*). Worldwide the conservation status of palm cockatoos is ‘least concern’, however the Australian sub-species (*P.a. mcgillivrayii*) is recognized as ‘vulnerable’ under International Union for the Conservation of Nature (IUCN) criteria (2012). Palm cockatoos have exceedingly slow reproduction as well as a specific association with rainforest within a larger matrix of woodland areas (Murphy et al. 2003). In previous studies we demonstrated genetic structure among Australian palm cockatoos either side of the northern portion of The Great Dividing Range on Cape York Peninsula. We also showed some degree of gene flow between otherwise genetically distinct populations (Keighley et al. 2019) that were also vocally differentiated (Keighley et al. 2016). Immigration may be especially important for maintaining one of the largest of these populations that could otherwise be undergoing rapid decline (Heinsohn et al. 2009). Little is known about dispersal in palm cockatoos. However

once acquired, mating pairs use the same breeding territories in subsequent seasons (Murphy et al. 2003). Philopatry leads to a high likelihood that vocal evolution aligns with dispersal and is therefore affected similarly to genetic variation (e.g. Bradbury et al. 2001). However, accurate vocal learning could also result in maintenance of dialect boundaries or gradients that are independent from genetic population structure resulting from dispersal (e.g. Baker 2008). Identification and preservation of landscape-scale movement corridors for dispersal could be especially important for preventing local extinctions in palm cockatoos. Due to the relative ease of making acoustic recordings, geographic vocal variation could facilitate initial connectivity assessments depending on how similarly both vocal and genetic variation align with landscape features.

We aimed to identify the key landscape features that influence movement of palm cockatoos throughout their Australian range and to determine whether they also affect vocal differentiation. We hypothesised firstly that palm cockatoos' association with narrow corridors of rainforest could cause isolation (restricted movement) and secondly that isolation could occur due to prominent topographic features such as The Great Dividing Range. We also tested a third (null) hypothesis that any isolation could in fact be due to geographic distance rather than landscape features.

Our movement predictions for palm cockatoos were derived from three model landscapes representing each hypothesis. We used electrical circuit theory in CIRCUITSCAPE (McRae 2006) to calculate resistance distance (cumulative movement cost of possible pathways) among individuals or populations in which high values mean more resistance to movement (i.e. isolation). Our hypotheses were then tested by comparing predicted resistance distances to genetic differentiation and three measures of acoustic differentiation. We predicted that both vocal and genetic differentiation would increase with increasing isolation by habitat and elevation, and that isolation by distance would have less of an effect. To test which scale of behavioural variation has conservation relevance and for a thorough representation of palm cockatoo vocal behaviour, we used population level call repertoires as well as individual level structural call variation in two call types.

## Methods

### Study species

Palm cockatoos (*P. aterrimus*) are large (up to 1 kg), charismatic parrots that inhabit lowland New Guinea, the Aru Islands, and Cape York Peninsula north of the Laura Basin (14.5°S) in mainland Australia. They are a sedentary canopy dwelling species, with pairs defending territories (approx. 1.5 km diameter) containing multiple nesting hollows in the ecotone between open woodland and rainforest. New Guinean palm cockatoos are found in the lowlands up to 1300 m elevation though are most common below 750 m (Juniper and Parr 1998). The distribution of palm cockatoos in Australia and New Guinea has been modelled (Keighley et al. 2019), and field studies have provided information about their habitat use (Murphy 2005).

Australian palm cockatoos occur in greatest density in woodland within 1 km of rainforest (Wood 1984), especially where there are small patches of rainforest or linear corridors of gallery forest (Murphy 2005). They occur at lower densities in continuous rainforest and do not cross large stretches of open water (Igg 2002; Murphy et al. 2003). Habitat contractions associated with aridification during the Pleistocene likely caused contractions in their distribution (Keighley et al. 2019) as in other rainforest dependent species (e.g. New Guinean bandicoots, *Echymipera rufescens*, Westerman et al. 2001, pademelons *Thylogale stigmatica*, Macqueen et al. 2010, and logrunners *Orthonyx* spp., Norman et al. 2002). Today, fluctuating regimes of fire frequency and intensity regulate the persistence of rainforest patches and the ecological processes that result in large, hollow trees for their nests (e.g. recruitment and termite density, Murphy and Legge 2007). On Cape York Peninsula, the largest patch of rainforest extends along the eastern coast and includes the Iron and McIlwraith Ranges, northern parts of the Great Dividing Range. This rainforest area supports what is thought to be one continuous palm cockatoo population, however demographic studies suggest this population is in severe decline unless supported by sufficient dispersal from populations elsewhere (Heinsohn et al. 2009).

## Study sites

This study used acoustic data presented in Keighley et al. (2016) who recorded palm cockatoos within six local ‘populations’ on Cape York Peninsula, Australia. These populations represented locations at which palm cockatoo habitat could be accessed on repeated occasions to make enough recordings for characterisation of a call repertoire. Geographic distance between populations ranged between 50 and 402 km. As the birds were not marked, individuals of the same sex were differentiated based on distance between their specific recording locations. We used the minimum of 1.5 km between specific recording locations as a proxy for individual identification (reflecting territory size), and the maximum distance between them was 40.7 km. This resulted in data from 68 individual palm cockatoos; 18 at Piccaninny Plains Wildlife Sanctuary, 10 at Steve Irwin Wildlife Reserve, and 8 near Moreton Telegraph Station (all of which are on major river systems inland on Cape York Peninsula). We recorded 23 individuals at the free-hold lands around Bamaga (on the northern tip of Cape York Peninsula), 4 near Port Stewart (at the southernmost point of the species’ recorded range) and a single bird in central Cape York Peninsula at Palm Creek 50 km north of Moreton Telegraph Station (Fig. 1i). Recordings of an additional five birds from the Iron Range National Park (on the eastern side of Cape York Peninsula) were contributed by C.N. Zdenek. Moulded feathers, combined with blood and skin samples from museum collections were used for genetic analyses in Keighley et al. (2019) (locations shown in Fig. 1i).

## Recordings and acoustic differentiation analyses

Recordings of unmarked, wild palm cockatoos were made and analysed for repertoire variation by Keighley et al. (2016), a brief summary of the methods and results relevant to the current analysis is presented here. Recordings were collected from June to October 2013, and from July to November 2014. By following individual birds on foot, on average 43 min  $57 \pm 48$  min 30 s (sd) of audio was recorded per specific recording location. RavenPro v. 1.5 (Charif et al. 2008) was used to create spectrograms which allowed initial call classification by eye followed by the measurement of acoustic characteristics using the

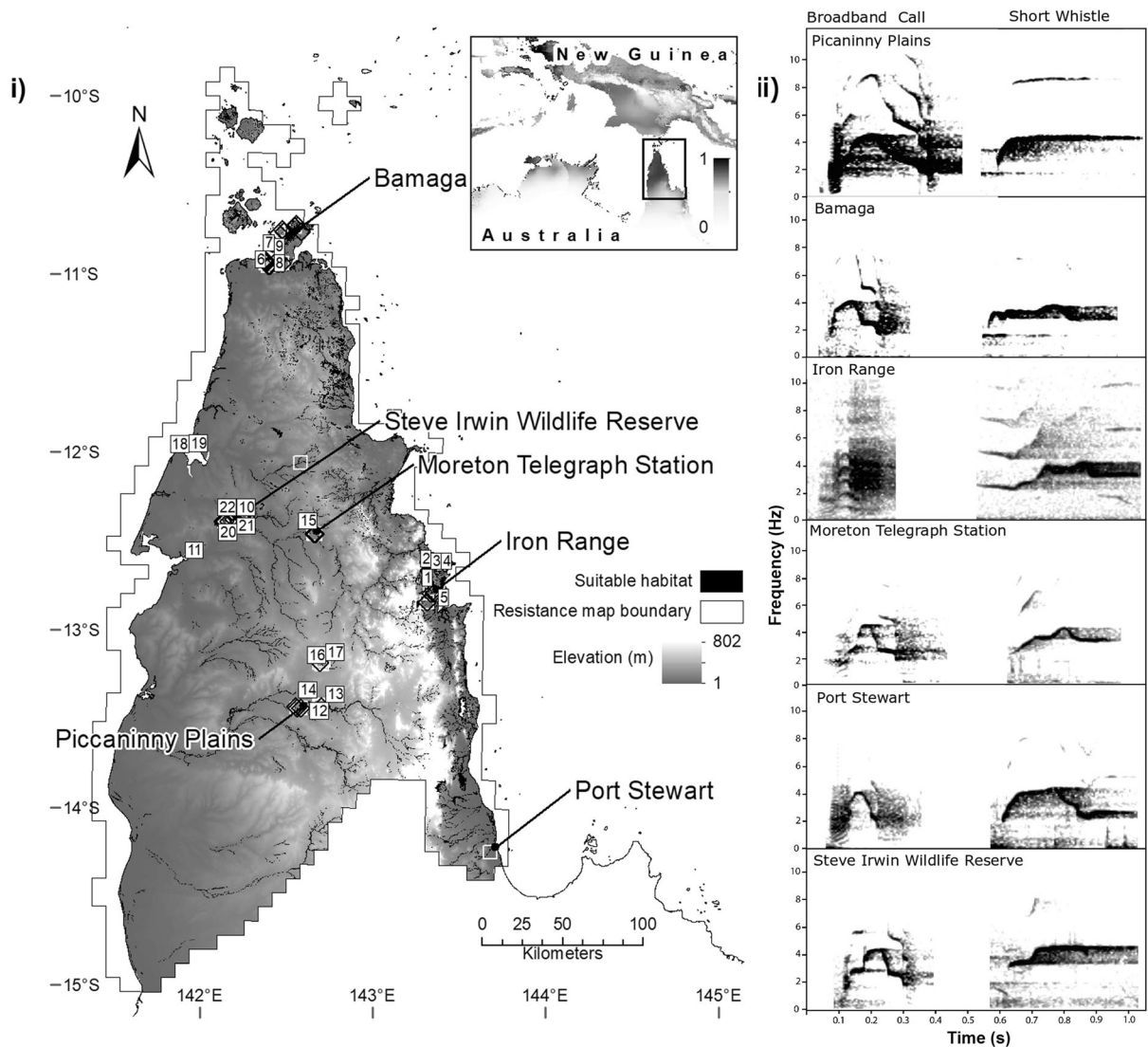
on-screen cursor. Twenty-two acoustic measurements were made in total and measurements using amplitude were excluded as recording distance was not controlled (Table S1.1, Supplementary Material). All measurements were used to statistically validate visual call classification within populations and then to compare call similarity between populations and individuals using discriminant function analyses (DFAs). These analyses validate category membership (population or individual call data) if there is no overlap between category confidence intervals. We used this to compare population repertoires. A measure of category differentiation is provided by the Mahalanobis distance between each category’s multivariate mean and provides a pairwise acoustic distance. We used this to compare individual call structure.

## Repertoire differences

We only included calls that were given at least three times by three separate individuals to ensure they were widespread within a population and not individually idiosyncratic. Based on population level pairwise DFAs, calls that were not significantly different between each of the six major populations’ repertoires were termed ‘shared’. The overall repertoire similarity was then quantified using a six by six matrix of pairwise Bray–Curtis dissimilarity values. To ensure an adequate proportion of each population’s repertoire was sampled, the full vocal repertoire size was estimated using rarefaction (Peshek and Blumstein 2011). Call classification yielded mean  $12.33 \pm 2.80$  sd call types per population representing mean  $76 \pm 12.18\%$  sd of their estimated full repertoire size (Table 1). Call sharing between populations was generally low (Supplementary Material, Table S1.2). The population at Iron Range, despite being relatively central in geographic location had the fewest calls shared with other populations. In contrast, the most distant population (Bamaga) shared more calls than others (Table S1.2, Supplementary Material; Keighley et al. 2016).

## Contact call differences

The two most common types of the contact call from each population that could be easily differentiated from each other were termed ‘short whistles’ and



**Fig. 1** i The topography, suitable habitat and bioclimatic distribution prediction for palm cockatoos (*Probosciger aterrimus*) on Cape York Peninsula with sampling locations ‘sources’ for genetic and acoustic data used in resistance modelling with CIRCUITSCAPE (McRae 2006). Genetic sources are numbered (individuals 1–22). Three groups of genetic samples shared sampling location (3 and 4, 6–9, 10 with 20, 21 and 22). Short whistles are black diamonds (31

individuals) and broadband calls are white squares (39 individuals). Population based acoustic data is represented by the centre points of the six major populations. ii Spectrograms of contact calls representative of six populations on Cape York Peninsula marked on the map; broadband calls and short whistles. Spectrograms were created in RavenPro v. 1.5 (Charif et al. 2008) (16-bit sample format, frame overlap = 50%, Hann Window, DFT = 512, frequency resolution = 124 Hz)

‘broadband calls’ (e.g. Fig. 1ii; Bradbury 2003; Zdenek et al. 2015). Based on initial inspection of the spectrograms, these calls appear to have different landscape level differentiation patterns (Keighley et al. 2016). Based on DFA, central Cape York Peninsula populations at Steve Irwin Wildlife Reserve and Moreton Telegraph Station shared similar short

whistles and broadband call structure while only sharing similar broadband call structure with Port Stevens. Bamaga only shared similar broadband call structure with Steve Irwin Wildlife Reserve. Both broadband calls and short whistles from Iron Range were distinctive despite this population’s more central geographic location (Figs. 1ii, S1.1, Supplementary



**Table 1** Repertoire and call sample size per population

Population	Repertoire			Call structure analysis	
	Number of individuals	Number of call types and proportion of estimated repertoire size <sup>a</sup>	Estimated repertoire size <sup>a</sup>	Broadband calls: number of individuals	Short whistles: number of individuals
AR	18	14 (58%)	24	9	5
BA	23	15 (88%)	17	13	14
IR	5	15 (70%)	20	4	4
MTS	8	11 (79%)	14	2	2
MU	4	8		1	
PC				1	
SI	10	11 (85%)	13	9	6
Total	68			39	31

AR Piccaninny Plains, BA Bamaga, IR Iron Range, MTS Moreton Telegraph Station, MU Port Stewart, PC Palm Creek, SI Steve Irwin Wildlife Reserve

<sup>a</sup>Estimated using rarefaction based on 20 randomly sampled calls from 11 recordings in each population, except MTS which only had 6 recordings with at least 20 calls (Keighley et al. 2016)

Material; Keighley et al. 2016). We used individual based data from both call types to distinguish which vocalization type was most relevant for non-invasive interpretation of movement patterns and genetic differentiation. To control for effects of spatial autocorrelation and to achieve a more stable representation of their call structure, for each call type we included in our DFAs a single recording of a randomly selected bird from each specific recording location which included at least four repetitions. This resulted in a matrix of Mahalanobis distances for each call type; short whistles ( $31 \times 31$ ) and broadband calls ( $39 \times 39$ ). Short whistle and broadband call datasets were also investigated for correlation and were found to reflect different patterns of differentiation (Mantel  $r = 0.648$ ,  $P = 0.001$  from  $N = 21$  paired sampling locations).

### Genetic structure

DNA from 22 palm cockatoo samples (5 blood, 4 skin and 13 moulted feathers) from Cape York Peninsula was extracted and the nuclear genome screened for anonymous SNPs at 342 loci in Keighley et al. (2019); sample details are in Table S2.1, Supplementary Material. Samples were selected to represent the greatest possible area on Cape York Peninsula with five from Piccaninny Plains, four from Steve Irwin

Wildlife Reserve, three from the west coast, one from Moreton Telegraph Station, four from Bamaga and five from Iron Range (Fig. 1). Extraction methodology and analysis are available in Keighley et al. (2019) as well as Supplementary Material (Part 2, Fig. S2.1; Table S2.2).

A  $22 \times 22$  matrix representing individual (percentage) differences at focal loci was extracted (as in Keighley et al. 2019) and used for comparison to vocal distance datasets. ANGSD was used for SNP filtering and genotype likelihood calculations (Korneliussen et al. 2014), and multiple filters were employed to obtain high quality SNPs for analyses. Only contigs with a minimum coverage of  $2 \times$  were used. SNPs that overlapped between populations were found using ngsTools so the resulting genetic distances were not biased to SNPs genotyped within a single population (Fumagalli et al. 2014). Contigs with  $> 5$  SNPs were filtered out to avoid putative repeat or paralogous regions ( $< 1\%$  of the contigs) and unlinked SNPs (only one SNP per locus) were used to determine population structure. The percent difference between individuals' nuclear genomes was recovered using ngsDist in the ngsTools kit (Fumagalli et al. 2014; Vieira et al. 2016), using the genotype likelihood output of ANGSD as input for ngsDist to incorporate the uncertainty in the distance measures.

For broad measures of genetic structure, population genetics summary statistics (including population divergence,  $D_{xy}$  and divergence after population split,  $DA$ ) were estimated from the allele frequencies derived from genotype likelihoods (Keighley et al. 2019). For the nuclear SNP loci, the Iron Range population came out as separate from the remaining Cape York samples (Fig. S2.2, Supplementary Material). The absolute divergence measure was  $D_{xy} = 4.98 \times 10^{-3}$  per site, with an equivalent relative divergence measure of  $DA = 4.97 \times 10^{-3}$  per site. This level of divergence is relatively high within subspecies of birds, but about average between subspecies (e.g. meliphagoid passerines; Peñalba et al. 2017). Several individuals sampled along the Wenlock River in central Cape York Peninsula displayed admixture (genetic characteristics of both populations), suggesting some importance of river corridor connectivity for gene flow (Figs. S2.3, S2.4, S2.5, Supplementary Material; Keighley et al. 2016).

#### Palm cockatoo suitable habitat

A distribution model for palm cockatoos was originally calculated using a maximum entropy method (MAXENT) in Keighley et al. (2019) and then modified for the current study. Information about the creation and evaluation of the original model are in Supplementary Material, here we describe the relevant modifications. From the total range of the bioclimatic distribution prediction (Fig. 1, inset), the area with over 0.35 probability of containing palm cockatoos was selected. This outer limit encompassed all palm cockatoo sightings in Australia and was then used for calculating palm cockatoos preferred habitat types at a finer scale in the following steps.

Our georeferenced sightings of palm cockatoos were supplemented with an unpublished sightings dataset maintained by Birdlife Australia. These combined sightings were used with maps of broad vegetation groups from the regional ecosystems classification scheme (Queensland Herbarium 2015) in ARCGIS 10.4 (ESRI 2011) to determine fine scale habitat preferences for palm cockatoos. We created 500 m buffers around each waypoint forming a sample area of 217 km<sup>2</sup>. We took the total area covered by 66 habitat types observed in our sample and calculated each area covered as proportional to the total area within the aforementioned map boundary from the

distribution model. The area of each habitat in our sample expected under random sampling was calculated by multiplying the proportion of each habitat within the map boundary by the total sample area. We tested if expected habitat area differed from that observed in our sample area using a  $\chi^2$  test. Habitat types in our sample that covered at least double their expected area were considered suitable habitat for palm cockatoos and were hypothesised to offer the least resistance to palm cockatoo movement in an “isolation by habitat” connectivity model (see below).

#### Landscape connectivity predictions

We constructed three model landscapes to represent each of four hypotheses regarding palm cockatoo population connectivity using the below method. Each model landscape was used to produce resistance values in pairwise fashion between samples (i.e. population centres for repertoire, individual locations for call structure or genetic distance) using electrical circuit theory and CIRCUITSCAPE (McRae 2006).

We used spatial analysis techniques in ARCGIS 10.4 (ESRI 2011) to create three landscape grid models of cell size 300 m  $\times$  300 m to represent our hypotheses for palm cockatoo movement. This cell size was chosen as it is smaller than individual palm cockatoos' home range size (approx. 1.5 km<sup>2</sup>) and is approximately the maximum distance from rainforest they choose to nest (Murphy et al. 2003). For the map area we started with the outer limit provided by the above habitat model. Boundary based limits to movement were of less interest than the effects of internal features within landscape models, so we inflated our map boundary by 1° (using the focal statistics tool in ARCGIS 10.4). The first model represented the isolation by distance hypothesis and all cells were attributed a value of 1. The second model represented isolation by habitat (suitable habitat determined above) with cell resistance value increasing linearly with distance from it. These values were calculated using the “cost distance” function in the Spatial Analyst toolbox (ARCGIS 10.4; ESRI 2011) based on individual cell resistance of 1 for suitable habitat cells and 2 for non-suitable habitat. The cost distance value at each cell represents the minimum cost per unit distance (in m) of reaching the cell from the nearest patch of suitable habitat and is calculated by multiplying cell resistance by its resolution while also

compensating for diagonal movement. Isolation by habitat's range of resistance values therefore ranged from 1 (adjacent to suitable habitat) to 58,595. The third model represented isolation by elevation using elevation data from the GEODATA 9 s digital elevation model version 3 and included resistance values ranging between 1 and 802 reflecting meters above sea level (Fig. 1i) (Hutchinson et al. 2009).

To test for effects of landscape models on acoustic and genetic distances we used mixed models. Linear mixed models allow model selection statistics (e.g. marginal  $R^2$ , AIC, AICc and BIC; Van Strien et al. 2012), control for interdependence among pairwise distance metrics and can test the effect of resistance distance matrices (independent predictor variables) on acoustic or genetic distances (dependent response variables). We used maximum likelihood (ML) population-effects models to fit response variables (genetic or acoustic distance) to resistance distances following procedures outlined in Van Strien et al. (2012) and Clarke et al. (2002). We mean centred all variables and scaled them by dividing by their standard deviation to ensure restricted ML (REML) estimates matched those from simple linear regression (Clarke et al. 2002). All variables were tested for multicollinearity using the variance inflation factor; values over 10 warranting exclusion (Belsley et al. 1980). Fixed effects in our models were the resistance distance matrices and each model included one of all possible combinations, i.e. alone or in combination. A random effect accounted for population or individual-level influence in all models (Clarke et al. 2002; Van Strien et al. 2012). All linear mixed model calculations were performed in the R package ResistanceGA with the function “mlpe\_rga”.

The resistance surface (or combination thereof) that best explained each response variable was selected by comparing each model's AIC values and variance components (marginal  $R^2$ GLMM, Nakagawa and Schielzeth 2013) using ML estimation. We used the function “aictab” in the R package AICcmodavg (Mazerolle 2019) to return AIC values for each linear mixed model. In accordance with Burnham and Anderson (2002) we selected models with  $\Delta AIC \leq 2.0$  as the best models. For repertoire and genetic distances second order AIC (AICc) was used due to small sample size ( $n/K < 40$ , where  $n$  is sample size and  $K$  is number of model parameters, Burnham and Anderson 2002). We also calculated marginal

$R^2$ GLMM using the function “r.squaredGLMM” in the R package MuMIn (Bartón 2016) for each model to further assist model selection. Finally, the influence of individual resistance surfaces was evaluated by the degree to which individual fixed effects explained the dependent variable using REML versions of each of the best model (as opposed to ML, Zuur et al. 2009). Significantly influential fixed effects were interpreted as those with an effect to standard error ratio greater than 2.

To identify areas which contributed most to connectivity between sample pairs we generated cumulative current maps with CIRCUITSCAPE (McRae et al. 2008). This was done for landscape models that were most strongly associated with each distance measure based on model evaluation. Maps were visualized in ARCGIS 10.4 (ESRI 2011).

## Results

### Range and habitat preferences

We used an earlier MAXENT distribution model for palm cockatoos including the 0.35 probability range (Keighley et al. 2019) which yielded 59,838 km<sup>2</sup> of climatically suitable area, encompassing the whole of Cape York Peninsula north of Princess Charlotte Bay. Of 51 types of broad vegetation group categories within this outer limit, 7 broad vegetation groups were disproportionately represented within 500 m of palm cockatoo sightings ( $\chi^2[1, N = 51] = 271.8, P = 0.05$ ). These were designated as ‘suitable habitat’ and included spring wetlands associated with bauxite deposits (34e), vine forests (4b, 2d, 2c, 2b, 3a) and *Maleleuca* wetlands (22c; Table S3.1, Supplementary Material). Their combined distribution is shown in Fig. 1.

### Testing landscape level connectivity

We assessed the effects of each of three isolation by resistance models (habitat, elevation and distance) on differentiation in vocal and genetic distance data using two lines of evidence; the models that provided the best fit to the distance data (Table 2) and the effect sizes relative to the standard error of the predictor variables (Table 3). We were also interested in how similar our acoustic distance results were to those



**Table 2** Results from the linear mixed models comparing resistance distance to acoustic and genetic distances among palm cockatoos sampled in Cape York Peninsula, Australia

Distance measure (dependent variable)	Movement model (predictor)	AIC <sup>a</sup>	Delta_AIC	AICWt	R <sup>2</sup> GLMM
Repertoire	<b>Null</b>	46.320	0.000	0.310	0.186
	<b>Elevation</b>	47.340	1.020	0.190	0.221
	<b>Habitat + Elevation</b>	47.850	1.530	0.150	0.501
	Elevation + Null	48.460	2.140	0.110	0.464
	Habitat	48.910	2.590	0.090	0.112
	Habitat + Elevation + Null	48.960	2.640	0.080	0.668
	Habitat + Null	49.240	2.920	0.070	0.320
Short whistle	<b>Elevation + Null</b>	634.620	0.000	0.590	0.503
	<b>Habitat + Elevation + Null</b>	635.310	0.690	0.410	0.509
	Habitat + Elevation	650.380	15.760	0.000	0.462
	Elevation	740.660	106.040	0.000	0.165
	Habitat + Null	758.090	123.470	0.000	0.195
	Null	810.380	175.760	0.000	0.031
	Habitat	824.670	190.050	0.000	0.019
Broadband call	<b>Habitat + Elevation</b>	650.750	0.000	0.570	0.379
	<b>Habitat + Elevation + Null</b>	651.320	0.570	0.430	0.382
	Elevation + Null	667.080	16.330	0.000	0.363
	Elevation	780.290	129.540	0.000	0.122
	Habitat + Null	840.730	189.980	0.000	0.137
	Null	886.380	235.630	0.000	0.022
	Habitat	907.170	256.420	0.000	0.011
Genetic distance	<b>Habitat + Elevation + Null</b>	318.680	0.000	0.560	0.631
	<b>Elevation + Null</b>	319.120	0.440	0.440	0.614
	Habitat + Elevation	373.150	54.470	0.000	0.562
	Elevation	400.090	81.410	0.000	0.344
	Habitat + Null	474.120	155.440	0.000	0.277
	Null	484.650	165.970	0.000	0.099
	Habitat	516.390	197.710	0.000	0.003

Repertoire distances were among the six major populations, whereas short whistle, broadband call and genetic distances were among 31, 39 and 22 individuals located throughout Cape York Peninsula respectively. Models with  $\Delta AIC \leq 2.0$  (best models) are in bold

<sup>a</sup>AIC used when  $n/K > 40$ , otherwise AICc was used

using genetic distance. We predicted stronger effects on differentiation for isolation by habitat and elevation than for isolation by distance. Overall, structural variation in both call types was explained by similar models to genetic distance; all three predictors together (the full model) featured in the best models and explained most variance in each case (full model  $R^2$  for short whistles 0.509, broadband calls 0.382 and genetic distance 0.631). Tests of individual predictors on acoustic and genetic differentiation showed that

isolation by elevation had the strongest effects on differentiation in all characteristics. Contrary to expectation we found a negative effect of isolation by distance on short whistle variation in each of the best models ( $\beta$ :  $SE = -11.216$  and  $-4.273$  respectively). We found the same with each of the best models explaining genetic differentiation ( $\beta$ :  $SE = -8.11$  and  $-7.693$ ). Although significant, the negative direction of isolation by distance allows rejection of the null model that distance would be the only

**Table 3** Best approximating models for the effects of the predictor variables on acoustic and genetic distance between palm cockatoos

Distance measure (independent variable)	Model description	Movement model (predictor)	Effect size ( $\beta$ )	Standard error (SE)	$\beta$ : SE	Variance (random effects)	Standard error (random effects)
Repertoire	Null	Intercept	> 0.001	0.554	> 0.001	0.431	0.657
		Isolation by distance	0.370	0.190	1.947		
	Elevation	Intercept	> 0.001	0.225	> 0.001	0.274	0.523
		Isolation by elevation	<b>0.517</b>	0.042	12.403		
	Habitat + Elevation	Intercept	> 0.001	0.250	> 0.001	0.338	0.582
		Isolation by habitat	– <b>0.498</b>	0.088	– 5.680		
Isolation by elevation		<b>0.635</b>	0.044	14.483			
Short whistle	Elevation + Null	Intercept	<b>0.000</b>	0.236	0.000	0.430	0.656
		Isolation by distance	– <b>0.594</b>	0.053	– 11.216		
		Isolation by elevation	<b>1.101</b>	0.074	14.907		
	Habitat + Elevation + Null	Intercept	0.000	0.242	0.000	0.611	0.782
		Isolation by distance	– <b>0.807</b>	0.189	– 4.273		
		Isolation by habitat	<b>0.169</b>	0.145	1.163		
Isolation by elevation		<b>1.175</b>	0.096	12.242			
Broadband call	Habitat + Elevation	Intercept	0.000	0.206	> 0.001	0.412	0.642
		Isolation by habitat	– <b>0.318</b>	0.026	– 12.036		
		Isolation by elevation	<b>0.651</b>	0.037	17.643		
	Habitat + Elevation + Null	Intercept	0.000	0.206	> 0.001	0.411	0.641
		Isolation by distance	– <b>0.090</b>	0.076	– 1.198		
		Isolation by habitat	– 0.254	0.060	– 4.242		
Isolation by elevation		<b>0.684</b>	0.046	14.809			
Genetic divergence	Habitat + Elevation + Null	Intercept	> 0.001	0.266	> 0.001	0.384	0.620
		Isolation by distance	– <b>0.647</b>	0.080	– 8.110		
		Isolation by habitat	– 0.148	0.092	– 1.603		
		Isolation by elevation	<b>1.180</b>	0.076	15.447		

**Table 3** continued

Distance measure (independent variable)	Model description	Movement model (predictor)	Effect size ( $\beta$ )	Standard error (SE)	$\beta$ : SE	Variance (random effects)	Standard error (random effects)
	Elevation + Null	Intercept	> 0.001	0.260	> 0.001		
			Isolation by distance	– <b>0.400</b>	0.052	– 7.693	0.523
			Isolation by elevation	<b>0.971</b>	0.073	13.362	0.723

explanator of variation. Also contrary to expectation, we found negative effects of isolation by habitat on repertoire differentiation ( $\beta$ :  $SE = -5.68$ ) and on broadband call differentiation ( $\beta$ :  $SE = -12.036$  and  $-4.242$ ).

The cumulative current maps for isolation by elevation between sampling locations for each distance measure (Fig. 2) show that connectivity relies on corridors to the east and west coasts of Cape York Peninsula. There are also corridors reaching into the centre of the peninsula that align with major rivers. Connectivity to the north appears better via the west coast than the east, and Piccaninny Plains individuals also appear slightly better connected to western and central individuals than to those in the east. A corridor along the Wenlock River appears particularly important for connecting central individuals to the west coast. This corridor also extends eastwards, close to corridors on the eastern side of the peninsula approximately 50 km south-east of Moreton Telegraph Station. Connectivity between broadband call recording locations also reveals a corridor along the east coast which extends south of Iron Range to Port Stephens.

## Discussion

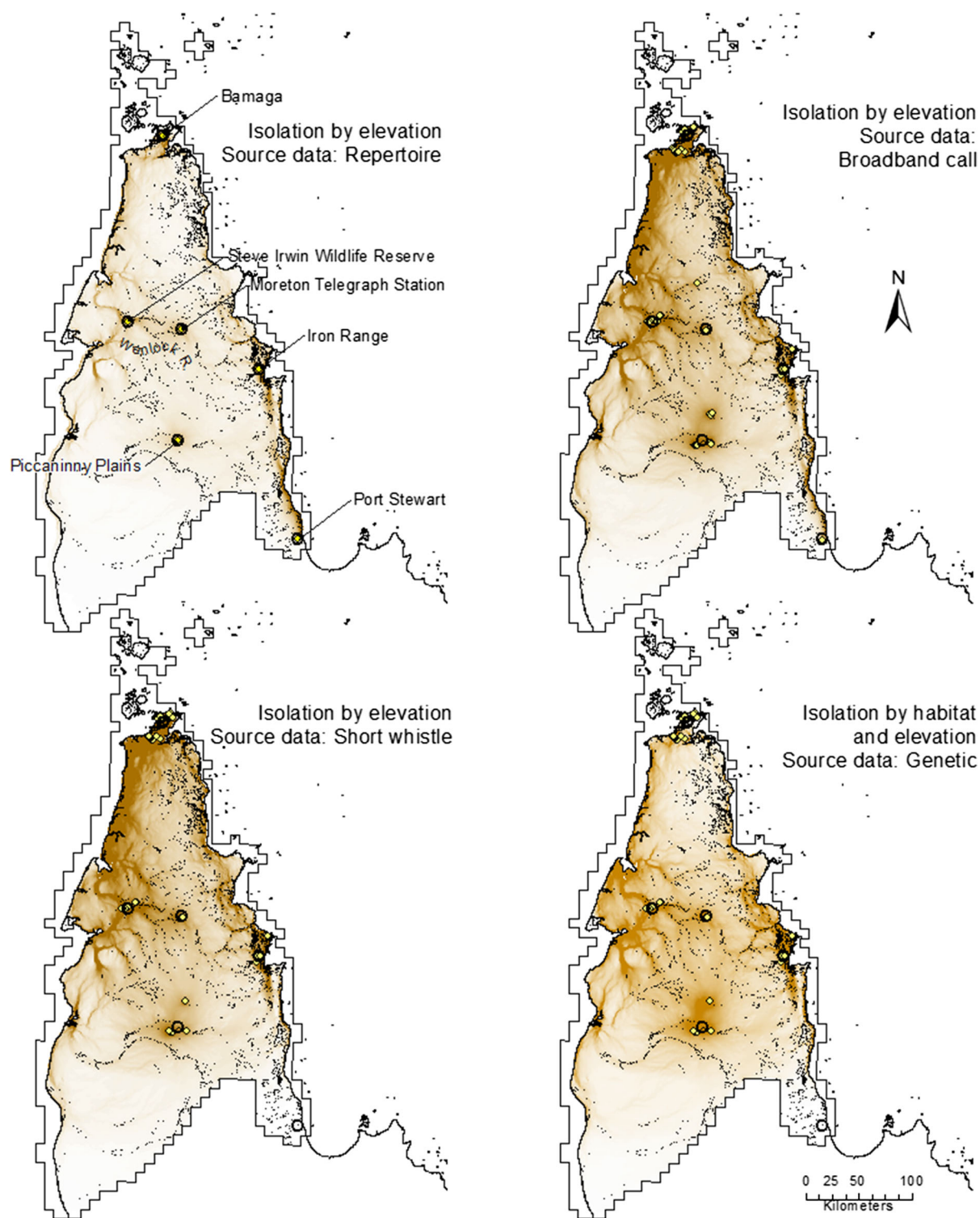
Determining the relative strength of dispersal pathways or barriers in heterogeneous landscapes is valuable for understanding the conservation status and management requirements of threatened species (McRae et al. 2008). We identified suitable habitat and tested predictions of population connectivity among palm cockatoos within their Australian range using electrical circuit theory and both genetic and vocal

data. Primarily, we found strong effects of isolation due to topographical features of the northern part of Great Dividing Range on Cape York Peninsula. Our multifaceted approach for identifying connectivity corridors provides an important example for species that may be difficult to capture and follow on an individual basis.

We note two main limitations of our study. First each of our datasets had a different sample size and distribution (e.g. 741 pairwise distances for broadband calls versus 231 for genetic data), which may have limited direct assessment of correlation between genetic and vocal data and resulted in inconsistency in the perceived effects of landscape resistance models. Second, our method for determining preferred habitat for palm cockatoos, comparing observed versus expected area covered by vegetation types, may have biased results towards habitat types with smaller areas (e.g. some rainforest types).

## Distribution and habitat

The bioclimatic envelope used for our analyses here aligned closely with previous range estimates (Juniper and Parr 1998; Higgins 1999), within which we identified seven broad vegetation types that are disproportionately associated with palm cockatoo occupation (Table S3.1, Supplementary Material). Previous studies found that palm cockatoos nest in woodland trees but feed in both woodland and rainforest, reaching their greatest density in savannah woodland close to rainforest patches or linear gallery forest corridors (Wood 1984; Murphy et al. 2003). Our findings therefore aligned with previous studies showing that rainforest is important habitat for an



**Fig. 2** Cumulative resistance maps of the CIRCUITScape (McRae 2006) models which correlated with either acoustic or genetic divergence among palm cockatoos (*Probosciger aterrimus*) on Cape York Peninsula, Australia. Population centre points are open circles, sampling locations (sources) are shown as yellow circles, areas of conductance are orange, areas of resistance are white and suitable habitat black. (Color figure online)

eastern sub-population of palm cockatoos (Murphy et al. 2003; Murphy 2005).

#### Landscape effects on genetic and vocal connectivity

All four of our vocal and genetic distance measures revealed strong effects of isolation by elevation between palm cockatoo populations separated by about 25 km of mountains higher than 500 m on Cape York Peninsula. These results align with similar studies which show elevated terrain can form natural barriers for dispersal even in large, strong flying parrots (scarlet macaw *Ara macau*, Masello et al. 2011; Olah et al. 2016). Our model of elevation resistance supports the Great Dividing Range functioning as a barrier causing or maintaining the genetic differentiation that generally distinguishes eastern, Iron Range, palm cockatoos from other individuals (Keighley et al. 2019).

It is not clear why palm cockatoos might avoid elevated terrain when dispersing but a lack of suitable vegetation communities at higher altitude is a possible explanation. The bioclimatic envelope we used for palm cockatoos includes the mountain range, however it was constructed using sightings from New Guinean and Australian birds (Keighley et al. 2019). Mountains on Cape York Peninsula are small compared to New Guinea where palm cockatoos occur up to 1300 m. Vegetation communities similar to New Guinea's would be found at lower elevations in Cape York Peninsula due to the latitudinal difference (Rapoport's rule) mirroring the effect of increasing altitude (Stevens 1992). Detailed telemetry data about dispersal in palm cockatoos are not available, although dispersal models show birds typically avoid risky dispersal regardless of their capacity for it (Shaw et al. 2014).

Few studies to our knowledge test vocal variation with landscape features in parrots. Repertoire dissimilarity and dialects in both broadband calls and short

whistles showed strong effects of isolation by elevation. As suggested for genetic evolution, call dialects and limited call sharing between populations could result from restricted contact between divergent populations. This would be similar to inferences made about vocal and genetic evolution associated with isolation by elevation in other avian taxa (e.g. greenish warbler *Phylloscopus trochiloides*, Irwin 2000). Acoustic variation aligns with subspecies boundaries in other parrots (e.g. Australian ringneck *Platycercus barnardius*, Baker 2008; crimson rosella *P. elegans*, Ribot et al. 2012) but not within sub-species (e.g. yellow-naped amazons *Amazona auropalliata*, Wright and Wilkinson 2001).

The question of whether differentiation in call structure can be used to approximate within subspecies genetic differentiation in palm cockatoos (see Laiolo 2010) is difficult to answer definitively because genetic and vocal samples were not taken from the same individuals. It does seem likely however for both individual level variation in the most common contact calls (short whistles and broadband calls) and population level variation in vocal repertoire (although more time-consuming to measure). This is supported by our finding that similar models best explained both genetic and acoustic differentiation and because of concordant effects of elevation on differentiation in each case.

The effect of isolation by elevation was stronger for genetic variation than structural variation in either call type (Table 3). A possible explanation is that isolation by elevation (Fig. 2) and individuals' genetic admixture (Figs. S2.3, S2.5, Supplementary Material, Keighley et al. 2019) both allow for some connectivity along the Wenlock River which flows westward through central Cape York Peninsula. It is possible that call dialects align with isolation by elevation less well than genetic data because fast and accurate learning of the local dialect by immigrating individuals maintains greater vocal distinction than predicted by isolation by elevation (e.g. Salinas-Melgoza and Wright 2012).

Our other hypotheses were that isolation by habitat or by distance would increase differentiation in vocal and genetic data. Neither hypothesis was supported by our results. Contrary to our predictions for isolation by habitat, we found less differentiation in repertoires and broadband calls with increasing resistance distance. It is unclear why this might be the case, apart from either



deficiency in the way our landscape resistance model for habitat reflected actual palm cockatoo ecology or as a side-effect of geographic positioning of the populations. Differentiation in short whistle and genetic divergence was also reduced, but with increasing isolation by geographic distance. The results with isolation by geographic distance (and perhaps also habitat) could reflect the spatially central position of the most vocally and genetically differentiated population at Iron Range.

### Implications for conservation

Understanding connectivity among geographically separate populations is important for estimates of species persistence (Frankham 2005; Keller et al. 2015) but for many vulnerable species this information is absent. Predictions of strong declines in numbers of Iron Range palm cockatoos contributed to recognition of their vulnerable status (Heinsohn et al. 2009; IUCN 2012) mainly due to their slow life-history (Murphy et al. 2003), but there are also several processes that threaten their patchy habitat distribution. The main threats are nest tree destruction from unsuitable fire regimes (Murphy and Legge 2007), habitat removal by bauxite mining on the west side of Cape York Peninsula and potential adverse effects on groundwater storage from removal of bauxite (Leblanc et al. 2015). Our results add to the evidence that river corridors such as the Wenlock River are likely to be necessary for the current level of connectivity, especially between the two populations we found to be separated by the Great Dividing Range. Future studies could assess whether the connectivity we determined is likely to bolster numbers for the declining Iron Range population for improved status estimates and conservation action planning.

### Conclusion

Our results demonstrate the effectiveness of a multifaceted, model validation approach for elucidating landscape scale processes via their influence on patterns in multiple kinds of data about inter-population interaction. We showed with palm cockatoos on Cape York Peninsula that topography could plausibly affect dispersal through alignment with genetic and acoustic differentiation. Although our samples were

limited and geographically unmatched, our data also revealed similar effects of elevation on genetic and acoustic connectivity, which supports the use of geographic variation in broadband calls for assessment of interpopulation connectivity. Using patterns of genetic and acoustic variation we also showed that particular corridors of habitat could provide valuable interpopulation connectivity despite a barrier formed by the Great Dividing Range. Our results raise concerns for the more isolated and declining population east of the mountains at Iron Range which may depend on dispersal through very specific corridors of suitable habitat.

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