Cultural diversity and meta-population dynamics in Australian palm cockatoos (*Probosciger aterrimus*), the legacy of landscape and biogeographic history.

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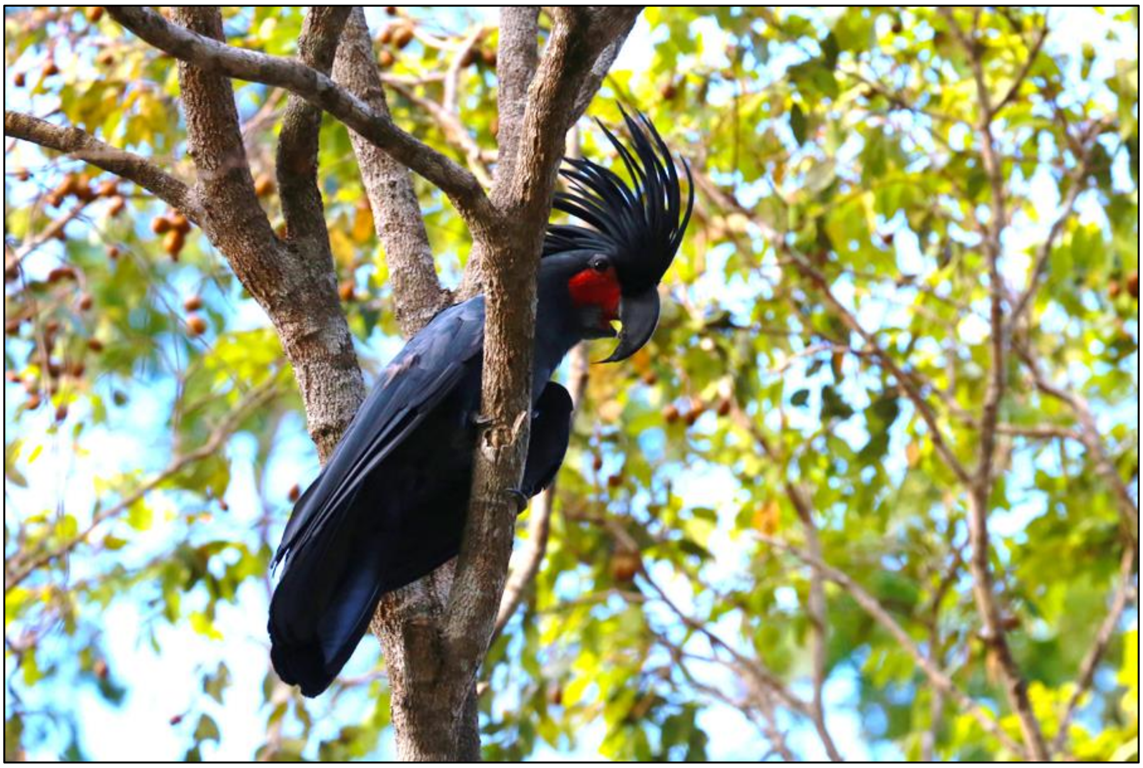
Thesis submitted for the degree of Doctorate of Philosophy
at the Fenner school of Environment and Society, Australian National University



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I certify that the majority of this thesis is my own original work. I have acknowledged all cases where contributions have been made by others in the *Author contribution* sections of each chapter.

A significant contribution was made by another author who wrote the supplementary methods section of Chapter 4 (2150 words) and conducted these methods and analyses.

Signed:

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Date: September 21, 2017

Acknowledgements

This thesis would not have neared completion if it wasn't for the encouragement and support of the wonderful people surrounding me; first and foremost, my patient and infectiously enthusiastic supervisors Rob Heinsohn and Naomi Langmore. Big thank you to Christina Zdeneck for passing on so much useful knowledge about palm cockatoo vocal behaviour and accommodating us during visits to Iron Range.

My family deserve much of the credit for the piece presented before you. My mum, Carol encouraged me to accept the position that I had applied for in the first place, and Dad helped to support me through my off-scholarship year. Through long phone calls, my brother James helped align my perspective keeping me functioning mentally and emotionally during fieldwork, and my other brother Matthew did the same during write-up in Denmark.

I owe much to Xénia for helping support me during most of my final year, and encouraging me over the significant hurdles involved with moving overseas and a nasty back injury. I also thank my super smart office-mates/co-sufferers for setting a good example; Ben, Darren, Nélida, Keshab, Wendy, and especially Claire Foster for pulling me back to the office from working at home. I am especially grateful to Claudia Benham for her support and for helping me adjust to PhD life. I thank also the Fenner School of Environment and Society for holding weekly morning teas, which are excellent.

Chris Sanderson, Maddie Castles, Zoe Reynolds, Richie Southerton and Andrew Neilen were high quality companions and skilled assistants for many weeks camping on Cape York Peninsula, and Piers Bairstow and Mauro Devanzo provided logistical equipment and advice, and a fully loaded four-wheel driving course.

Baz and Shelley Lyon provided the ‘Palmy army’ with a second home at Boulder Bend and a second family. Thanks Terry Irwin and Australia Zoo for putting me on a crocodile twice, and for generally being eager to help with the project. And thanks to the Australian Wildlife Conservancy, Graham Woods and Sally Gray and Eridani Mulder for such professional assistance with fieldwork on Piccaninny Plains.

A big thanks to Steve Murphy, for his hard work collecting demographic data on this special but difficult study species, and to my co-authors Josh Penalba and Steve Haslett for their respective contributions and abundant skill. Brian Venables’ kind offer of a beer turned into emergency post-prang accommodation and assistance in Cairns. Thanks also John Pritchard for sharing your idyllic home among the canopy, and of course for all the fish.

I also thank my Danish hosts Torben Dabelsteen, Nina Simonsen, Concalo Cordoso, Thomas Læssøe and Ulrik Søchting for conversation, an office with a view and the all important ‘hæve sinke bord’ (height adjustable table).

I thank the Australian Government for my Australian Postgraduate Award, Birdlife Australia, the Hermon Slade Foundation and the National Geographic Society for the valuable funding they provided for field and lab work. I also thank the staff at the Australian, Western Australian, South Australian and Queensland Museums as well as at the Australian National Wildlife Collection for providing valuable palm cockatoo tissue samples to the project.

Overall abstract

Understanding dispersal dynamics is important for conservation of vulnerable species because they effect whether populations recover or disappear following decline or disturbance, especially in species with slow life-histories that cannot replenish quickly. Palm cockatoos have one of the slowest reproductive rates for any parrot, and likely face steep decline in at least one location on Cape York Peninsula (CYP), north-eastern Australia. Traditional methods of measuring dispersal, such as capture and fitting of tracking devices, identification markers or tissue sampling for genetic analyses, are inappropriate in this species due to their susceptibility to stress. While handling chicks for DNA sample collection does not cause harm, locating nests requires too much focused effort at spatial scales relevant for conservation. In this thesis, I assess the utility of cultural methods for determining population connectivity based on published literature, and employ a combination of cultural and genetic methods to assess connectivity among Australian palm cockatoo populations. I then use a landscape 'resistance' modelling approach based on electrical circuit theory to identify connectivity corridors. Finally, I use population viability analysis (PVA) to determine the effects of dispersal dynamics on viability for both individual populations and the combined meta-population in Australia.

Based on the literature I concluded that geographic variation in cultural behaviour among populations of a species can help fill important knowledge gaps about their population level processes, especially when comparisons to similar species and alternative data are available. My assessments of vocal and genetic variation among populations revealed differentiation among populations on Cape York Peninsula, separating east coast palm cockatoos at Iron Range from other Australian populations with some evidence of gene flow between them. My landscape 'resistance' analysis

identified the Great Dividing Range as a barrier, and rainforest patches as important corridors for interaction among separate populations. However, the level of connectivity we determined appears not to provide enough support via dispersal to buffer the decline predicted for Iron Range. Furthermore, other populations require much better reproductive success than data suggests for Iron Range if individuals dispersing to there are to be replenished. I emphasise the importance of managing local declines for the preservation of genetic and behavioural diversity in Australian palm cockatoos.

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Chapter 1: Introduction

Parrots are a highly charismatic and popular animal group. Their intelligence, bright colours and vocal mimicry have captivated humans throughout history and they have become favourite pets worldwide. Parrots are enchanting perhaps in part for their unique behavioral similarities to humans; they form strong monogamous pair bonds, can learn to imitate words throughout life and are among very few species capable of moving to a rhythmic beat (Pepperberg 2009; Bradbury and Balsby 2016; Heinsohn *et al.* 2017). Like us, wild parrots are social, vocal and use their brains and manual expertise to survive in an incredibly diverse range of habitats. Historically, our fondness for parrot companions has been to their detriment. Hunting and trapping for the pet trade alongside other forms of human interference have endangered many species in the wild (Olah *et al.* 2016a). Furthermore, populations of wild parrots are generally more vulnerable to decline than comparable bird groups (Olah *et al.* 2016a), and difficulties associated with studying parrots in the wild have resulted in many species with unknown or unconfirmed conservation status.

The parrot order *Psittaciformes* (398 spp.) has 28% of its species considered under threat (categorized as Critically Endangered, Endangered or Vulnerable, IUCN 2014), more than the other large avian orders *Passeriformes* (5913 spp., 10% threatened), *Caprimulgiformes* (593 spp., 9% threatened) and *Piciformes* (484 spp., 7% threatened). While a significant proportion of parrot species are threatened by anthropogenic environmental alterations, those with the greatest risk of extinction tend to have 1) large body size, 2) slow reproduction, 3) dependence on forest and 4) small historical distribution (Olah 2016). Those confined to islands seem to be especially at risk with 20 of the 24 extinct parrot species falling into this category. Three of the remaining extinct species were restricted to or highly dependent on specific habitat types within a ‘matrix’ of unsuitable area and therefore effectively had small range sizes (e.g. Spix’s, glaucus and Lear’s macaws) (Toft and Wright 2015).

Species that have restricted distributions are at greater risk of overall extinction than those with uniform or continuous distributions. Separate or small populations are more vulnerable to local extinction from local threats and stochastic fluctuations in numbers, and subsequent loss of genetic and cultural diversity results in lower adaptability to change, which can increase a whole species’ vulnerability to extinction (Frankham 2005). Local declines can however, be buffered by replenishment by dispersal from connected populations. Connectivity via dispersal conveys upon small populations the benefits of increased effective population sizes and lower extinction vulnerability (Frankham 2005; Sunnucks 2011). In this way, connectivity is important for determining whether species or populations of species with restricted habitat distributions are more likely to recover or to disappear given random or human-induced fluctuation in numbers.

Assessing connectivity through population structure and dispersal

Traditional methods

Assessing connectivity among populations usually involves capturing an individual (either chick or an adult), and marking them (e.g. with a uniquely numbered leg-band or wing-tag, or a unique combination of coloured leg-bands) and subsequently identifying them from a distance or after capture. Specific individuals can also be tracked using radio or GPS tracking devices, reliably providing the individual’s location at points in time of interest to the investigator. While capable of providing life-history and behavioural data that is useful for conservation and management, these methods can involve unintended negative impacts to marked individuals including direct costs of the capture and handling process (Nimon et al., 1995), subsequent decreased immune response due to stress, altered sex-ratio of their offspring (Moorhouse and Macdonald, 2005) and loss of subsequent reproductive success (Saraux et al., 2011), as well as increased predation (Saunders, 1988) and mortality rates (Castelli and Trost, 1996; Saraux et al., 2011). There are often logistical issues such as the habitat and/or behaviour of some species hindering or even preventing the capture process. For example, some species are very difficult to catch (e.g. Black-throated Divers *Gavia arctica*, Gilbert et al., 1994; palm cockatoos *Probosciger aterrimus*, pers. comm., R. Heinsohn). Such welfare and logistical issues create a requirement for less invasive methods to assess dispersal and population connectivity, including assessment of vocal similarity, population genetics, and habitat connectivity. These approaches are discussed below.

Cultural variation in vocal dialects

Vocal learning through imitation has evolved in three avian taxa: songbirds (suborder Oscines) (Thorpe 1958), parrots (order Psittaciformes) (Pepperberg & Neapolitan 1988) and hummingbirds (family Trochilidae) (Sigler Ficken et al. 2000). Learned vocalizations diverge readily between geographically separate populations, giving rise to vocal dialects (Catchpole & Slater 1995). New vocal dialects are thought to emerge under similar ‘cultural’ processes to new languages in humans, i.e. through the social learning process. One mechanism, known as the side effect or “epiphenomenon” theory of dialect evolution occurs through the incorporation of copying errors, such as adding or omitting parts of the call as well as structural changes to call elements through drift (Andrew 1962; Catchpole & Slater 1995; Podos & Warren 2007). This mechanism facilitates dialect evolution where dispersal, and therefore contact is limited among localities (Slater 1989). Correspondingly, many species show greater similarity in vocal structure within a population than between distant sites, which in many cases faithfully indicates the degree of interaction (Catchpole & Slater 1995; e.g. Irwin 2000).

Population or landscape genetics

Another less invasive assessment of dispersal throughout a landscape can be achieved using genetics (e.g. Manel *et al.* 2003). Landscape genetic techniques involve tissue sampling many individuals from separate locations, sequencing their DNA at multiple homologous loci and assessing the frequency of shared genotypes across them. Genetic variation can indicate the amount of interaction between populations through the mixing of genetic information when immigrant individuals reproduce successfully in their new location. Taking tissue samples can be less invasive if taken from chicks, which are less susceptible to negative effects of capture and handling than adult birds. Newer ‘next-gen’ sequencing methods (e.g. Suchan *et al.* 2016) are even capable of returning many hundreds of loci from old or otherwise degraded DNA, for example from museum specimens, or moulted feathers found on the ground (Penalba and Keighley, unpublished data).

Connectivity modelling

Dispersal is theoretically influenced by the spatial distribution of landscape features such as habitat distribution. However elucidating any individual landscape feature’s influence on dispersal is difficult without tracking devices, which may not be feasible for reasons discussed above. Electrical circuit theory and model landscapes can be used to make predictions about movement through hypothetical resistance surfaces representing known influences of the landscape on occupancy (McRae *et al.* 2008). Movement predictions can be verified with additional data known to vary with landscape level interaction patterns (e.g. genetic or variation in learned vocalisations) enabling the models to contribute to more complete understanding of the landscape's influence on inter-population connectivity.

Predicting the viability of small populations

Software (e.g. *VORTEX*) can be used to simulate the deterministic and stochastic forces that effect the persistence of small populations, and can provide insight into the relative importance of different parameters, events or treatments. These forces are modelled as constants or as random variables following specified distributions and since random events can strongly influence population outcomes, models are typically repeated many times (e.g. 1000) revealing a distribution of outcomes given their set of parameters. Catastrophes that affect survival and reproduction can also be included in the models, as well as transmission of genes to incorporate the effect of inbreeding depression on population viability. Model outputs summarize population growth, extinction probability over the simulated time period, time until extinction as well as the average size and genetic variation in extant populations.

Thesis structure and rationale

The aim of this thesis is to increase our understanding of the meta-population dynamics of a charismatic but vulnerable rainforest edge species by developing alternative methods to inform landscape-scale conservation management.

The thesis is written in the context of each chapter being a self-contained scientific paper with its own comprehensive Introduction, Methods, Results and Discussion. Chapter 3 is published, Chapters 2 and 4 are 'under revision' and 'review' respectively, and Chapters 5 and 6 are not yet submitted.

Study species

Conservation of a small inter-connected meta-population: the case of Australian palm cockatoos.

The palm cockatoo (*Probosciger aterrimus*) is found in woodlands of New Guinea and northern Cape York Peninsula (Queensland, Australia). Typical of parrot species that have already become extinct, it is large (the largest in the family Cacatuinae), has exceedingly slow reproduction and a specific association with rainforest within a larger matrix of woodland area (Murphy *et al.* 2003). This species probably underwent distribution contractions during arid periods in the Pleistocene, and historically they were hunted for the pet trade. Current threats include chicks being taken at low numbers by subsistence hunters in New Guinea, and in Australia portions of their habitat lie within lands under lease for the mining of bauxite, the ore of aluminium. Fire frequency and intensity regulate the ecological processes that result in large, hollow trees for nests (e.g. recruitment and termite density, Murphy and Legge 2007), for which they compete with other cockatoos (Murphy *et al.* 2003). Palm cockatoos are currently recognized as 'least concern' worldwide and 'vulnerable' within Australia (IUCN criteria) but may be more threatened, especially since severe declines have been predicted for at least one major Australian population (Heinsohn *et al.* 2009).

The Iron and McIlwraith Ranges, eastern Cape York Peninsula can theoretically support a population of about 1000 individuals. However, individuals there probably cannot live long enough (over 100 years) to sustain numbers given their slow reproductive rate of 0.11 offspring per year (Murphy *et al.* 2003; Heinsohn *et al.* 2009). It remains unknown whether other populations have similarly slow reproduction, or whether this population is buffered by dispersal from other populations connected by corridors of suitable habitat. Palm cockatoos are usually found within 1 km of rainforest (Wood 1984) the largest areas occurring at the Iron/McIlwraith Ranges and northern Cape York Peninsula, but also near the gallery forest lining major waterways that run nearly the whole way across the peninsula. If palm cockatoos occupying these narrow corridors form separate, small populations, and have similarly slow reproduction, they are likely to be as vulnerable to extinction from local threats or stochastic fluctuations in numbers as the population at Iron Range (Frankham 2005; Pavlova *et al.* 2012); possibly resulting in their disappearance from Australia within 100 years (Heinsohn *et al.* 2009).

In the context of local declines and the non-uniform distribution of palm cockatoo habitat at the landscape scale on Cape York Peninsula, the key questions for their conservation are:

1. What is the structure of the meta population?
2. What aspects of the landscape facilitate or prevent interpopulation movement?
3. Can connectivity buffer low reproductive success and prevent local declines?

Traditional methods for assessing connectivity of sub-populations via dispersal potential (such as banding and tracking of individual birds) are impractical for this species due to the difficulty of capture and stress to the birds (Heinsohn pers. comm.). Because they breed infrequently and their nests take much focussed effort to locate, finding chicks for population genetics sampling is less feasible than using tissue from museum specimens or feathers collected from the ground which have less, and degraded DNA (Suchan *et al.* 2016). However, palm cockatoos are particularly vocal and have an unusually large vocal repertoire compared to other parrots. The only detailed study revealed 30 discrete call types within the Iron Range population alone (Zdenek *et al.* 2015). Their propensity to vocalise presents an ideal opportunity to trial cultural methods of assessing dispersal connectivity, alongside the other afore-mentioned alternatives of landscape genetics and connectivity modelling.

The impetus for this study was to use information about variation in palm cockatoo vocal characteristics to complement genetic variation in an assessment of inter-population connectivity, providing the information needed to answer the above three questions. This broad aims of this thesis are to investigate the interaction between cultural and genetic evolution among populations of parrots at scales relevant for their conservation, and apply any insights gained to interpretation of genetic and cultural variation among palm cockatoo populations to inform their actual conservation status in Australia.

Context statement

This thesis investigates the interaction of animal culture with meta-population processes at a spatial scale relevant for conservation management. As stated above it is written in the context of each chapter being a self-contained scientific paper (apart from Chapters 1 and 7, Introduction and Conclusion respectively) and is written in accordance with the Fenner School of Environment and Society guidelines for a Thesis by Compilation. Chapter 2 is ‘under revision’, Chapter 3 is published, Chapter 4 is ‘under review’ and Chapters 5 and 6 are not yet submitted. An outline of the rationale for each Chapter and the relationship between Chapters is provided below.

Chapter 1: In the introduction to this thesis I have discussed humanity’s fascination with parrots and the specific risks threatening their persistence in the wild. I describe the study species which is the focus of this research and outline knowledge gaps relevant to its conservation. I discuss the importance of and methods for assessing interpopulation connectivity and its role in buffering separate populations from local extinction in the context of research presented in this thesis.

Chapter 2: In the process of reviewing the literature about how culture interacts with species' ecology and population processes I outline how parrots present a special case. I discuss the importance of cultural behaviour in parrot ecology, finding it more so than in other non-human taxa. Making frequent comparison to human cultural evolution, this chapter discusses several unique cultural characteristics of parrots and whether they are generally more suitable models for the role of culture in evolution than traditional non-human model taxa such as primates and songbirds.

Chapter 3: As a step towards assessing links between behavioural variation and population connectivity in palm cockatoos, in this Chapter I quantified the geographic structural variation of contact calls within and between six major populations in Australia, as well as the extent to which frequently given call types are shared. Detailed information about vocal characteristics were already being recorded as part of an ongoing field study of palm cockatoos at Iron Range, so I visited and recorded palm cockatoo calls at five additional populations on Cape York Peninsula.

We found that palm cockatoos from the east coast at Iron Range National Park possess unique contact calls and have fewer call types in common with other locations. Based on literature reviewed in Chapter 2, we tested hypotheses about the evolution of vocal differentiation, which form the basis for the structure of the following Chapters. Unique vocal dialects at Iron Range could reflect contemporary barriers that affect interaction and sharing of vocal characteristics among populations (including elevation and restriction to sparse habitat, see Chapter 5), but other explanations are also plausible. Alternatively, dialects may have evolved historically during long-term isolation in rainforest habitat refugia (on the eastern Cape York Peninsula escarpment), and are maintained today by accurate learning of dispersing individuals (see Chapter 4).

Chapter 4: Species persistence and maintenance of genetic diversity are strongly affected by dispersal and historic distribution, especially when species depend on habitat that is non-uniform or fluctuates dramatically with changing climate. The distribution of rainforest in the Australo-Papuan region has changed dramatically, particularly since the last glacial maximum (around 20kya). To understand how pre-historic climate fluctuation effected population connectivity and genetic diversity in palm cockatoos, I provided 27 palm cockatoo samples from Cape York Peninsula (north-eastern Australia) and southern New Guinea to a collaborator for screening in 1132 single nucleotide polymorphisms (SNPs) in 342 nuclear loci and the mitochondrial ND2 gene. We also modelled their distribution at present, mid-Holocene (~6 kya) and the last glacial maximum (~21 kya). The results showed genetic differentiation among Australian palm cockatoos that can be explained by a historical, refugial distribution with admixture from subsequent gene-flow.

Chapter 5: Landscape level processes such as dispersal are often difficult to observe in real time, yet have serious consequences for the persistence of local populations and entire species. Dispersal is theoretically influenced by the spatial distribution of landscape features such as habitat, and can be inferred from interaction patterns among populations, for example with landscape genetics approaches (Chapter 4). However, elucidating any individual landscape feature’s influence on dispersal is difficult without tracking devices, which are rarely feasible for large birds that are difficult-to-capture and are easily stressed. In this Chapter, I used electrical circuit theory to predict landscape-scale palm cockatoo movement through their range in north-eastern Australia using hypothetical ‘resistance’ surfaces representing known habitat use and elevation. We verified the movement predictions with genetic (Chapter 4) and behavioural data (Chapter 3) known to vary with landscape level interaction patterns in the species.

Our results indicate that elevation and narrow rainforest corridors influence landscape-scale movement in this large, difficult-to-capture parrot species, reveal specific areas of importance for connectivity, and confirm that the declining Iron Range population is probably more isolated than others because of its geographic location.

Chapter 6: The previous chapters outlined the possibility of some (perhaps restricted) movement between separate populations of palm cockatoos on Cape York Peninsula, however it is unknown whether dispersal could be sufficient to support slow reproduction at Iron Range. Furthermore, while we have uncommonly good demographic and abundance data for the Iron/McIlwraith Ranges population from the previous field study, neither population trajectories nor abundance are known for other Australian populations which would influence their likelihood of providing support via dispersal.

In this chapter I explored the connectivity and demographic conditions that would be required for all populations on Cape York Peninsula to be stable enough to prevent local extinction. Starting population sizes were grounded in basic data about abundance that I indirectly collected during fieldwork (Chapter 3), and calculated using generalized linear modelling. I used three dispersal scenarios based on field data from similar species and the results from Chapter 5, as well as a fourth hypothetical scenario of liberal dispersal. All other parameters were carried from the previous Population Viability Analysis on this species, however reproductive success was experimentally increased outside the Iron/McIlwraith Ranges in some scenarios in case it is unusually low at the Iron/McIlwraith Ranges population.

My analysis showed that palm cockatoos are at greater risk than previously supposed. Our simulations on average show a > 50% decline in the Australian metapopulation over a three generation period, and the best case scenario involving restricted connectivity and experimentally increased reproductive success resulted in a 62.3% decline. These results support a change in conservation status from ‘vulnerable’ to ‘endangered’ based on IUCN Criterion A3c (IUCN, 2012).

Chapter 7: To conclude, I discuss the findings of this research that used information from multiple sources to understand patterns in a species’ meta-population processes. In the context of palm cockatoo conservation, I synthesise the importance of my research to conservation planning relating to maintenance of habitat connectivity, and whether specific populations require focussed attention.

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Submitted to *Emu,* received feedback 29th August, under revision for resubmission.

Chapter 2: Parrots as non-human models for cultural evolution

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Abstract

Culture in non-human animals is of great interest to investigators of evolution, especially for the perspective it provides on its evolution in humans. Theory about language evolution and technological sophistication in humans has been honed with insight from cultural characteristics like vocal learning and tool use in animals, traditionally exemplified by songbirds and non-human primates. We review the literature about such cultural characteristics in parrots asking whether they can shed more light on human cultural evolution moving forward, and discuss several reasons why they might. Firstly, the breadth of social learning in parrot vocal communication as well as use of visual gesture, and the unique importance of learning in their ecology is altogether more comparable to humans than other model taxa. Furthermore, the apparent convergence may result from human language and parrot vocal communication having similar, ecological evolutionary roots. The cognitive capacity for tool manufacture and rudimentary music also make parrots the best models for exploring evolution of a diversity of cultural behaviours. Finally, vocal dialect patterns reveal interaction between cultural and demographic processes in both parrots and humans contributing to parrots' overall suitability as models for cultural evolution in non-human animals.

Introduction

The dissemination and preservation of successful behaviour in humans (Homo sapiens) has been facilitated by the use of sophisticated language (Durham 1991; Reynolds 1993). With language, *Homo sapiens*, literally ‘wise man’, have been able to efficiently and accurately transmit knowledge and behaviour across generations at such a rate that the resulting technological advancement distinguishes *Homo* from other animals (Morell 1996). However it remains debatable whether language is inextricably linked to *Homo’s* technological advances (Hauser *et al.* 2002). Sophistication and diversification of learned behaviour appear to occur through other kinds of social learning mechanisms in non-human animals, despite the absence of language (Slater and Ince 1979; Whiten *et al.* 1999; Rutz *et al.* 2012). Although the products of animal social learning initially seem less sophisticated than *Homo*’*s*, they also undergo ‘cultural’ evolution, and whether this process is analogous to that which creates cultural change among humans has been a major question in biology.

Cultural behaviour is learned, therefore it has the potential to change due to similar processes to those involved in other types of evolution, often at rates rapid enough to be observed (Slater and Ince 1979; chaffinch Fringella coelebs song, Jenkins and Baker 1984; e.g. chimpanzee Pan troglodytes tool use, Biro *et al.* 2003; human language, Greenhill *et al.* 2010). Debate about animal culture has centred around the proportion of variation in animals’ traits owed to social learning processes, versus other modes of inheritance or adaptation (Galef 1992; Galef and Laland 2005). The major models for cultural processes in non-humans have been chimpanzees’ behavioural repertoire including tool use, and songbirds’ (order Passeriformes) vocal learning and dialects. Chimpanzees show geographic variation between populations in many complex, probably learned behaviours (Whiten *et al.* 1999; Lonsdorf *et al.* 2010), and songbirds often use complex, syntactically organised vocalisations comprising learned elements that vary geographically like languages (Krebs and Kroodsma 1980; Jarvis 2004; Podos and Warren 2007; Bolhuis and Everaert 2013). Much of our evidence for culture in non-human animals comes from examining these evolutionary models of tool use, language and music. In some cases however other taxa may provide better, more comprehensive models than non-human primates (order Primates) or songbirds.

The animal culture debate has refined the way our concept of culture encompasses both humans and other animals, and has resulted in distinct, testable hypotheses about social learning and its many adaptive functions (Fitch 2000; Byrne *et al.* 2004; Laland and Janik 2006; e.g. Bradbury and Balsby 2016). The most detailed insights into animal learning processes come from studies of captive birds (e.g. novel object handling and lid opening crows *Corvus corvax*, Fritz and Kotrschal 2008, Schwab *et al.* 2008; feeding preferences in zebra finches *Taeniopygia guttata*, Benskin *et al.* 2002, and chickens *Gallus gallus*, Nicol 2004) . However, having the capacity to learn socially does not predicate social inheritance of behaviour in wild populations. The role of social learning in establishing adaptive traits in wild populations is proving surprisingly important given detailed evidence from recent field studies (e.g. great tits Parus major Aplin *et al.* 2015). Further empirical study is essential to support any inferences made about social learning from observation of geographic variation in learnt behaviours (e.g. Laland and Janik 2006; Rutz *et al.* 2012; Kopps *et al.* 2014).

Our understanding of social learning in wild animals has advanced considerably, and we outline below how evidence from wild populations of parrots suggests an important role of social learning in the evolution of human-like capacities for language. Parrots (order Psittaciformes) are sister taxa to songbirds, major models for language evolution, and also display geographic variation in socially learned vocalisations among wild populations. However, social and foraging ecology as well as individual fitness are perhaps more strongly influenced by cultural processes in parrots. Integration of vocal learning and ecology in parrots may have accompanied evolution of impressive cognitive skills and vocal control (Pepperberg 2009), making them suitable models for language evolution and supporting the strong role of social learning in this process (Bradbury and Balsby 2016). Parrots also use gestural communication, a possible precursor of language that occurs in our sister taxa, apes (superfamily Hominoidea, Corballis 1999; Diamond and Bond 1999), though learning of gestures in wild populations has scarcely been investigated. Spontaneous tool use in captive parrots further illustrates their innovative ability as being comparable to primates and the more intelligent of songbirds (Auersperg *et al.* 2011; Auersperg *et al.* 2012; Auersperg *et al.* 2014). However, parrots differ from their sister taxa like we do from ours in an ability to produce a rhythmic beat (Heinsohn *et al.* 2017) and to synchronise action with rhythmic beat (Patel *et al.* 2009), including the only example of sound tool manufacture and use among animals (Wood 1984) which makes parrots the primary models for evolution of instrumental musical abilities.

We review the literature on cultural characteristics in parrots and discuss the following key points; (1) the importance of vocal learning for parrot communication in many contexts, as well as the use of visual gestures, make parrots the most comprehensive model for language evolution among non-human species. (2) The Psittacine capacity for tool manufacture and use, and (3) their rudimentary musical abilities make them the best models for diverse cultural processes that are analogous to those in humans. (4) Deep interactions between cultural and demographic processes in parrots are evident in their patterns of geographic variation in vocalisations. Throughout our review we identify pertinent research areas for improving our understanding of cultural processes in parrots, to maximise their value as non-human models for the evolution of cultural processes.

1. Communication

Studies of animal communication often draw comparisons with human language, and classify their degree of complexity within the context of language (Corballis 1999; Jarvis 2004; Bolhuis and Everaert 2013). Primates are the understandable models for language evolution when investigating likely precursors in the ancestors of humans. Great apes can understand relatively complex sentences (Savage-Rumbaugh *et al.* 1993), use vocalisations to refer to objects and converge vocally within groups, displaying limited learning ability (Watson *et al.* 2015). Gestural communication in apes can be learnt throughout life in the same way as humans learn language, suggesting gestural roots to language in humans (Corballis 1999). Use of sign language by a captive gorilla (*Gorilla gorilla*) (Patterson 1978) and sentence completion with pointing to symbols by a chimpanzee (Rumbaugh *et al.* 1973) display the capacity for grammatical organisation of referential elements comparable to human children (Hurford 2011). Non-human primates cannot however, learn and reproduce novel sounds (Hauser *et al.* 2002). Songbirds were primary models for language evolution in non-primates because they learn vocalisations, and their songs have syntactical organisation (Jarvis 2004; Bolhuis and Everaert 2013). Although they can learn and use referential alarm calls (Langmore *et al.* 2012), learned novel songs and song elements lack referential utility (Hurford 2011). Other taxa can also learn vocalisations throughout life and use gestural communication, perhaps greater similarity with language can be found in the vocal communication systems outside these traditional models.

Vocal learning

Reproducing learned vocalisations is a primary component of human language (Jarvis 2004; Bolhuis and Everaert 2013), and has evolved in humans since we diverged from our last common ancestor with chimpanzees (Fitch 2000). Convergent evolution of vocal learning in other species provides insights into biological constraints influencing evolution of such complex communication systems as language. In addition to humans and songbirds, vocal learning evolved independently in two other avian orders; parrots and hummingbirds (Apodiformes, González and Francisco Ornelas 2009), as well as several other mammalian orders, including bats (order Chiroptera, Esser 1994), whales and dolphins (Noad *et al.* 2000, Reiss and McCowan 1993, order Cetartiodactyla), seals (Sanvito *et al.* 2007, order Carnivora) and elephants (Poole *et al.* 2005, order Proboscidea). Parrots and bottlenose dolphins (*Tursiops truncatus*) use novel learned vocalisations (other than alarm calls) referentially, making them more suitable models for the evolution of language (Pepperberg 1990; Janik 2013). Famous tests on an African grey parrot (*Psittacus erithacus*) revealed that parrots probably have the most language-like combination of sophisticated vocal control and cognition. After learning the appropriate words, the parrot could answer complex questions vocally (Pepperberg 2009) which apes achieve by pointing at symbols (Savage-Rumbaugh *et al.* 1993). Parrots make vocal adjustments when referring to specific individuals, and respond more to their special calls when made by a mate than by others (Wanker *et al.* 1998; Wanker *et al.* 2005). Individual recognition might be used primarily for group cohesion in groups of wild parrots (e.g. Buhrman-Deever *et al.* 2008). Acoustic labels like this are also used by dolphins (Janik 2013) and involve the association of meaning with arbitrary, learned sounds independent of arousal state (e.g. Pepperberg 1990; Pepperberg 2009); a cognitive capacity regarded as a cornerstone for sophisticated language (Durham 1991).

Vocal learning shares some functions in parrots and songbirds, such as mate attraction and territory defence (songbirds, Byers and Kroodsma, 2009; Catchpole and Slater, 1995; Searcy and Andersson, 1986, e.g. vocal duets in psittacines, Farabaugh and Dooling, 1996). Parrots also use vocal learning to manage extra-pair social and possibly even foraging dynamics, and these functions have been proposed to drive more complex and human-like vocal communication (Bradbury and Balsby 2016). Here, we make the additional points that such broad integration between cultural processes, including vocal learning, visual communication, tool use and music, with ecology and mating dynamics is unique to parrots and supports their status as a primary model for cultural evolution in animals.

Studies on both wild and captive parrots show that vocal imitation helps them to manage their social relationships, both within and outside the pair bond, suggesting that vocal learning is deeply integrated with important biological functions such as mating and group organisation (Farabaugh and Dooling 1996). Parrot contact calls are often learned from conspecifics, and resemble most closely the calls of mates or social partners (Farabaugh and Dooling 1996; Wright 1996; Baker 2000; Hile *et al.* 2000; Baker 2003; Bradbury 2004; Hile *et al.* 2005; Kleeman and Gilardi 2005). Studies on captive male budgerigars (*Melopsittacus undulatus*) have shown they use vocal mimicry to strengthen their strong pair bonds (Hile *et al.* 2000; Hile *et al.* 2005; Moravec *et al.* 2006; Moravec *et al.* 2010). Parrots may also use vocal learning to coordinate the large groups within which they forage. Groups of female budgerigars imitate each other for social integration and individual labelling purposes (Dahlin *et al.* 2014), but they match vocalisations more slowly than males (Hile and Striedter 2000). Across age-classes, wild juvenile and adult keas (*Nestor notabilis*) have call cultures specific to their separate social environments (Bond and Diamond 2005), which share similarities with ethnic or age related sub-culture dialects in humans (Pika *et al.* 2003) (Stenström and Jørgensen 2009).

Any differences in vocal learning (and corresponding differences in neural mapping, Chakraborty *et al.* 2015) between parrots and their songbird sister taxa may result from contrasting foraging behaviours (Bradbury and Balsby, 2016). Rather than defending discrete territories with quality food sources as songbirds often do (Catchpole and Slater 1995), parrots typically forage in fission-fusion groups throughout overlapping home ranges (Juniper and Parr 1998). Parrots specialise on complicated foods such as unripe seeds with toxins, or hard shells that are difficult to penetrate. To maximise nutritive value, these require time to digest, mineral supplements to bind toxins, or manual expertise. Parrots avoid poisoning by being highly neophobic (Mettke-Hofmann *et al.* 2002; Fox and Millam 2007), and might rely on social information and learned vocal cues to learn what, when and how to exploit these marginal food sources over greater geographic areas than songbirds. Thought to live in dispersed and nomadic groups, the ancestors of humanity would have faced similar ecological challenges. Pressure to gain knowledge about sparse food or water sources from neighbouring groups may have contributed greatly to evolution of their sophisticated social learning and communication capacities (Aiello and Dunbar 1993).

Other primates also exploit social information when foraging (King *et al.* 2011), with evidence from apes that vocal learning capacities enhance social foraging (Galef and Giraldeau 2001). For parrots foraging in canopies, the limited visual contact between individuals may have led to selection for imitation, referential signaling and individual recognition. The advantages of sophisticated vocal communication in environments with poor visibility has been shown in other species, for example the coordination of group foraging by dolphins in murky water (Reiss and McCowan 1993; Janik 2013).

Dolphin groups can show local specialisations in foraging behaviour which are likely to be socially learned (Kopps *et al.* 2014). Similar learnt specialisations probably exist among parrot groups, which authors have suggested might be reflected in geographic variation in vocalisations (Wright *et al.* 2005).

By delivering fitness benefits through improved pair-bonds, social integration and perhaps also information transmission, vocal learning is as necessary to parrot communicative systems as it is for humans. Parrot vocal learning is remarkable, but to fully evaluate their suitability as cultural analogues to humans we cannot overlook another potentially cultural trait in their communicative repertoire, visual communication with gesture.

Visual communication

Visual signals often supplement vocalisations in the communication systems of humans (Goldin-Meadow 1999), primates (Corballis 1999), parrots (e.g. Merton *et al.* 1984, Serpell 1981, Wirminghaus *et al.* 2000, Saunders 1974, 1983) and other birds (Prum 1990; Kennedy *et al.* 1996; Dalziell *et al.* 2013). Visual communication can be highly complex and informative. Human symbolic gestures can function like language independently of speech, express unspoken thoughts and be understood by untrained individuals (Goldin-Meadow 1999). In our species, making and understanding symbolic gestures shares a common neural processing system with spoken language (Xu *et al.* 2009). Apes are capable of understanding relatively complex human language and responding with symbolic gestural communication (Savage-Rumbaugh *et al.* 1993), leading to the hypothesis that gesture forms a stepping stone towards complex vocal language in humans (Corballis 1999). Communicative visual gestures, like learned vocalisations, may be transmitted socially and display cultural variation as they do in humans (e.g. Brodsky 1987).

Geographic variation in communicative displays within species supports cultural diversity in chimpanzees (Tomasello 1994; Whiten *et al.* 1999) and might be socially learned in other apes (Pika *et al.* 2003, 2005). Great apes are the best models so far, perhaps because possession of free limbs with arms, hands and fingers improves their gestural dexterity. However, we need not limit investigation to systems that morphologically resemble humans. For example, cockatoos' erectile crests enhance their capacity for body language beyond that of other birds. Parrots, like humans use visual gestures and displays to supplement their vocal repertoires (e.g. Diamond and Bond 1999), although we do not yet know whether visual signals are learned alongside vocalisations or how important they are in parrot communication. Advances in the field of visual behaviour analysis using digital recordings might facilitate detection of variation in visual communication systems among conspecific populations as a first step to identifying cultural variation (e.g. Peters *et al.* 2002). Historically, courtship displays have been assessed for usefulness as phylogenetic characters (Lorenz 1941, e.g. Prum 1990, de Queiroz and Wimberger 1993, Kennedy *et al*. 1996). Visual display variation often aligns with phylogenetic relationships (Lorenz 1955; Prum 1990; Kennedy *et al.* 1996; How *et al.* 2009), however caution is advised when drawing phylogenetic inference from behaviour alone as learning may constrain behavioural phenotype (Tinbergen 1959; Freeberg 2000; Slabbekoorn and Smith 2002).

Visual communication adds another avenue to explore cultural characteristics in parrots. This, combined with the importance of vocal learning to parrot ecology, strengthens the argument for parrot communication as an informative comparison to the complexity of human communication and language evolution. Parrots' capacity for tool manufacture and use further adds to the diversity of cultural characteristics they display, perhaps earning them equal status with apes as human cultural analogues.

2. Tool manufacture

Humans are fascinated by tool manufacture in other taxa because it defines our genus; *H. habilis* (handy man) is recognised as the earliest *Homo* species because their tool construction was markedly more sophisticated than the *Australopithecines'* before them (Morell 1996). The most famous example of tool manufacture in non-human species occurs in *Homo's* closest extant relative, *Pan* (chimpanzees), which (among other examples) manufactures stick tools to facilitate foraging for ants (Goodall 1964; Whiten *et al.* 1999). Tool manufacture has been documented in two phyla (Arthropoda and Chordata) for many functions (e.g. to aid foraging, physical maintenance, mate attraction, nest construction and predator defence, Bentley-Condit and Smith 2010). Studies have provided insight into cognitive demands of tool manufacture (e.g. corvid passerines and primates reviewed in Emery and Clayton 2004) and its cultural transmission (e.g. Biro *et al.* 2003; Rutz *et al.* 2012; Kopps *et al.* 2014). Tools in birds are best defined as an object used to extend the body's function that is held directly in the foot or mouth; for example as probes, hammers, sponges or scoops (Lefebvre *et al.* 2002). Parrots have few examples of tool manufacture and use compared with primates and songbirds (Bentley-Condit and Smith 2010) which is surprising given their cognitive capacity (Lefebvre *et al.* 2004; Pepperberg 2009), however this may to some extent reflect the adequacy of their powerful mandibular toolkits for most tasks, or difficulties with making observations in the wild which are considerable compared to habituated groups of primates. Parrots use tools spontaneously to solve problems related to foraging, and might be the only non-human taxa to use manufactured tools for display (Heinsohn *et al.* 2017), a function formerly thought to be unique to humans (Fitch 2006).

Tool use in parrots: spontaneous or cultural?

The first observation of a tool using parrot was made by Alfred Russel Wallace (1869) during his travels to the Aru islands. He observed a palm cockatoo (*Probosciger aterrimus*) manipulating a kanary-nut using a leaf to aid its grip.

> *... it takes hold of the nut with its foot and, biting off a piece of leaf, retains it in the deep notch of the upper mandible, and again seizing the nut, which is prevented from slipping by the elastic tissue of the leaf, fixes the edge of the lower mandible in the notch, and by a powerful nip breaks off a piece of the shell.*

Wallace (1869) also observed captive hyacinth macaws (*Anodorhynchus hyacinthinus*) using a similar technique to improve their grip on slippery food with a leaf in the beak. He noted that the

> *technique would keep the mandible from slipping on the slippery stones of fruits known to be eaten by Hyacinths in the wild.*

Other than hyacinth macaws and palm cockatoos, very few natural cases of tool use have been documented among wild parrots. Sometimes individuals in captivity demonstrate spontaneous tool use, illustrating ample cognitive capacity for tool use tasks (Borsari and Ottoni 2005; Auersperg *et al.* 2011; Auersperg *et al.* 2012). For example, keas were first observed to use tools as part of an experiment involving multiple ways to access a puzzle box for rewards (Auersperg et al. 2011) and a single African grey parrot has been observed using a splinter tool held in the foot to scratch the back of its head (Janzen *et al.* 1976). Whether tool use behavior undergoes cultural transmission in wild parrots remains to be seen. Social interactions that contribute to learning are often difficult to observe in the wild. Even evidence of cultural processes creating variation in nut cracking behaviour in a wild population of chimpanzees required 16 years of longitudinal study of identifiable individuals and three different approaches (Biro *et al.* 2003). Tool use in the foraging context might be less relevant to the study of culture in parrots than in songbirds and primates because parrots have impressive mandibular toolkits for accessing difficult foods (eg hard seedpods), so might have less need to develop novel solutions while foraging.

A very small number of studies in captive populations have tried to determine whether tool use behaviour undergoes cultural transmission processes in parrots. Cultural inheritance of nut gripping with leaves in the beak remains uncertain for captive hyacinth macaws (Borsari and Ottoni 2005) and has not been investigated further in palm cockatoos. Goffin's cockatoos (*Cacatua goffini*) were not known to use tools before recent observations of a captive male making and using splinter tools, which were held in the beak to rake in out-of-reach objects (Auersperg *et al.* 2012). Male onlookers emulated the same outcome by making and using their own tools in the same way, which suggests that social transmission of tool use behaviour is possible in this species (Auersperg *et al.* 2014). The male bias may be due to sexual selection, if tool use is selected by females of the species as a display of intelligence.

While tool use is rarely observed in wild parrots, captive individuals demonstrate ample capacity for spontaneous tool use in the foraging and perhaps also grooming contexts. Tool use and manufacture appears to be socially transmissible in some examples in captive parrots, yet controlled experiments in more species are required to elucidate this process' generality among the parrot order. Further experimentation or at least observation of tool use and manufacture in wild parrots is needed to assess social transmissibility, but initial results suggest this capacity, among others, will contribute to their standing as the foremost models for cultural processes in non-humans. The particular capacity that sets parrots apart is their sensitivity to rhythm in music;

something outlined as an important stepping stone to evolution of language by Darwin (1881).

3. Musical parrots

As with the search for evolutionary models for language, the uniquely human capacity for musical expression has been broken down into components for more informative comparison to non-human animals. A summary is given by Bispham (2006) and although a mosaic of different abilities appear to be required (Dunbar 2012), of primary importance is the capacity to perceive temporally organized events. This ability mirrors the hypothesized prerequisites for language evolution (Fitch 2000), and interestingly aligns with Charles Darwin’s hypothesis that language evolved via a “musical protolanguage” (1881). It remains unclear whether music and language have common evolutionary roots. The adaptive advantages of language seem clear, whereas those of music are less so and remain a debated topic (Miller 2000; Fitch 2006; Dunbar 2012).

Hypotheses to explain the evolution of human musical ability include social selection, sexual selection and that it evolved as a byproduct of vocal learning. The emotional effects of music may stem from an earlier group bonding function, an idea linked to the hypothesis that music and language evolved to replace grooming as group size increased (Dunbar 2012). Musical ability might otherwise be under selection through mate choice for the valuable characteristics it requires as part of courtship displays, including physical coordination, cognitive health and memory (Miller 2000). Alternatively, synchronization of action and rhythm (a necessary component of musical ability) may have evolved as a side effect of vocal learning ability (Schachner *et al.* 2009). The latter idea has its basis in the neural structures of species that can learn novel vocalisations; overlapping control centers for audio perception and motor control are plausible requirements for synchronization of action and rhythm (Jarvis 2004). It is even possible that all three scenarios reinforced one another in humans to bring about our unique musicality; the pronounced vocal learning abilities and sociality of parrots also present some of these hypothesized prerequisites.

Parrot rhythm and sound tools

The ability to produce, or synchronise movement to a rhythmic beat is rare in animals and is best known in parrots (e.g. synchronisation in sulphur crested cockatoos Cacatua galerita, Patel *et al.* 2009; African greys, Schachner *et al.* 2009; production in palm cockatoos, Heinsohn *et al.* 2017). Hypotheses to explain the origin of this ability in parrots include the possibilities that it is a by-product of vocal learning, or the outcome of sexual selection.

Parrots are well known vocal learners, and this ability has been argued to support the hypothesis that music and language evolved in tandem as a by-product of vocal learning (Patel 2006). However, further evidence from other vocal learning taxa is required for conclusive support of the by-product hypothesis.

The sexual selection hypothesis states that conspicuous sex differences in animals (e.g. body size, ornamentation) may have evolved to facilitate choice and alleviate competition for mates (Darwin 1881). Sexual selection might drive the only known non-human example of musical expression through the use of a sound tool; drumming in Australian palm cockatoos. Males manufacture drum sticks and drum on their nest hollows as part of their courtship displays (Wood 1984). Like human music, drumming is rhythmic and shows individual styles (Heinsohn *et al.* 2017). Although the links between fitness and drumming are yet to be explored, the sex specificity of the trait, its use when females are present and individuality in drumming styles all suggest a role for sexual selection (Heinsohn *et al.* 2017). Tool use occurs among intelligent animals which have adapted cognitively to the demands of their environment (Emery and Clayton 2004). Cognitive ability might be a particularly valuable trait for survival in parrots given their social pressures and dietary challenges. Drumming using a manufactured tool could be an honest display of cognitive ability, resulting from sexual selection for cognitive traits (Miller 2000; Heinsohn *et al.* 2017). However whether drumming is culturally transmitted, and can therefore provide a model system for cultural evolution, is not yet known.

Convergent evolution of musical ability (or at least its precursors) in a number of species of parrots support the hypotheses that human musical ability could have evolved through sexual selection or as a by-product vocal learning ability. Although there remains scope for further investigation across many taxa, the parrot group is perhaps most suitable for more detailed tests of these hypotheses in the future. Despite strong variation in musical expression among human cultures, its broad occurrence suggests the capacity is innate. Whether musical displays in animals show geographic variation due to similar cultural processes is an intriguing avenue for future work, and much about the cultural manifestation of learned vocalisations has already been learned from geographic variation among wild populations.

4. Geographic variation and change over time

Language is a highly variable cultural characteristic among humans and although it can be learnt throughout life it is most commonly learnt by offspring from their parents. The predominant theory about language diversification is that errors in learning cause passive modification with descent, contributing to geographic variation where interaction between distant groups is more limited than neighbouring groups (Creanza *et al.* 2015). In the search for greater insight into language evolution, discrete vocal differences (dialects) among separate animal populations have received much attention, mostly among songbirds (reviewed in Podos and Warren 2007). Wright and Dahlin provide a detailed review of the field as it relates to parrots (manuscript in preparation), but here we outline how the processes behind vocal geographic variation in parrots support their case as leading models for cultural evolution in humans.

Dialect modification by learning is possible where dispersal is constrained, and therefore contact between localities is limited (Slater 1989), the same logic allowed inference about demographic movements from dialect patterns in humans (Creanza *et al.* 2015). Authors argue that geographic variation in animal vocal characteristics due to learning represents cultural variation akin to human languages, unless attributable to other processes (e.g. variation due to habitat) (Catchpole and Slater 1995; Podos and Warren 2007). Many parrots show greater similarity in vocal structure within a population than between distant sites (e.g. orange-fronted conures *Aratinga pertinax*, Bradbury *et al.*, 2001; keas, Bond and Diamond, 2005; and palm cockatoos, Keighley *et al.* 2016; but not thick-billed parrots *Rhynchopsitta pachyrhyncha*, Guerra *et al.*, 2008), contributing to similar theories of evolution being a result of learning in parrots and humans (Andrew 1962; Catchpole and Slater 1995; Podos and Warren 2007). Wild chimpanzee populations also display geographic variation in vocalisations by actively differentiating their vocalisations from neighbouring groups (Crockford *et al.* 2004) while converging on similar vocal characteristics within groups (Marshall *et al.* 1999; Watson *et al.* 2015).

In parrots, dialects may be maintained through time either if the vocally divergent populations have little contact, if the species is sedentary (e.g. Kleeman and Gilardi 2005), or if local vocalizations are learnt especially quickly and accurately by immigrant birds (e.g. Salinas-Melgoza and Wright 2012). Dialect boundaries survived for thousands of years regardless of admixture in the western Australian ring-necked parrot *Platycercus zonarius,* even following reunification and hybridisation of morphologically divergent subspecies (Baker 2008). Not only can migration affect vocalisation structure, vocal incompatibility may enable ongoing genetic divergence among vocally distinct varieties. Illustrating this point are the crimson rosella *Platycercus elegans* species complex in south-eastern Australia (Ribot *et al.* 2012), and the greenish warbler *Phyllloscopus trochiloides* ring species around the Tibetan plateau (Irwin 2000).

The developmental period at which vocal learning occurs in parrots may determine whether dialect boundaries are distinct (Wright 1996; Baker 2003; Ribot *et al.* 2009) or gradual (Bradbury *et al.* 2001; Bond and Diamond 2005). Gradual change in vocalisations over distance may be characteristic of mobile fission-fusion flocks, which require constant adjustment for individual labelling or adaptation to a highly plastic social environment (Bradbury *et al.* 2001; Bradbury and Balsby 2016). Distinct vocal dialects often do not correspond with genetic population structure, which has been interpreted as evidence of life-long learning encompassing movement of birds throughout their life (Wright 2005, Baker 2008, but see Ribot *et al.* 2012). However, distinct dialects may instead result from a sensitive period for learning in early life that extends only long enough for individuals to disperse and assimilate into their new population (e.g. Salinas-Melgoza and Wright 2012).

The consensus among investigators is that vocal characteristics in parrots display variation due to learning, instead of being adjustments to specific ecological conditions (although diet remains to be investigated). Landscape scale variation in vocal characteristics seem to be effected by life history scenarios and learning regimes in predictable ways. For example, in species that learn vocalisations early in life like humans, and have short distance dispersal, we see sharp boundaries resembling those between languages (e.g. yellow-naped amazons Salinas-Melgoza and Wright 2012). It appears that such strong links between vocal learning, social and demographic processes in parrots may allow inference about one to be made from the other.

Applications of cultural information

Behavioural comparisons across populations can offer insight into demographic processes and reveal new behavioural diversity and peculiarities. This extra information is of both intrinsic and conservation value and offers particular benefit for parrot conservation because they are difficult to study in the field. Correspondence between genetic and language data across worldwide human populations has led to important discoveries regarding the evolution of language and demographic movements (Creanza *et al.* 2015). For example, human genetic and language divergence patterns are qualitatively correlated (Cavalli-Sforza *et al.* 1988) with language boundaries a likely cause of the genetic distinction (Barbujani and Sokal 1990). Similar relationships between vocal and genetic characteristics have been observed in songbirds (e.g. Irwin 2000) and parrots (e.g. Ribot *et al.* 2012).

The geographic pattern of vocalisations is often important for inferring crucial aspects of a species' ecology at the landscape scale when that information is difficult to acquire directly (Laiolo 2010). Geographic variation in behaviour of the St Lucia parrot (*Amazona versicolour*) suggests that it is relatively sedentary, since vocal variation was maintained over distances of less than 100km, and also because the species has not reclaimed a historical part of its range (Kleeman and Gilardi 2005). Distinct vocal dialects may also be maintained by the dual processes of short range dispersal by juveniles and accurate vocal learning in yellow-naped amazon parrots (*Amazona auropalliata*) (Salinas-Melgoza and Wright 2012). Translocated adult yellow-naped amazons do not integrate vocally or socially, which is valuable information when considering re-introducing captive reared individuals to wild populations. In contrast, gradual vocal changes might be more characteristic of mobile flocks with overlapping home-ranges (e.g. orange-fronted conures, Bradbury *et al.* 2001). Knowledge of the underlying processes controlling vocal dynamics in well-known species that still occupy much of their historical range are important not only for their own species information, but also as there may be similar processes in species that are more difficult to study, or that only occupy remnants of their historical range, or for which wild geographic variation is either lost or limited.

Most studies on parrot calls focus on only a small fraction of their repertoire (but see Guerra *et al.* 2008; Zdenek *et al.* 2015; Keighley *et al.* 2016) however the inferred geographic patterns of variation may vary between calls with different functions (e.g. Farabaugh and Dooling, 1996; Beebee, 2002; Baker and Gamon, 2006; Kroodsma 1996, Nelson 2016). Therefore, it is crucial for studies to explore differential geographic variation in calls depending on their function to obtain a more complete picture of vocal culture and the underlying demographic processes (e.g. songbirds Byers and Kroodsma, 1992; Nelson 2016, and parrots, Guerra *et al.* 2008). Given the challenges of sampling a large proportion of a bird’s repertoire, and further difficulties inferring for what reason call types are used, taxa such as parrots with small vocal repertoires (Bradbury 2004) are the most promising model. It may be possible to garner social or spatial information pertaining to the communication environment associated with specific call types in parrots (Baker 2011; Keighley *et al.* 2016), or even the status of populations based on vocal data (e.g. Baker 2008).

Many parrot species are threatened in the wild due to habitat fragmentation (Olah *et al.* 2016a), so awareness of the extent of dispersal and genetic connectivity among populations is vital for conservation efforts. Learning has a large impact on acquisition and maintenance of vocalisations in parrots (discussed above) making it unreasonable to use vocal data as a surrogate for genetic connectivity and population dynamics without additional data. However, behavioural data (including vocalisations) are important when planning wildlife reserves, re-introduction schemes or conservation monitoring programs (e.g. implications for social integration, Guerra *et al.* 2008, Saranathan *et al.* 2007) as behavioural incompatibility may affect individual survival in the short term (e.g. social isolation Salinas-Melgoza and Wright 2012). Behavioural data is important above the individual level as an indicator or population viability and for the preservation of diversity (Laiolo *et al.* 2008; e.g. loss of diversity, Baker and Gammon 2006). Documentation of unique behaviours can also add to the conservation value of particular sub-species or populations (Kidjo *et al.* 2008; Keighley *et al.* 2016).

Considering geographic variation in species' cultural characteristics is increasingly recognised as important for conservation management, and is especially useful when combined with life history and demographic information. The relevance of such information for management is further increased in species with strong integration between ecology and cultural characteristics, such as parrots.

Conclusion

We aimed to discuss the nature of cultural characteristics in parrots and how understanding their evolutionary and ecological context in wild populations can benefit our understanding of cultural evolution in humans. The large body of evidence for cultural processes influencing the use of vocal communication in parrots suggests culture is perhaps as embedded in parrot communicative systems as it is for humans. The referential utility and prolific use of learned vocalisations in parrot communication bears better resemblance to language than any other currently known animal communication system. Further, examples of gestural communication and social learning of tool use, especially for music, improve further their comparability with humans to rival even that of traditional model species.

Evidence from wild parrots has been hard-won, and compared to primates (e.g. Biro *et al.* 2003), songbirds (e.g. Aplin *et al.* 2015) and dolphins (e.g. Kopps *et al.* 2014) further exploration of social transmission among wild populations of parrots will be similarly if not more difficult. A recent review highlights specifically the processes of obtaining and communicating knowledge about the complex or ephemeral food sources on which parrots often specialise as pertinent for further exploration of the evolution of language-like complex vocal communication systems (e.g. Bradbury and Balsby 2016). Presenting challenging novel foods to flocks of individually identifiable parrots and observing transmission of specialist knowledge might provide insight into the communicative content of vocal and gestural activity.

Gestural communication is understudied in parrots, and yet to be confirmed as socially learned, as is tool use (especially for music) in wild parrots. Experimental designs for testing social learning of vocalisations may be adapted for gesture in captive systems. Continued investigation of social learning and geographic variation in vocalisations, tool use and visual gestures among wild populations will allow us to gauge integration of cultural mechanisms in the foraging, social and sexual ecology of wild parrot populations, for more complete comparisons with humans and other animals.

Acknowledgements

This research is supported by an Australian Government Research Training Program Scholarship. We wish to thank Xenia Weber for helpful comments on the manuscript, and Christina Zdenek for valuable thoughts and discussion.

Author contributions

This review was conducted by M.V.K. to inform further investigation under the aims of this thesis. R.H. encouraged expansion of the chapters' scope and alongside N.E.L. contributed substantial edits to the manuscript.

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Bioacoustics, 2016
Vol. 26, No. 1, 91 – 108, http://dx.doi.org/ 10.1080/09524622.2016.1201778
Received 15 Mar 2016, Accepted 31 May 2016, Published online: 24 Jun 2016

Chapter 3: Geographic variation in vocal characteristics of Australian palm cockatoos (*Probosciger aterrimus*).

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Abstract

Vocal dialects have been well studied in songbirds, but there have been fewer examples from parrots. The Australian population of palm cockatoos (*Probosciger aterrimus aterrimus*) from Cape York Peninsula in far north Queensland has an unusually large vocal repertoire for a parrot. Most calls are made during their unique display ritual, which also includes a variety of postures, gestures, and the use of a manufactured sound tool. Here we quantify the geographic structural variation of contact calls within and between six major populations of palm cockatoos in Australia, as well as the extent to which frequently given call types are shared. We found that palm cockatoos from the east coast (Iron Range National Park) possess unique contact calls and have fewer call types in common with other locations. This may have resulted from their long term isolation in rainforest habitat refugia. Such variety in vocal traits presents a rare opportunity to investigate the evolutionary forces creating behavioural diversity in wild parrots. This is also a step towards assessing links between behavioural variation and population connectivity, which is important information for determining the conservation status of palm cockatoos.

Introduction

Observing and analysing geographical patterns in genetics, morphology or behaviour can give insights into evolutionary processes that are difficult to observe in real time. Contemporary geographic variation in behaviour can sometimes reflect historic evolutionary changes within species and is especially informative where social learning and cultural processes lead to faster evolution (e.g. Jenkins 1978) The learned vocalizations of birds diverge readily between geographically separate populations, giving rise to vocal cultures or dialects (Catchpole and Slater 1995). Vocal learning through imitation has evolved in three avian taxa: songbirds (Suborder Oscines) (Thorpe 1958), parrots (Order Psittaciformes) (Pepperberg and Neapolitan 1988) and hummingbirds (Family Trochilidae) (Sigler Ficken *et al.* 2000). In these groups, geographic variation in vocalizations can arise as a side effect or 'epiphenomenon' of learning through the incorporation of copying errors, such as adding or omitting parts of the call as well as structural changes to call elements through drift (Andrew 1962; Catchpole and Slater 1995; Podos and Warren 2007). This mechanism facilitates dialect evolution where dispersal, and therefore contact is limited among localities (Slater 1989). Correspondingly, many species show greater similarity in vocal structure within a population than between distant sites (Catchpole and Slater 1995; e.g. Irwin 2000). Dialects may be maintained through time either if the vocally divergent populations have little contact, or if vocalizations are learnt especially quickly and accurately by immigrant birds through a process called 'social adaptation' (e.g. Salinas-Melgoza and Wright 2012). Social adaptation refers to an enhanced ability to learn new vocalizations throughout adulthood which provides reproductive and territorial benefits to immigrant birds (e.g. parrots: Farabaugh *et al.* 1994; Catchpole and Slater 1995; Farabaugh and Dooling 1996).

Many studies have explored differences in vocalizations between localities to understand how dialects are formed (reviewed by Podos and Warren 2007), which in turn may inform our understanding of connectivity between localities (reviewed by Laiolo 2010). Connectivity can be inferred where dialects arise as an epiphenomenon of learning because decreasing similarity occurs between sites with decreasing connectivity. In this way geographic variation in vocalizations could be indicative of how birds disperse through fragmented habitat, potentially making the study of vocal variation a non-invasive tool for assessment of population connectivity (Kroodsma 1996; Laiolo 2010; Pavlova *et al.* 2012).

By contrast, less information about ongoing population connectivity may be acquired where vocalizations are learned through social adaptation because individuals can imitate local call types after dispersal to their breeding population (Laiolo 2010). However social adaptation may preserve geographic patterns in vocalizations that originated from historical meta-population structure, despite contemporary population mixing (Wright *et al.* 2005; Baker 2008; Salinas-Melgoza and Wright 2012).

Here we quantify geographic variation in the calls of an Australian parrot, the palm cockatoo *Probosciger aterrimus aterrimus*, and assess call variation as a tool for measuring population connectivity across its Australian range. A previous population viability analysis (Heinsohn *et al.* 2009) at a single site on Cape York Peninsula (CYP) (Iron Range region of the east coast, see Figure 1) suggested that the population was in steep decline and led to palm cockatoos in Australia attaining ‘vulnerable’ status under IUCN criteria (Department of the Environment 2015). However further studies are required, especially on the connectivity between the Iron Range and other populations, to evaluate fully the conservation status of the entire Australian meta-population of palm cockatoos (Heinsohn *et al.* 2009). Behavioural assessments of connectivity could be particularly important for this species because traditional methods of assessing population level dynamics (such as capture and marking of individuals and genetic sampling) are hampered in palm cockatoos because of the difficulty of catching parrots in remote locations (Murphy *et al.* 2003; Zdenek *et al.* 2015).

Palm cockatoos are restricted to New Guinea and some of its offshore islands, as well as northern CYP (Queensland, Australia). On CYP they are usually found within 1km of rainforest (Wood 1984) but it is unknown whether populations associated with discontinuous rainforest patches are connected. Palm cockatoos have a slow life history strategy with females laying a single egg on average every 2.2 years (Murphy *et al.* 2003). Australian palm cockatoos are non-flocking and form monogamous pairs with nest site fidelity. Pairs defend territories containing a number of hollow trees used for nesting and displays (Murphy *et al.* 2003), typically found in savannah woodland adjacent to rainforest including gallery forest that lines major waterways. Rainforest on CYP is naturally fragmented; its distribution adhering closely to drainage patterns (gallery forest) throughout most of CYP. Otherwise small areas of suitable soil and topography create patches of rainforest among sclerophyl woodland (Webb and Tracey 1981), which expand and contract according to fire frequency and intensity (e.g. Iron Range; Russell-Smith *et al.* 2004). The largest patch of rainforest extends south on the east coast from Iron Range National Park to the McIlwraith Ranges (Figure 1). Palm cockatoos found throughout this region are thought to form one population, but it remains unknown whether the gallery forest corridors of the Wenlock and Archer Rivers (both flowing west of the Great Dividing Range), provide habitat that connects populations across CYP.

Palm cockatoos have an unusually large vocal repertoire compared to other parrots. The only detailed study to date showed 30 discrete call types, or 'syllables' within the Iron Range population alone. A syllable was defined following Zdeneck *et al.* (2015) as 'either a single element (continuous line on the spectrogram; Catchpole and Slater 1995), or a cluster of elements that always occur together in a cohesive unit and in a distinct order with a maximum of 0.2 seconds between them'. The syllables were shown to be 'mixed and matched' to create more complex vocalizations. The degree of variation and whether or not other populations in Australia and New Guinea have similarly large vocal repertoires, remains unknown.

Methods

Study sites

Recordings were made between June-October 2013, and from July-November 2014, corresponding with the time of year with most vocal activity and including the breeding season (palm cockatoos in the Iron Range lay eggs throughout eight months of the year) (Murphy *et al.* 2003). A total of 232 putative individuals were recorded over 44 sites across CYP. The sites were spread across the following major known populations: Iron Range National Park is on the eastern side of CYP, the Steve Irwin Wildlife Reserve is on the western side of CYP, Piccaninny Plains Wildlife Sanctuary (Archer River), and Moreton Telegraph Station are both on major river systems inland on CYP, and the free-hold lands around Bamaga are on the northern tip of CYP (Figure 1). An additional site was used at the southernmost point of the birds' recorded range near Musgrave Roadhouse (Figure 1). The distance between populations ranged between 50km and 402km. Within each population, sites were chosen based on accessibility of suitable habitat (Murphy *et al.* 2003), and occupation by palm cockatoos. Most sites had a dirt road with infrequent vehicle traffic, though some were only accessible by foot. Distances between sites ranged from 1.5 to 40.7km, and each site was visited at least once in the morning and once in the afternoon on a minimum of two occasions each year, coinciding with longer stays at each population (except those at Bamaga and Musgrave). The Bamaga sites were only visited in 2014, and the single Musgrave site was only visited one morning in 2014. Each site was visited a mean of 3.9 ± 4.3sd times, and we ceased visiting sites once we acquired approximately 15 minutes of calling behavior, but site visits were resumed once returning to the population on a separate occasion. Data from Iron Range were collected by CNZ during the 2014 season, while the other populations were visited sequentially by MVK and volunteer research assistants in 2013 and 2014.

Recordings

In total we collected 34 hours of non-continuous recordings from unmarked, wild palm cockatoos at a distance of 20-60m. Males and females were easy to distinguish for trained observers by relative beak size, males having the larger beak (Higgins 1999). Recordings of both sexes were used in this study even though males tend to vocalize more (Zdenek *et al.* 2015). Birds that had calls recorded but were not seen were included if the observer was confident of attributing calls to the correct individual based on the territory. Where there were multiple callers, caller ID was annotated verbally by the observer in the field or determined visually later if video footage was available.

As individual birds were not marked, individuals of the same sex were differentiated based on distance; we used a minimum of 1.5km between recorded individuals (also the minimum distance between sites) as a proxy for individual identification. This distance was used because, as hollows are frequently defended against conspecific intruders, it is unlikely for a pair to defend multiple hollows across this distance in a single morning or afternoon. However, because pairs defend multiple hollows within their territory (Murphy *et al.* 2003), misidentification may have occurred on some occasions across adjacent territories. We could not distinguish between individuals recorded at the same location on different occasions if they were the same sex.

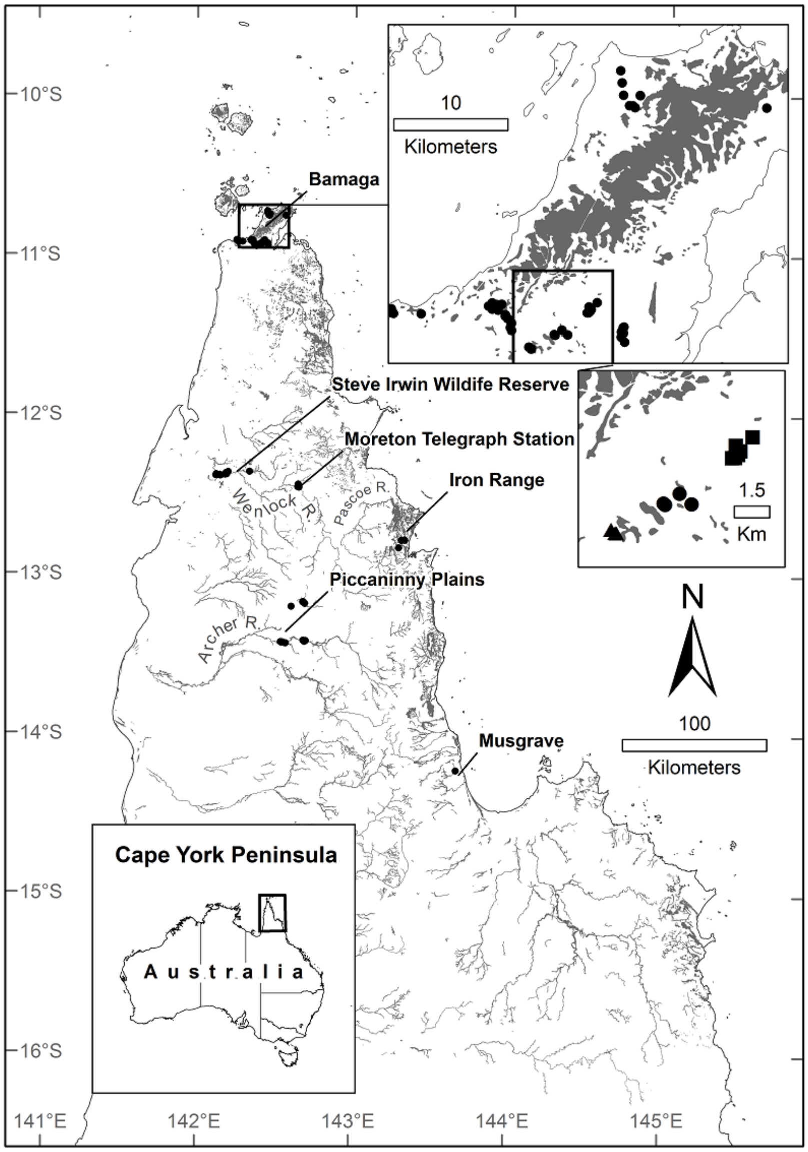

Figure 1. Palm cockatoo population study locations, showing distribution of rainforest and gallery forest corridors in grey. The Bamaga population is enlarged, with another inset illustrating three separate recording sites with different shapes.

Recordings from the Iron Range were made with a Canon EOS 5D Mark III camera with a 400mm EF 5.6L IS USM lens and a directional Rode VideoMic pro external microphone (with a windshield) set to 0dB gain boost. All other recordings were made using a Canon 600D DSLR camera with 100-400mm EF 4.5-5.6L IS USM lens and Beachtek DSA-SLR audio adapter connected to a Sennheiser ME66/K6 shotgun microphone (with windshield). The adapter was set to mono, and automatic gain control was turned on with a gain boost of 15dB. For both equipment sets the HD video recording function of the camera was used to make recordings from which audio data were isolated using Xilisoft video conversion software. Due to variation in recording distance, no measurements involving amplitude were made at the analysis stage. To test comparability between the equipment sets, recordings of four birds at Iron range were made using the equipment used at the other sites, and were then tested for statistical correlation at the analysis stage.

Individual birds were followed on foot and recorded for as long as possible (mean ± SD = 4 min 43 s ± 3 min 14 s, totaling to means of 43 min 57 s ± 48 min 30 s per site), and if birds appeared disturbed by an observer’s presence data collection ceased and the area was vacated. Recordings were not made in excessively windy weather or during rain. Spectrograms of audio data were created, viewed and analyzed using RavenPro v. 1.5 (Bioacoustics Research Program 2014) (16-bit sample format; frame overlap = 50%; Hann Window, DFT = 512; frequency resolution = 124 Hz).

Call Classification

Palm cockatoo vocalizations are harmonically rich, appearing as vertically stacked lines (harmonics and sidebands) on the spectrogram. The most energy occurs in the fundamental frequency (i.e. lowest frequency harmonic), which was measured in a standard, semi-automatic way using RavenPro v. 1.5 (Charif *et al.* 2008). Semi-automatic measurements were made by drawing a selection box around each call manually using the on-screen cursor. To reduce subjectivity of manual measurements, the beginning and end of calls were aligned with a marked change in amplitude using the time-aligned waveform (energy versus time). Acoustic parameters were calculated automatically within the selection.

Calls were initially classified by ear and visual inspection of the spectrograms and then refined based on the statistical information derived from 22 acoustic parameters calculated in RavenPro (Table 1). For this and all subsequent call analyses we focused on call types given at least three times by the same individual and took the mean of their call measurements, but we treated the same call type from different individuals within recording sites as independent. We restricted this analysis to call types given by at least three individuals as we were interested in call diversity at the population scale. Within each population the suite of visually determined call types that occurred commonly enough for these thresholds were compared using Discriminant Function Analysis (DFA) wherein the acoustic parameters were the predictor variables (JMP 10, SAS Institute Inc.).

For each population an average of 12.33 ± 2.81sd call types were sufficiently widespread to be included in the analysis. Many additional call types were recorded at each site (33.67 ± 16.85), but were not recorded from enough individuals to be included in the DFA, and therefore did not undergo the classification procedure. DFA labels each call type with its multivariate mean in canonical space together with 95% confidence intervals . Overlapping confidence interval indicate categories (calls) that are not significantly different, and non-overlapping circles indicate significantly different categories. Calls which were not significantly different were combined under the same call label, unless they had other obvious distinguishing features.

We used rarefaction (Peshek and Blumstein 2011) in the *vegan* package in *R (R Development Core Team 2016)* to estimate the size of each population's full vocal repertoire, which gave the proportion represented by the common calls we compared above. To achieve an equal subsample of each population's repertoire which is necessary for rarefaction, we randomly selected 20 calls from 11 recordings which were also selected randomly from each population.

Musgrave was excluded for lack of any recordings with at least 20 calls. Moreton Telegraph Station only had 6 recordings with 20 calls which may cause underestimation of repertoire size for this population (Peshek and Blumstein 2011). Keeping a uniform recording number across populations was trialled by restricting all sites to 6 recordings, however repertoire size estimates were more stable with the larger number of recordings when the random sampling procedure was repeated several times, so we present the results of the larger sample size of recordings.

Geographic variation in palm cockatoo calls

Two separate analytical approaches were taken to quantify the geographic variation in calls. Firstly, we calculated the number of shared call types between populations, and secondly we calculated differences in the structure of the two most commonly produced call types.

Table 1. Acoustic Parameters.

Measurement	**Unit**	**Description (Raven Pro User Manual: Charif, *et al.* 2008)**
Length	Frames	The number of frames contained in a selection.
Centre time*	s	The duration at which the selection is divided into two time intervals of equal energy.
1st quartile time*	s	The point in time within the selection that divides the call into blocks containing the first 25% and last 75% of the energy.
3rd quartile time*	s	The point in time within the selection that divides the call into blocks containing the first 75% and last 25% of the energy.
Interquartile duration	s	The time between the 1st and 3rd quartile times.
Delta time	s	The time from the start of the selection to the end.
Duration 90%	s	The duration of the interval between time points marking the first and last 5% of the energy in the selection.
High frequency	Hz	The highest frequency marked by the top of the selection border.
Low frequency	Hz	The lowest frequency marked by the bottom of the selection border.
Delta frequency	Hz	The bandwidth between the upper and lower frequency limits of the selection.
Bandwidth 90%	Hz	The bandwidth between the 5% and 95% frequencies.
1st quartile frequency	Hz	The frequency that divides the selection into two frequency intervals containing the first 25% and last 75% of the energy.
3rd quartile frequency	Hz	The frequency that divides the selection into two frequency intervals containing the first 75% and last 25% of the energy.
Frequency 5%	Hz	The frequency that divides the selection into two frequency intervals containing 5% and 95% of the energy in the selection.
Frequency 95%	Hz	The frequency that divides the selection into two frequency intervals containing 95% and 5% of the energy in the selection.
Peak frequency	Hz	The frequency at which maximum energy occurs within the selection.
Aggregate entropy	bits	The disorder of energy in a sound, measured by analyzing the energy distribution within a selection.
Average entropy	bits	The average entropy of each frame in the selection.
Max entropy	bits	The maximum entropy across all frames within the selection.
Min entropy	bits	The minimum entropy across all frames within the selection.

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*RavenPro records 1st and 3rd quartile and centre times as relative to the beginning the recording. To standardize these measurements for each call, the time at the beginning of the selection was subtracted from each to give a time in seconds relative to the start of the selection.

Common call sharing

To ascertain which call types were shared between populations the candidate sets of common calls from each population were compared in a series of pairwise DFAs between populations. Call categorization was based on confidence interval, but when confidence interval failed to distinguish between visually distinct call types categorization was aided by the proportion of calls which were correctly classified by the DFA procedure as per Ribot *et al.* (2009). Where DFA assigned two overlapping call types to the correct population more than 85% of the time they were treated as different calls. Conversely, calls that were misclassified in more than 15% of cases were treated as shared calls.

To control for some populations having more call types that met the recording number threshold than others and therefore being more likely to share calls with other populations, the Bray-Curtis (BC) index of dissimilarity was used for pairwise population comparisons and a matrix of BC indices was constructed. The index gives a value between 0 and 1; 0 meaning no dissimilarity between two populations' set of candidate calls (all calls shared), and 1 meaning complete dissimilarity (no shared calls). To test whether fewer calls were shared with increasing geographic distance between populations, the BC values for both analyses were compared to geographic distance using a Mantel test in R with 9999 permutations (R Development Core Team 2016, package: ade4). Geographic distance between populations was calculated using the great circle distance formula (Longley 2005):

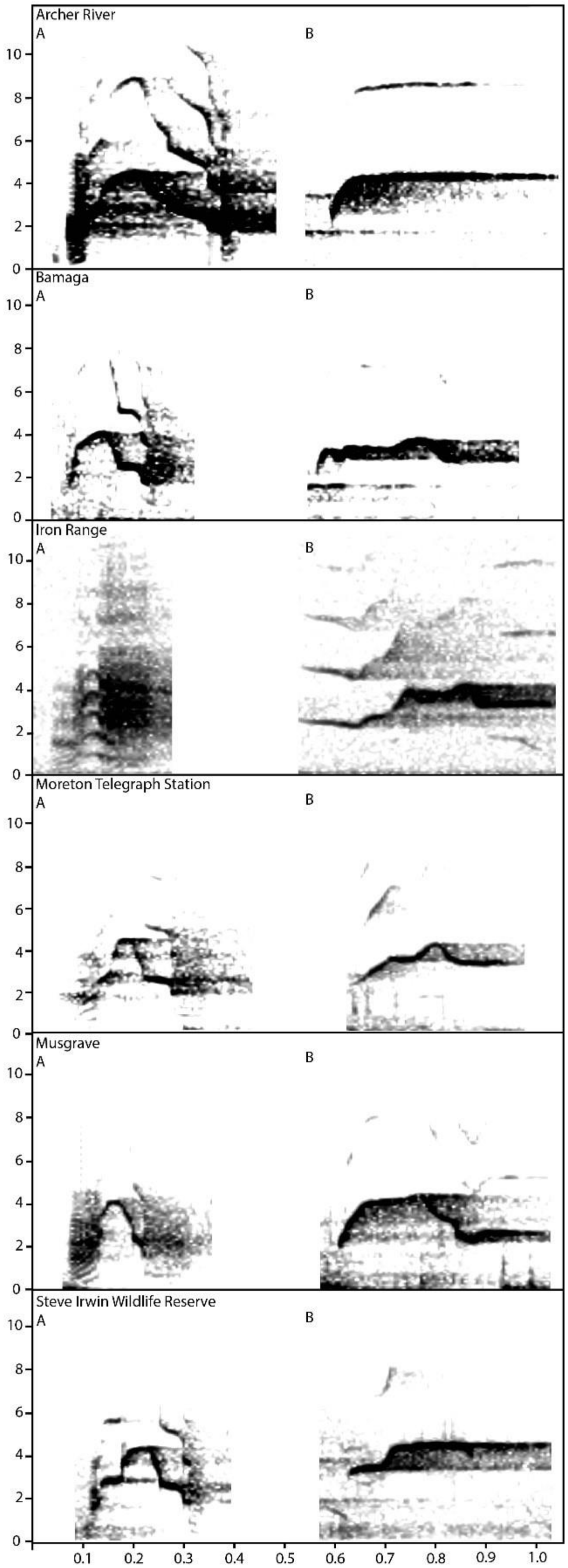

Figure 2. Representative spectrograms of the contact calls that were used in the structural comparison between populations, A = broadband contact calls, and B = short whistles. Spectrograms were created in RavenPro v. 1.5 (Charif *et al.* 2008) (16-bit sample format; frame overlap = 50%; Hann Window, DFT = 512; frequency resolution = 124 Hz).

Distance d, i.e. the arc length for a sphere of radius r (in this case Earth with radius 6371km) is given by:

$$d = \arccos(\sin\phi_1 \sin\phi_2 + \cos\phi_1 \cos\phi_2 \cos\Delta\lambda)r$$

where ϕ_1, λ_1 and ϕ_2, λ_2 are geographical latitude and longitude (in radians) of two points 1 and 2, and $\Delta\phi$, $\Delta\lambda$ are their absolute differences.

Structural differences in contact calls

To investigate geographic variation of specific call types within and between populations, the two most common and distinct varieties of the contact call (Bradbury 2003; Zdenek *et al.* 2015) from each population were compared; a broadband call and a short whistle (for sample sizes see Table 2). Each chosen call was the most common among several that appeared to cluster together in canonical space at the classification stage, yet did not necessarily have overlapping confidence intervals. Comparisons of each call type were made using a DFA for both between and within populations. Between populations, call variation was assessed based on the multivariate mean for each population's call data, and associated confidence interval. Generally, calls that were significantly different had non-intersecting confidence intervals, but the proportion of correct classifications was also taken into account when assessing dissimilarity between sites. To determine any effect of using different equipment (see *Recordings* section), a separate DFA was conducted with broadband contact call recordings from all populations and four Iron Range birds recorded with the equipment used at all other sites.

Table 2. Common call set and call sample size per population.

			Broadband contact calls		Short whistles	
Population	Number of common call types and proportion of estimated repertoire size*	Estimated repertoire size*	No. Sites	No. Individuals	No. Sites	No. Individuals
AR	14 (58%)	24	11	42	10	33
BA	15 (88%)	17	16	78	16	64
IR	15 (70%)	20	6	15	6	13
MTS	11 (79%)	14	1	9	1	7
MU	8		1	3	1	4
SI	11 (85%)	13	10	36	9	20
Total			45	183	43	141

*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.

For the within population comparison, the mean of each recording site was used, and only sites with at least three individuals were used for robust call classification. We restricted the within population analysis to the four populations that had separate recording sites at least 1.5km apart within them (Iron Range, Bamaga, Steve Irwin Wildlife Reserve and Archer River). We included data from every population in the one DFA to ensure that all within population acoustic distances were constructed on the same scale, and subsequent analysis was based on the within population acoustic distances (rather than intersecting confidence intervals, or proportions of correct classification). Assessment of which variables had the most influence on category membership was not conducted to avoid unreliable results due to multicollinearity among parameters (Farrar and Glauber 1967). Effect sizes were calculated as the squared canonical correlation for each discriminant function with a loading of more than 0.5. Regularization was used where there was singularity within the covariance matrices (Friedman 1989).

To test whether call dissimilarity increased with distance, a measure of acoustic distance between calls was compared to geographic distance between populations and between sites within populations. The acoustic distance of each individual's call data to the centroid of each group (population or site, depending on analysis scale) was given by DFA (Mahalanobis distance), and a matrix was constructed of each group's mean acoustic distance to each other group. The acoustic distance matrix was then compared to a matrix of geographic distances between the same groups using Mantel tests with 9999 permutations in R (R Development Core Team 2016).

Permission for this study was sought and received from the traditional owners of the Kalaw Kawaw Ya, Uutaalnganu, Kanthanampu and Kuuku Ya'u language groups. This research was conducted under an Australian National University Animal Experimentation Ethics Committee approval (Protocol No. A2012/36).

Results

Population differences in common call types

Using the statistical classification method sites had mean 12.33 ± 2.80sd common call types representing mean 76% ± 12.18%sd of their estimated repertoire size (Table 2). The proportion of shared call types between sites was generally low; no sites shared more than half their candidate calls with any other site, and four out of 15 pairwise comparisons between sites revealed that no calls were shared at all (i.e. Bray Curtis dissimilarity =1, Table 3). Common call sharing did not correlate with straight line geographic distance between the populations (Mantel test r = 0.22, p = 0.308) (Table 5), despite the geographically closest sites (Moreton Telegraph Station and Steve Irwin Wildlife Reserve) having the lowest dissimilarity value (Table 3). In fact, the population that shared the greatest number of common call types with others, Bamaga (mean BC = 0.73), was actually the furthest away from all other sites (mean distance = 251km). The site with the fewest shared calls, Iron Range (mean BC = 0.96), was relatively close to most of the other sites (mean distance = 143km, Figure 1).

Table 3. Bray-Curtis index of common call sharing between sites.

	Bray Curtis dissimilarity				
	AR	BA	IR	MTS	MU
BA	0.586				
IR	0.931	0.933			
MTS	0.68	0.692	0.923		
MU	1	0.739	1	1	
SI	0.6	0.692	1	0.545	0.895

Values between 0 and 1 indicate repertoire dissimilarity (0 = all calls shared, 1 = no calls shared) between population for five populations, Archer River (AR), Bamaga (BA), Iron Range (IR), Moreton Telegraph Station (MTS) and Musgrave (MU).

Within population analyses on contact calls

To investigate whether call structure changed with increasing distance within a continuous population, we compared call structure within the four largest populations. Discriminant function analysis on broadband contact calls from each site within the four populations yielded 22 dimensions; seven with eigenvalue loadings above 0.5 (Table 4). The solution classified 77.86% of all individuals into their correct site. Mantel tests yielded significant positive relationships between broadband contact call similarity and straight line geographic distance between sites within all populations except Steve Irwin Wildlife

Reserve. Particularly strong relationships were found within Archer River (r = 0.53, p < 0.001) and Iron Range populations (r = 0.402, p = 0. 006) (Table 5).

Table 4. Discriminant function loadings for site categories.

Discriminant Function	Eigenvalue	Percent variation	Effect Size	P value
Population comparison				
Broadband call				
DF1	6.500	66.460	0.867	<0.001*
DF2	1.639	16.800	0.621	<0.001*
DF3	1.055	10.800	0.513	<0.001*
Short whistle				
DF1	6.016	51.500	0.857	<0.001*
DF2	3.121	26.700	0.757	<0.001*
DF3	1.248	10.700	0.555	<0.001*
DF4	0.928	8.410	0.495	<0.001*
Within population comparison				
Broadband call				
DF1	14.034	53.948	0.933	<0.001*
DF2	4.285	16.473	0.811	<0.001*
DF3	1.925	7.400	0.658	<0.001*
DF4	1.093	4.201	0.522	0.047*
DF5	0.934	3.592	0.483	0.349
DF6	0.792	3.043	0.442	0.806
DF7	0.612	2.354	0.380	0.981
Short Whistle				
DF1	9.562	28.670	0.905	<.001*
DF2	5.44	16.319	0.844	<.001*
DF3	3.147	9.438	0.758	<.001*
DF4	2.759	8.273	0.734	<.001*
DF5	2.259	6.774	0.693	0.001*
DF6	1.572	4.714	0.611	0.062
DF7	1.398	4.193	0.583	0.315
DF8	1.179	3.537	0.541	0.716
DF9	1.136	3.407	0.531	0.936
DF10	0.957	2.871	0.489	0.996
DF11	0.713	2.138	0.416	1.000
DF12	0.688	2.065	0.407	1.000
DF13	0.519	1.557	0.341	1.000

Discriminant function analysis on short whistles from each site yielded 22 dimensions; 13 with eigenvalue loadings above 0.5 (Table 4). The solution classified 79.43% of all individuals into their correct site. Mantel tests showed that only the sites within Bamaga had a significant positive association between short whistle difference and straight line distance between them (Mantel test r = 0.899, p = 0.018) (Table 5).

Table 5. Test results for acoustic distance versus geographic distance within and between four populations.

Geographic scale		Acoustic distance measure	Mantel test	
			r	*P*
Between all populations*		Common call set	0.220	0.308
		Short whistle	0.295	0.227
		Broadband contact call	-0.141	0.460
Within populations	Archer River	Short whistle	-0.063	0.709
		Broadband contact call	**0.530**	<0.001
	Bamaga	Short whistle	**0.899**	0.018
		Broadband contact call	**0.117**	0.022
	Iron Range	Short whistle	0.568	0.107
		Broadband contact call	**0.402**	0.009
	Steve Irwin Wildlife Reserve	Short whistle	-0.404	0.997
		Broadband contact call	-0.112	0.832

Mantel tests conducted with 9999 repetitions. Results with *P* values <0.05 are in bold.
* Including Moreton Telegraph Station and Musgrave which weren't analyzed at within population scale due to their small geographic area.

Between population scale analyses on contact calls

Discriminant function analysis on broadband contact calls from each population yielded seven dimensions (Table 4). The solution classified 86.3% of all individuals into their correct population (Figure 3a). Every site had a distinctive version of the broadband contact call except Archer River which had fewer than 85% correctly classified calls

(81%). Moreton Telegraph Station and Musgrave had very good classification rates (100%), which may have been inflated due to smaller sample sizes at these sites (N = 9 and 3 respectively). Moreton Telegraph Station's call was not significantly different to Musgrave and Steve Irwin Wildlife Reserve. In addition Steve Irwin Wildlife Reserve and Bamaga's calls were also not significantly different. Broadband contact calls from Iron Range and Archer River remained significantly different. Broadband contact calls from Iron Range were more distinctive than those of other populations (99.4% correctly classified: Figure 3a), despite its central position geographically. There was no significant correlation between acoustic distance and geographic distance between populations (Mantel test r = -0.141, p = 0.46) (Table 5). The comparability of the two sets of equipment was validated by the lack of significant difference between broadband contact calls within Iron Range. This was shown by a DFA that yielded eight dimensions, only the first of which had an eigenvalue > 0.5 (Wilks' Lambda = 0.003, $p < 0.001$).

The short whistles from the six populations varied along seven dimensions in DF analysis (Table 3). The solution classified 94.3% of all individuals into their correct populations (Figure 3b). All populations had unique short whistle contact calls that had 90% correct classification; however Steve Irwin Wildlife Reserve and Moreton Telegraph Station short whistle calls weren't significantly different in structure. Perfect classification rates within Iron Range, Moreton Telegraph Station and Musgrave indicate distinctive calls at Iron Range but may have once again been inflated due to fewer samples at Moreton Telegraph Station and Musgrave (N = 7 and 4 respectively). A Mantel test showed no correlation

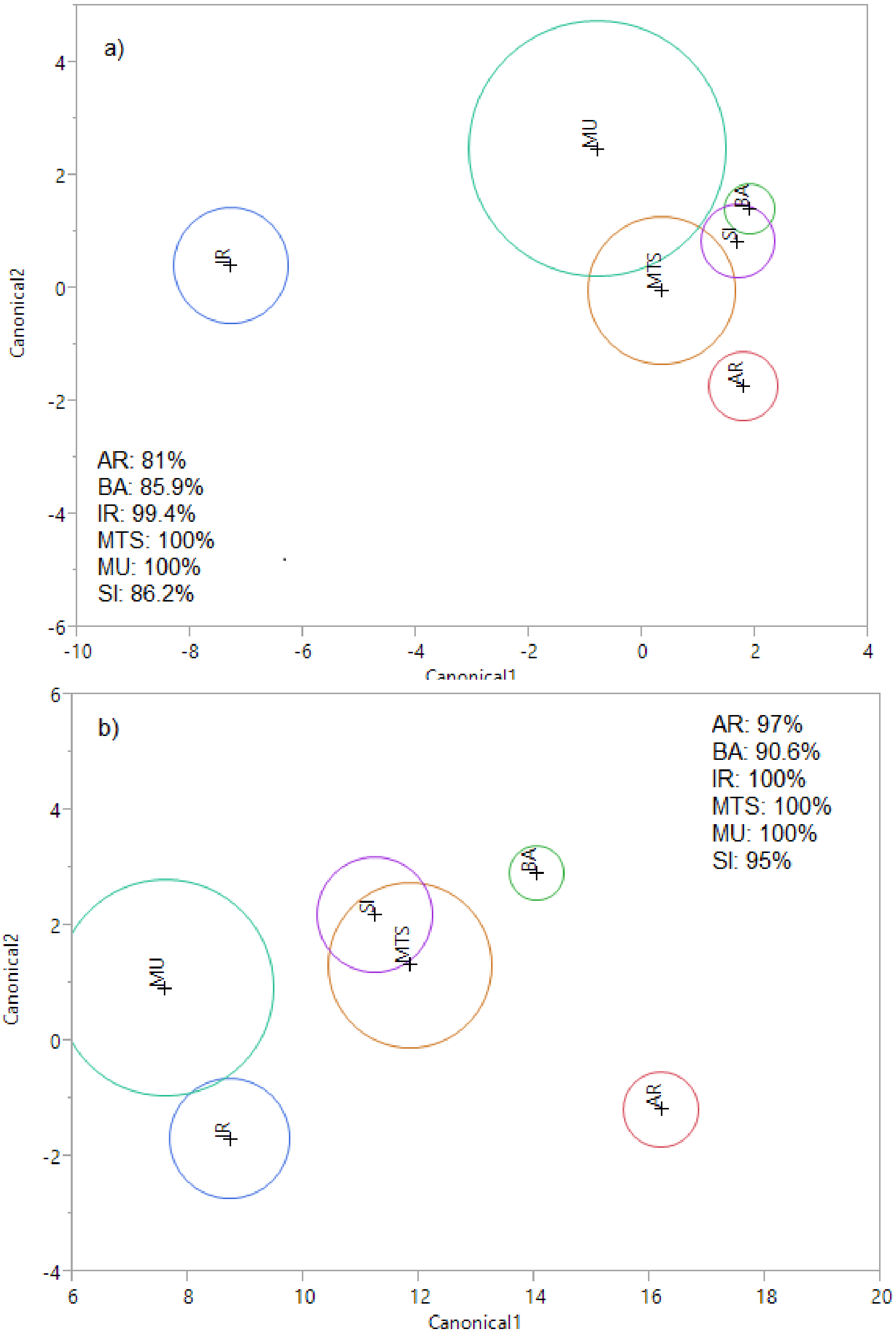

Figure 3. Discriminant function analysis based on the 22 acoustic parameters of (a) broadband contact calls and (b) short whistles from each of the 6 populations (AR: Archer River, BA: Bamaga, IR: Iron Range, MTS: Moreton Telegraph Station, MU: Musgrave, SI: Steve Irwin Wildlife Reserve). Each point represents an individual's mean call data, the '+' represents the centroid for individuals in each population and the circles represent 95% confidence surrounding each population's centroid. Overlapping confidence interval circles indicate acoustic data that are not significantly different. The proportion of correct classifications for each population is also given.

between short whistle similarity and geographic distance overall (r = 0.295, p = 0.227) (Table 5).

Discussion

We found spatial patterns in call sharing and structure both within and between palm cockatoo populations on CYP. Although full repertoires were not obtained we compared sharing of the most common call types between populations. The population at Iron Range on the east coast had the fewest shared calls and the most distinctively structured broadband contact call. The two populations that were geographically closest to one another (Steve Irwin Wildlife Reserve and Moreton Telegraph Station) had the most shared calls and were the only populations without distinctive short whistle structures. We found positive relationships between geographic distance and call structure differences within all populations for broadband contact calls, but the same relationship was only found at Bamaga for short whistles. Between populations there was no correlation, except between the two closest sites. Observed geographical variation in the vocal characteristics of palm cockatoos may have arisen due to social learning, biogeographic history and population connectivity with differing effects depending on geographic scale and call type.

Observed geographical variation in the vocal characteristics of palm cockatoos is comparable to levels of variation recorded from several other species of parrots (Wright 1996; Baker 2000; Bradbury *et al.* 2001; Baker 2003; Bond and Diamond 2005; but see Guerra *et al.* 2008). Variation in short whistles resembles locally convergent calls in gallahs *Cacatua roseicapilla*,(Baker 2003), yellow naped amazons *Amazona auropalliata* (Wright 1996) and ringneck parrots *Barnardius zonarius* (Baker 2000). Palm cockatoo broadband contact calls change gradually within populations, on a similar scale to the contact calls of orange fronted parakeets *Aratinga canicularis(Bradbury et al. 2001)*. However the distinctive call at Iron range is more comparable to distinct dialect variation in yellow-naped amazon flight calls (Wright 1996).

Within population analyses on common contact calls

Strong relationships between geographic distance and call similarity could support the epiphenomenon hypothesis as a result of the accumulation of copy errors and drift (Krebs and Kroodsma 1980). We observed possible evidence of this process in broadband contact calls within all, but not between populations, through positive correlation between geographic distance and call dissimilarity. Interestingly, two populations with strong positive correlations, Iron Range and Archer River, also had significantly distinctive broadband contact calls compared to other populations.

For short whistles there was a general lack of correlation between geographic and acoustic distance within populations, most likely caused by similarity in call structure within populations rather than variation without geographic structure. A correlation was observed at Bamaga where sites had the greatest dispersion (over 40.7km). The correlation may indicate that distances of this magnitude are required to resolve any geographic structure in short whistle variation, which supports accumulation of copy errors and drift to divergent forms in short whistles.

Between population analyses of common contact calls

Broadband contact call differences correlated with geographic distance within but not between populations. Under the epiphenomenon hypothesis, this is possible if accumulating vocal differences occur unevenly across space at the between population scale. The fragmented distribution of rainforest habitat, known to be important for palm cockatoos, might explain the lack of correlation. However elucidating any relationship between vocal divergence and the geospatial pattern of habitat requires further analysis, perhaps using a connectivity modelling approach.

Broadband contact calls had a lower overall rate of successful classification with DFA than short whistles between populations and were therefore generally more similar. The similarity in broadband contact calls outside of Iron Range unrelated to geographic separation suggests that this call type evolved more slowly than short whistles. Iron Range had the most distinctive broadband contact call based on DFA. This distinctiveness suggests that some degree of contemporary, or historic isolation of the Iron Range population from more western populations provided an opportunity to develop such different vocal characteristics.

Short whistles were more diverse than broadband contact calls as they showed greater divergence between populations and had a higher classification success rate. This is potentially due to a more rapid accumulation of copy errors in short whistles. However, lack of correlation between short whistles and geographic distance both between and within populations suggests a less random mechanism. Parrots are known to imitate social companions in captivity (e.g. budgerigars Melopsittacus undulatus, Farabaugh *et al.* 1994; Hile *et al.* 2000; Hile and Striedter 2000; Dahlin *et al.* 2014) making social adaptation a likely explanation for similar results in other species (Wright 1996; Baker 2000, 2003) and may explain discreet short whistle types in geographically separate populations of phylopatric palm cockatoos.

Vocalization patterns and biogeography

Without data about population genetics, forming conclusions about the origin and maintenance of geographic variation in vocal characteristics of palm cockatoos would be undermined by the Psittacine ability to adjust vocally to their social environment (see Farabaugh *et al.* 1994; Hile *et al.* 2000; Hile and Striedter 2000; Dahlin *et al.* 2014). To guide further research we suggest two mutually plausible explanations for the variation in vocal characteristics documented here; summarized as the dynamic historical biogeography of CYP, and contemporary biogeographical influences.

There have been considerable expansions and contractions of rainforest on CYP occurring together with the repeated formation and loss of a land bridge between CYP and New Guinea, which correspond with glacial cycles throughout the Pleistocene (Nix and Kalma 1972; Webb and Tracey 1981). The Iron and McIlwraith Ranges on the east coast are likely to have acted as refugia for rainforest reliant palm cockatoos by maintaining pockets of suitable habitat during arid periods when rainforest disappeared elsewhere. The high degree of species level endemism of the Iron McIlwraith Ranges (20%: Crisp *et al.* 2001; Legge *et al.* 2004) supports this region's role as rainforest refugia. During wetter periods habitat connections may have allowed population replenishment from New Guinea enabling more vocal similarity among populations outside of the already occupied Iron-McIlwraith Ranges. This is supported by the distinctiveness of broadband contact call and other common call types at Iron Range, as well as presence of unique mitochondrial haplotypes found by Murphy *et al.* (2007).

Alternatively, the distinctiveness of vocal characteristics of the Iron Range palm cockatoos may be influenced by contemporary population isolation. The Iron Range is located among the east-flowing river systems of CYP, where the other populations are located on west-flowing rivers, and these river systems are separated by the northern section of the Great Dividing Range. This could potentially reduce population connectivity to the Iron Range since palm cockatoo habitat tends to follow the gallery forest of river systems closely. However the small distance between the Wenlock (west flowing) and the Pascoe (east flowing) at one point along their length (3km) may allow sufficient dispersal to prevent population divergence. The Great Dividing Range to the west of Iron Range is a more plausible barrier to dispersal, indeed mountains explain population structure in large parrots (e.g. scarlet macaws *Ara macao,* Olah in prep). In later contributions we will investigate the role of topography in determining the observed vocal patterns, and using recent molecular techniques (Suchan *et al.* 2015) whether phylogeographic analyses support an ancient, contemporary or neither isolation hypotheses for the Iron Range population of palm cockatoos.

Acknowledgements

We gratefully acknowledge Barry and Shelley Lyon, Australia Zoo and the Australian Wildlife Conservancy for their hospitality. Chris Sanderson, Maddie Castles, Zoe Reynolds, Claudia Benham, Richie Southerton and Andrew Neilen provided invaluable assistance and companionship in the field. We thank Steve Murphy, Raoul Ribot and Xénia Weber for their feedback on drafts of this paper and the anonymous reviewers for their comments. Logistical and technical support was provided by Barry Croke, John Griffith and Brian Venables.

Funding

Funding for this study was provided by an Australian Government Research Training Grant, The Hermon Slade Foundation, The National Geographic Society, Birdlife Australia and the Fenner School of Environment and Society, Australian National University.

Author contributions

M.V.K. conducted fieldwork, performed sound and statistical analyses and wrote the manuscript. C.N.Z contributed sound files from her field site, assisted logistically and commented on the manuscript. N.E.L. assisted with analysis, commented on the manuscript and sought funding. R.H. conceived the idea for the project, sought funding, guided the project and commented on the manuscript.

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Chapter 3: Geographic variation in vocal characteristics of Australian palm cockatoos (*Probosciger aterrimus*)

Zdenek, C., Heinsohn, R., Langmore, N. (2015). Vocal complexity in the palm cockatoo (*Probosciger aterrimus*). *Bioacoustics* **24,** 253-267.

Submitted to *Emu*

Chapter 4: Genomic population structure supports vocal dialect boundaries in palm cockatoos (Proboscistiger aterrimus) and a refugial late-Quaternary distribution model.

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Abstract

Species persistence and maintenance of genetic diversity are strongly affected by dispersal and historic distribution, especially when species depend on habitat that is non-uniform or fluctuates dramatically with changing climate. Rainforest in the Australo-Papuan region has fluctuated dramatically since the last glacial maximum (around 20kya). To understand how pre-historic climate fluctuation affected population connectivity and genetic diversity in a large rainforest edge species, we screened 27 Palm Cockatoo samples from Cape York Peninsula (Australia) and southern Papua New Guinea (PNG) in 1132 single nucleotide polymorphisms in 342 nuclear loci and the mitochondrial ND2 gene. We also modelled the birds' distribution at present, mid-Holocene (~6 kya) and the last glacial maximum (~21 kya). Population differentiation in nuclear genomic data among Australian populations aligns with distribution contraction to mountainous refugia at the mid-Holocene (~6ka). Lack of nuclear divergence between PNG and Australia may reflect late-Holocene recolonization, but different ND2 haplotypes suggest early stages of divergence. Although admixed individuals suggest some gene-flow, recent movement restriction to/from Australian refugia is suggested by a unique ND2 haplotype, genomic divergence and a

vocal dialect boundary shown previously. Our results show how pre-historic climate fluctuation affects present-day and future species conservation in dynamic rainforest edge ecosystems.

Funding details

This research is supported by an Australian Government Research Training Program Scholarship. We would like to thank the Hermon Slade Foundation and the National Geographic Society for funding field work, and Birdlife Australia for funding lab costs through the Stuart Leslie Bird Research Award.

Introduction

Understanding contemporary structure of wild avian populations has great value for informing species conservation, especially where species distributions are non-uniform or fragmented throughout the landscape (Pavlova *et al.* 2012). Fragmentation of species distributions, either naturally (through past and present biogeographical influences) or human-induced (through land-use, e.g. vegetation clearing for agriculture), creates separate, small populations which are more vulnerable to local decline from local threats or stochastic fluctuations in population size (Frankham 2005). Population declines can cause loss of genetic and cultural diversity resulting in lower adaptability to change, consequently increasing the species' vulnerability to extinction (Frankham 2005). However, local declines can be buffered by replenishment from connected populations, which convey the benefits of increased effective population sizes and lower extinction vulnerability in small populations (Frankham 2005; Sunnucks 2011). These dynamics are important in determining which species or populations of species recover or disappear following dramatic changes in distribution due to climate or disturbance.

The present day distribution of rainforest species in the Australia-New Guinea region reflects dramatic worldwide climate and sea level changes during the Pleistocene (1.6 Mya – 10ka) creating complex biogeographical histories for many species. A land bridge between the two landmasses was exposed for most of the past 250ka (Chappell and Shackleton 1986) resulting in the rainforests of Cape York Peninsula, north-eastern Queensland, sharing greater floral (Webb and Tracey 1981; Barlow and Hyland 1988; Crisp *et al.* 2001) and faunal (Kikkawa *et al.* 1981) similarity with New Guinean rainforests than other rainforests within Australia. Global climate change in the recent past has caused these rainforest patches to contract greatly (Nix and Kalma 1972) making it unclear how population level dynamics of rainforest species have been affected. Dynamics such as where they persisted or recolonized following re-expansion of rainforests and how populations are connected in the present are even less clear for species occupying the ecotone between rainforest and woodland (e.g., Sooty Owls Tyto tenebricosa, Norman *et al.* 2002). The rainforest edge species, Palm Cockatoos (*Probosciger aterrimus),* are ideal for investigating these effects because information about their population structure is also urgently required to forecast the rate of future population declines and predicting viability (Murphy *et al.* 2003).

Palm cockatoo populations in eastern New Guinea and Australia have not diverged sufficiently to be considered separate sub-species, yet their aversion to crossing open water separates these populations for conservation purposes. In Australia, Palm Cockatoos have low breeding success; on average, each pair lays just one egg every two years and only 20 per cent of their eggs result in a fledgling (Murphy *et al.* 2003). Moreover, they are threatened with habitat loss both from changing fire regimes and vegetation clearing due to mining activity in the west of Cape York Peninsula, Northern Australia (Murphy *et al.* 2003; Heinsohn *et al.* 2009). Globally Palm Cockatoos are 'least concern' (Birdlife International 2016), however the 'vulnerable' status of Australian Palm Cockatoos is owed to an unsubstantiated estimate of between 2,500 and 10,000 individuals assumed to form a single sub-population, as well as predicted declines with probability of extinction greater than 10 per cent in the next 100 years (Heinsohn *et al.* 2009; IUCN criteria C and E, Department of the Environment 2015). The assumption that Australian Palm Cockatoos form a single sub-population may be inaccurate, given that they occur in fragmented rainforest patches and poor connectivity between patches may restrict gene flow.

Palm Cockatoos breed in monogamous pairs which defend nests in hollow trees within 1km of rainforest which is required for feeding (Murphy *et al.* 2003). Rainforest adheres to drainage patterns and patches of suitable soil or topography among sclerophyll woodland (Webb and Tracey 1981). The extent to which sub-populations of Palm Cockatoos are inter-connected on Cape York Peninsula could profoundly influence their persistence because some may act as sinks and others as sources (Diffendorfer 1998). Whether discontinuous rainforest patches allow connectivity among separate sub-populations is unknown, though unique cultural characteristics among Australian Palm Cockatoos suggest connectivity is disrupted (ref).

Palm Cockatoos conduct unique displays including postures, gestures, and the use of a manufactured sound tool to 'drum' on their nest hollow (Wood 1984). Although the drumming behaviour is widespread within Cape York Peninsula (personal observation), Palm Cockatoos from the Iron and McIlwraith ranges region (considered one coherent population due to habitat continuity, hereafter 'Iron Range') appear to use sound tools more frequently (Heinsohn pers. comm.), and have a unique vocal dialect in the contact call compared to other Cape York populations (Figure 1a) (Keighley *et al.* 2016). These cultural differences probably reflect disruption in connectivity between Iron Range and other populations (Freeberg 2000; Podos and Warren 2007). It is unknown whether this disruption is 1) contemporary with behaviour undergoing divergence, 2) historical and maintained by learning despite ongoing connectivity, or 3) purely an artefact of learning without separation. Identifying the basis for this disruption is crucial for conservation management and increasing understanding of interaction between cultural diversity and population level processes. To provide additional data about historical and recent population dynamics we examine variation in genome-wide single nucleotide polymorphisms (SNPs) within the nuclear and mitochondrial genomes of Palm Cockatoos from Australia and southern Papua New Guinea. To investigate potential biogeographical causes for population structure we compare our genomic data with present and past distribution models.

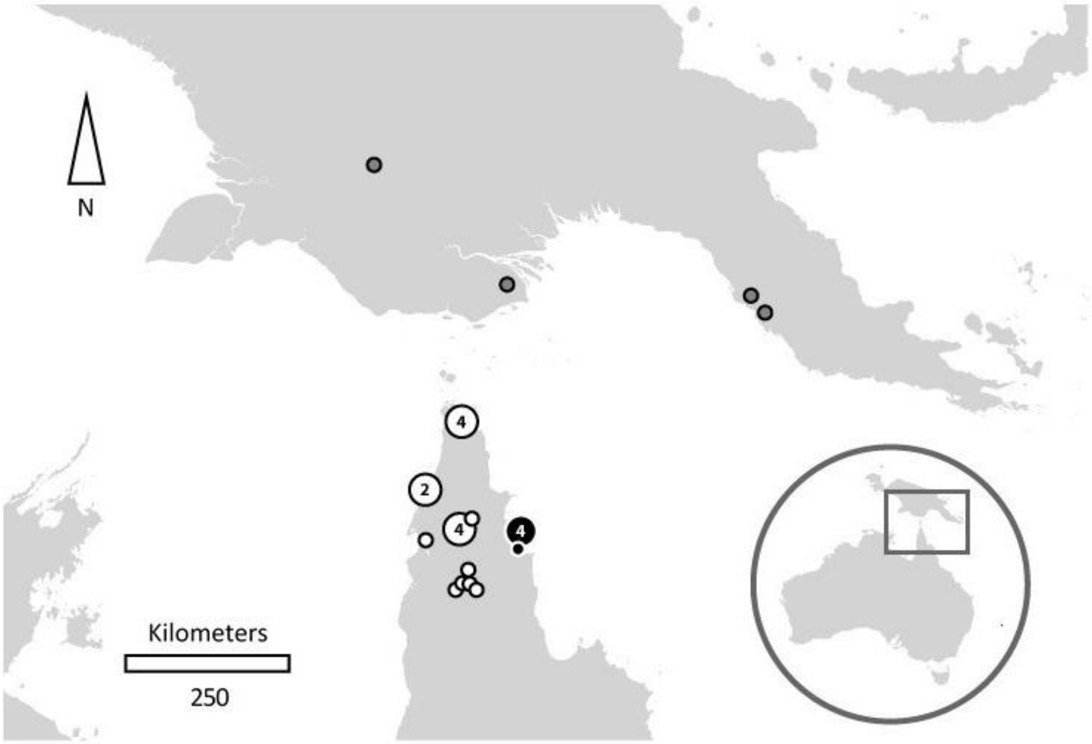


Figure 1a. Geographic sampling
The map depicts the geographic sampling of the Palm Cockatoo populations in Australia and Papua New Guinea. Black circles indicate samples from the Iron Range, white circles indicate samples from the rest of Cape York Peninsula, and grey circles indicate samples from Papua New Guinea. Numbers within circles represent sample sizes in the corresponding area.

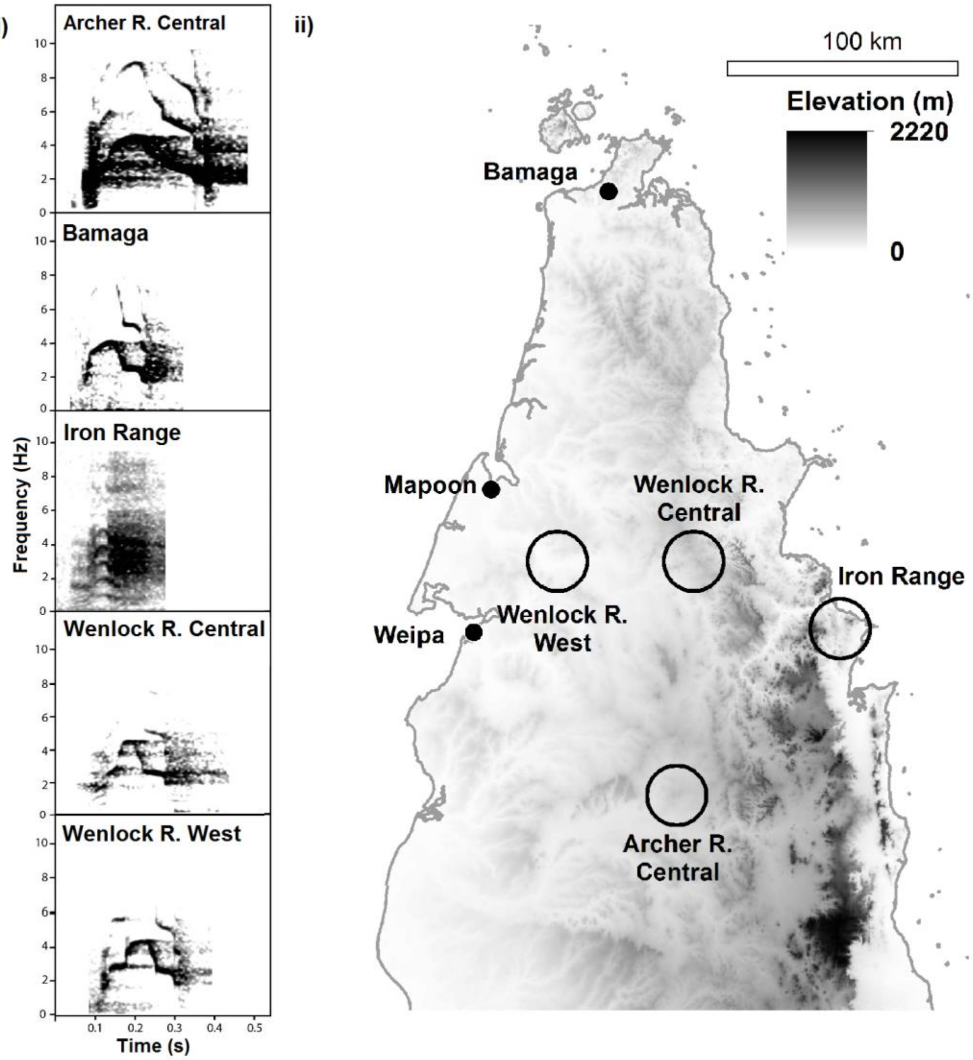


Figure 1b. Contact calls and elevation
(i) Sectrograms of representative contact calls from five locations on Cape York Peninsula marked on the elevation map in (ii). Note: Spectrograms were created in RavenPro v. 1.5 (Charif *et al.* 2008) (16-bit sample format; frame overlap = 50%; Hann Window, DFT = 512; frequency resolution = 124 Hz).

Methods

Sampling

We used a total of twenty-seven Palm Cockatoo samples for genetic screening (Table 1). Of these, 22 samples were from Cape York Peninsula, Australia, including five from the Iron Range, and five were from Papua New Guinea (Figure 1b). The DNA from the Iron Range population were all extracted from blood samples using the Qiagen DNeasy kit

(Qiagen, Valencia, CA, USA). The samples from Bamaga on Cape York Peninsula, Australia and the rest of Papua New Guinea were extracted from museum toe-pad samples. The blood and toe-pad samples were obtained and DNA was extracted for a previous project and the details of the extraction procedure is outlined in (Murphy *et al.* 2007). The remaining DNA samples were extracted noninvasively from moulted feathers collected throughout the range of the Cape York population. Apart from one feather from a captive individual at Weipa (western Cape York Peninsula), samples were collected from the ground by MVK and volunteer assistants or contributed with location data by third party individuals. Collection locations were at least 2 km apart, which probably exceeds different individuals' territorial separation (Murphy *et al.* 2003). The extraction method used is as described in (Horváth *et al.* 2005). The feathers were extracted using a Qiagen DNeasy Kit. From flight feathers, we took a ~8 x 5 mm portion of the quill adjacent to where the barbs end. From contour feathers we used the entire calamus. The samples were digested in 180ul ATL Buffer, 20uL ProK, and 10uL 1M dithiothrietol at 65°C overnight. Following the remaining steps of the standard Qiagen protocol, the samples were eluted in two sets of 150uL AE Buffer and concentrated using a SpeedVac.

DNA sequencing

A summary of our methods for molecular sequencing, data processing and calculation of population structure and statistics are presented here with full details in supplementary material. We used a modified version of the 'hyRAD' protocol (Suchan *et al.* 2016) to screen the nuclear genome for anonymous SNPs. The protocol combines the efficiency of restriction associated DNA sequencing (RADseq) with the accuracy and power of hybridization capture methods, allowing utilization of poorly preserved DNA from moulted feathers or historically sampled museum specimens. The hyRAD protocol uses double-digest restriction digest (ddRAD) sequencing libraries as probes for a sequence capture (Peterson *et al.* 2012; Suchan *et al.* 2016).

Probes for the hyRAD protocol were designed from ddRAD libraries of the four Iron Range samples due to their high DNA quality following a protocol similar to Penalba (Peñalba *et al.* 2014). The Iron Range ddRAD libraries were built with restriction enzymes PstI and EcoRI (Peterson *et al.* 2012) and fragments were size selected to 345-407bp. After probe design, the ddRAD Iron Range libraries were sequenced along with captured hyRAD libraries of all other sites as paired-end reads using an Illumina high-throughput NextSeq500 at the ACRF Biomolecular Resource Facility.

Whole mitochondrial genomes were obtained as a by-product of hyRAD capture except for samples from the Iron Range which were not included. For the Iron Range samples the mitochondrial ND2 (NADH dehydrogenase subunit 2) gene was amplified with primers L5204 and H6312 (Sorenson *et al.* 1999). The ND2 marker was chosen to complement previous mitochondrial studies (Murphy *et al.* 2007) and due to its' relatively fast mutation rate (Pacheco *et al.* 2011).

Data processing

The hyRAD and ddRAD-derived data sets were filtered using existing and custom pipelines. In particular, ddRAD data were filtered for low complexity reads and both hyRAD and ddRAD were trimmed for low quality sites, barcodes and restriction cut sites. A reference nuclear sequence set was assembled from the cleaned Iron Range ddRAD data. This reference contig set was used to map all the individuals. Genotype likelihood calculations (suited to low-coverage data) (Nielsen *et al.* 2011; Nielsen *et al.* 2012) and

SNP filtering based on coverage, overlap between populations or putative repeats and paralogous regions were conducted with ANGSD (Korneliussen *et al.* 2014). Unlinked SNPs were used for population structure and all SNPs within all loci were carried through for the other population genetic statistics. A *de novo* assembly of the mitochondrial genome was obtained using four samples, with subsequent mapping of cleaned reads. ND2 sequences were then extracted, inspected for possible heterozygosity and coverage and aligned.

Population structure and statistics

We recovered the nuclear genome population structure using ngsTools kit (Fumagalli *et al.* 2014; Vieira *et al.* 2016) using genotype likelihoods. The output from ngsTools was used to create a network in SplitsTree (Dress *et al.* 1996) and to summarize distance information using multidimensional scaling (MDS). The mitochondrial ND2 population structure was visualized using haplotype networking in PopArt (Leigh and Bryant 2015). To try to detect additional population structure and estimate admixture between populations we used ngsAdmix (Skotte *et al* 2013).

Population genetics summary statistics were based off allele frequencies from genotype likelihoods and included an estimation of population differentiation (FST, Reynolds *et al.* 1983), population divergence (d_{xy}), per site heterozygosity (θ), per site nucleotide diversity (π) and divergence after population split (D_A).

Species distribution modeling

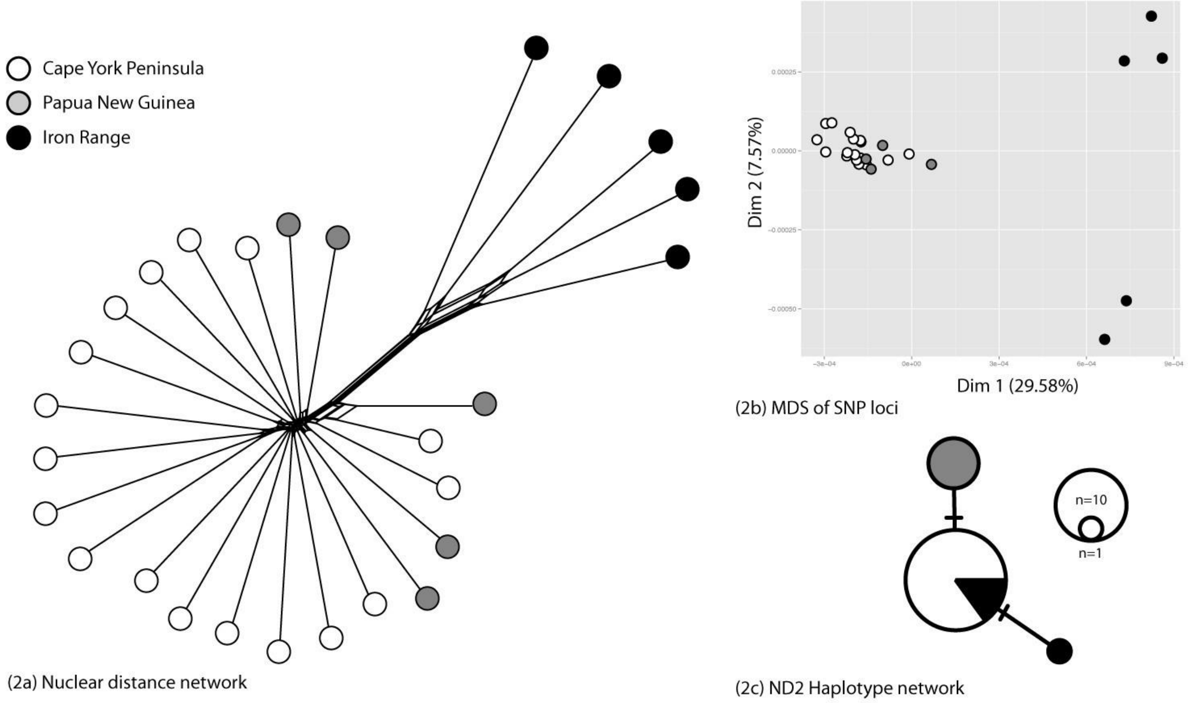
To determine whether observed genetic population structure had historic or contemporary origins we modelled Palm Cockatoo distributions using environmental data from the present, the mid-Holocene (~6ka years ago) and the last glacial maximum (~21ka years ago) from the WorldClim database (http://worldclim.com). In these databases, past climate was obtained by downscaling and calibrating based on present data (http://www.worldclim.org/downscaling). To acquire environmental data representative of Palm Cockatoo habitat requirements, we used data from the present climate database at geographic locations of museum voucher occurrence points from the Atlas of Living Australia Database (http://www.ala.org.au Accessed 12 Oct 2016). Spurious localities and duplicate points were removed and to compensate for bias due to sampling effort we only used one occurrence point in a 0.5 cell. To ensure parsimonious distribution models we removed covariable bioclimatic variables (Spearman Rank Correlation test $\rho \leq 0.7$) from the total set (available at: http://www.worldclim.org/bioclim). We used both BIOCLIM and MAXENT models to predict the species range (Phillips *et al.* 2006; Booth *et al.* 2014). We generated 5000 background points within the extent 135, 150, -18, -5. We used 5-fold partitioned occurrence and background data to train the model and the remaining samples to test the model. To evaluate the models we calculated the area under the receiver-operator curve (AUC) by averaging out the AUC values for each 4/5 training data subset. We also calculated a null model calibrated AUC (cAUC) value with the spatial sorting bias (SSB) removed as the background extent may affect the initial AUC calculation. Models with an AUC value of > 0.7 tend to be regarded as informative, though the same models tend to have a cAUC value of ~ 0.5 after removing SSB. (Hijmans 2012).

Results

Population structure and admixture

Population structure of both nuclear and mitochondrial loci can be found in Figure 2. After rigorous SNP filtering we recovered 342 contigs with 1132 SNPs in a total of 83,093 bp.

For the nuclear SNP loci, the Iron Range population comes out as a separate population from the remaining Cape York and Papua New Guinea samples. This is evident in the network (Figure 2A) and in the MDS plot where the first dimension separating the population contains 21.88% of the variation (Figure 2B). The ND2 network shows only 3 haplotypes, one representing all Papua New Guinea samples, one containing samples from Cape York Peninsula and the Iron Range, and one unique haplotype in the Iron Range (Figure 2C). Each ND2 haplotype is only differentiated by two mutations. One sample from Iron Range that was sequenced using both the ddRAD and hyRAD protocols consistently fell in the same population, providing evidence that the population structure is biological and not due to sequencing method.



(2a) Nuclear distance network

(2b) MDS of SNP loci

(2c) ND2 Haplotype network

Figure 2. Population structure
Each plot represents population structure with the colors of the samples corresponding to the sample map. (a) represents a network of the distance matrix derived from genotype likelihoods of the nuclear SNPs between each sample (b) represents a multidimensional scaling plot also derived from the distance matrix from the genotype likelihoods, and (c)

shows a haplotype network of a segment of the mitochondrial ND2 locus.

The results of our admixture analysis show the increase in (delta) likelihood is much greater at K = 2, than with subsequent K values, and division into three clusters adds little useful information based on Figure 4A, therefore we discuss structure shown by analyses at K = 2. The analysis shows support for differentiation between the Iron Ranges and the rest of the individuals, but two admixed individuals within the Iron Ranges provide evidence for gene flow from the Cape York Peninsula populations into the Iron Ranges (Figure 4A). Individuals from Cape York Peninsula west of the Iron Ranges also show evidence of admixture and therefore gene flow from the Iron Range populations outwards (Figure 5). A single individual from Aroa, Papua New Guinea also comes out as being admixed of the two nuclear populations (Figures 4A,5).

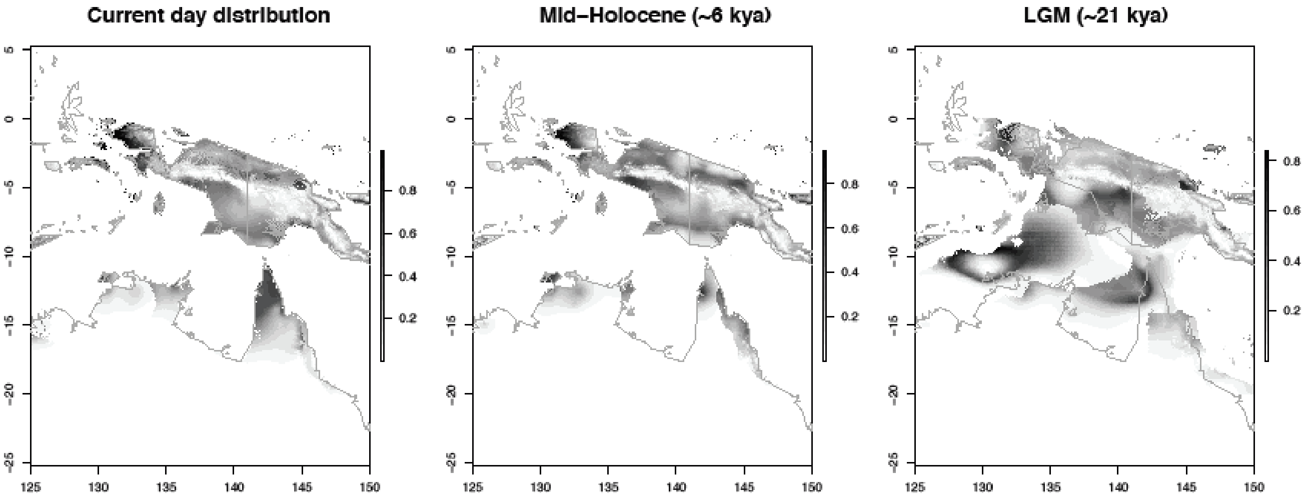
Population genetics statistics

The F_{ST} estimate between the Iron Range (IR) population and the combined Cape York Peninsula (CYP) and Papua New Guinea (PNG) population is 0.514, and the absolute divergence measure is D_{xy} = 4.98e-3 per site with an equivalent relative divergence measure of D_A = 4.97e-3 per site. The per site heterozygosity (Watterson’s θ) within each population is θ_{IR} = 5.42e-6 and $\theta_{CYP\&PNG}$ = 5.19e-6. The per site nucleotide diversity (π) within each population is π_{IR} = 6.38e-6 and $\pi_{CYP\&PNG}$ = 8.39e-6.

Species distribution modeling

After filtering the occurrence points, we had 37 occurrence points remaining for our model training and testing. The resulting species distribution model predictions for current day, mid-Holocene, and last glacial maximum for both MAXENT and BIOCLIM models can be found in Figure 3. After filtering against correlated bioclimatic variables we were left with temperature seasonality (BIO4), minimum temperature of coldest month (BIO6), mean temperature of wettest quarter (BIO8), precipitation of wettest quarter (BIO16), and precipitation of warmest quarter (BIO18) as our predictor variables. The average AUC value for the MAXENT model is 0.87.

(3a) MAXENT



(3b) BIOCLIM

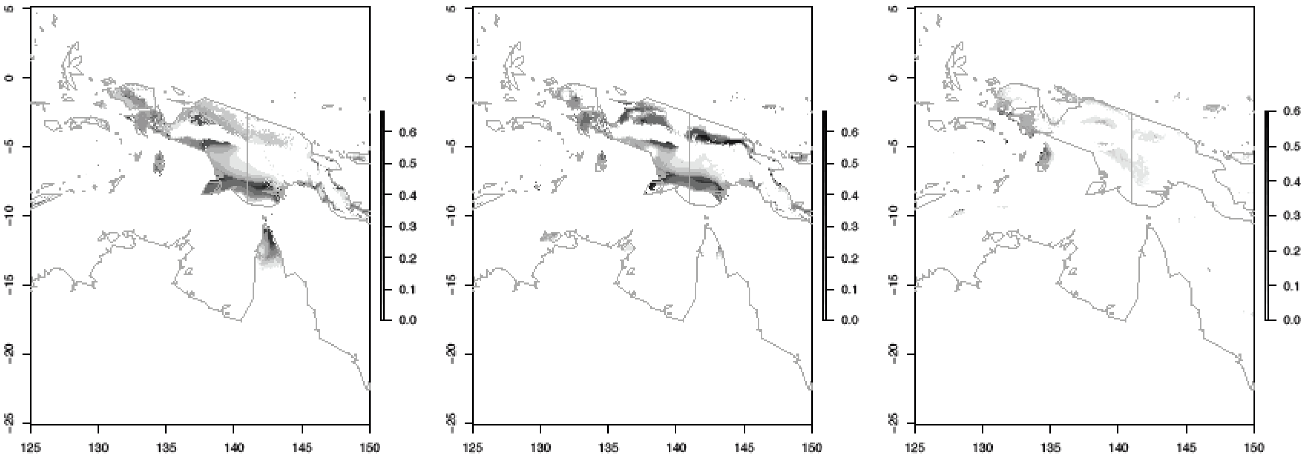
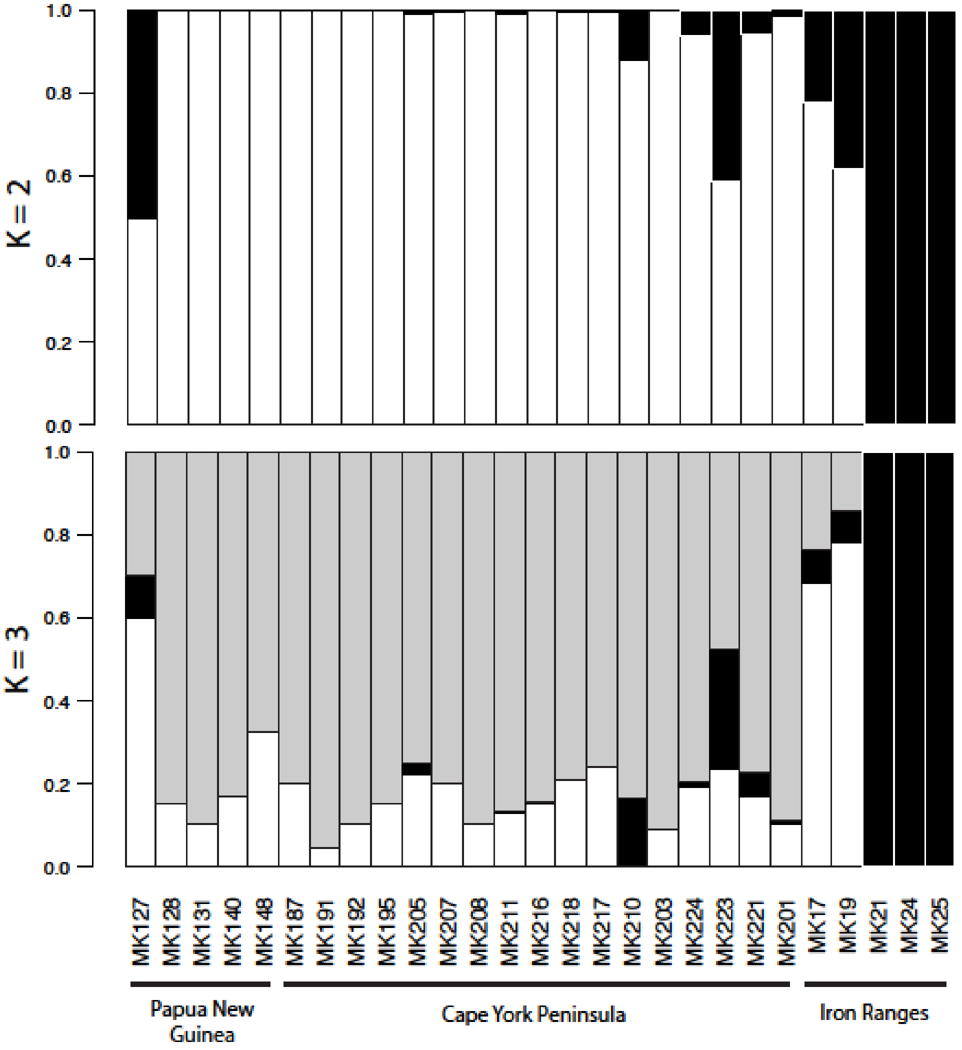


Figure 3. Species distribution modeling: Each map shows the predicted suitable range for the Palm Cockatoo species in Australia and Papua New Guinea with shading indicating % likelihood of occupation. (A) The top row corresponds to suitability predictions from a maximum entropy (MAXENT) model while (B) the bottom row corresponds to suitability predictions from a climate-envelope BIOCLIM model. The left column represents predictions for current day habitat suitability, the middle column projects the predicted model to climate of the mid-Holocene (~6 kya), and the third column projects the predicted model to the last glacial maximum (~21 kya).



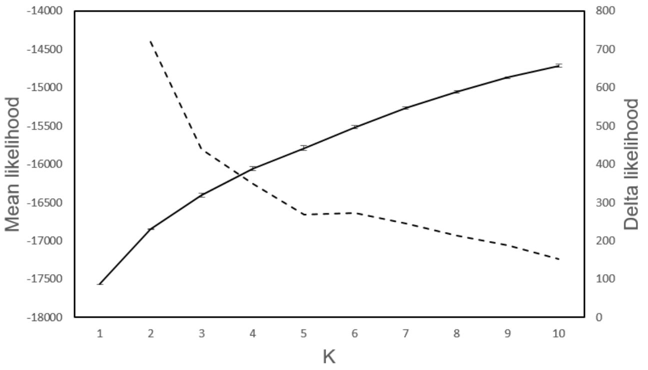


Figure 4. Admixture analysis These figures represent our results from the admixture analysis for (top) two clusters (K = 2) and 3 clusters (K =3), as well as (bottom) the change in mean (delta) likelihood by increasing number of clusters for each value of K from 2 to 5 (solid line: mean log likelihood ± s.d. in 10 repetitions for each number of clusters; broken line: delta likelihood with increasing K).

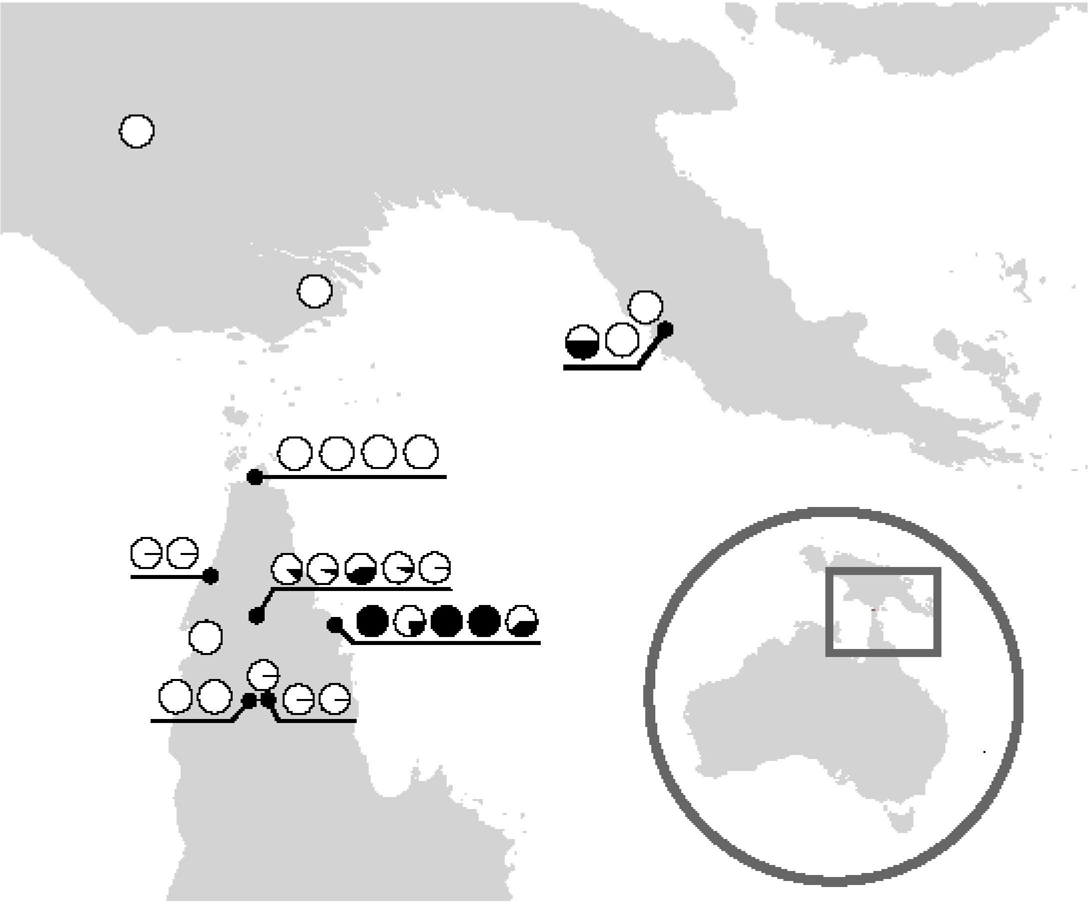


Figure 5. Admixture map
The map depicts the assortment of nuclear genomic SNP variation across individuals into two clusters (K = 2) with admixture analysis. Differentiation can be seen between Iron Range and other individuals from Cape York Peninsula and Papua New Guinea (PNG), though there is one mixed individual at Aroa, PNG. Central Cape York Peninsula individuals are more admixed than others, and two Iron Range individuals also display admixture.

After correcting for SSB, the cAUC resulted in 0.65. The average AUC value for the BIOCLIM model is 0.75. After correcting for SSB, the cAUC resulted in 0.58.

For all distribution projections, the climate-envelope BIOCLIM model had more conservative predictions than MAXENT. The mid-Holocene distribution projections of both models are more restricted than the present yet both methods show the Iron Range as suitable habitat at this time, which is the only area of suitable habitat on Cape York

Peninsula according to the BIOCLIM model. Both modelled predictions for the last glacial maximum show that Palm Cockatoo habitat was even more restricted than in the mid-Holocene, with no suitable habitat predicted on Cape York Peninsula predicted by BIOCLIM. The MAXENT prediction has suitable habitat on Cape York Peninsula at the last glacial maximum, and while there is a gap in suitable habitat to Papua New Guinea an expansive land-bridge is present.

Discussion

Our results demonstrate the importance of examining population connectivity both in the context of historical biogeographic processes, and from the viewpoint of modern population biology and cultural processes. We found shallow nuclear genomic structure within Cape York Peninsula separating Iron Range Palm Cockatoos from other Australian populations, a pattern not reflected in mitochondrial data. Admixture in SNP data suggests gene flow between Iron Range and other locations on Cape York Peninsula, though mostly in one location. We also found shallow partitioning in mitochondrial haplotypes but not nuclear SNPs between New Guinean and Australian birds. Our reconstructions of Palm Cockatoo past and present distribution had differing results depending on the method (BIOCLIM or MAXENT), though both suggest Palm Cockatoos have progressively expanded in distribution since the last glacial maximum. Below we explore in detail patterns of Palm Cockatoo persistence and recolonization with regards to changing climate, effects on population connectivity, and the likely role of these processes in determining vocal characteristics.

Genetic similarity between Cape York Peninsula and Papua New Guinea

Our data on nuclear SNPs show similarity between Cape York Peninsula Palm Cockatoos outside the Iron Range and individuals from Papua New Guinea, and is consistent with sharing of haplotypes in the mitochondrial control region found by Murphy *et al.* (2007). This lack of differentiation supports either recent recolonization of Cape York Peninsula from New Guinea following local extinctions, or ongoing connectivity between extant populations until loss of the Torresian land-bridge.

Our conservative distribution reconstruction (BIOCLIM) suggests absence of Palm Cockatoos on Cape York Peninsula at the last glacial maximum, with only small areas available by the mid-Holocene. Replenishment of Australian rainforest flora and fauna has been suggested via a connection during a short period ~7 kya when a warm-wet climate allowed expansive rainforest all along the Torresian land-bridge which was not yet submerged (Nix and Kalma 1972). However even during serious aridity, rainforest may have remained as small patches adhering to drainage routes or topographic features on Cape York Peninsula and the Torresian land-bridge (Nix and Kalma 1972), which would make complete local extinction and recolonization of Palm Cockatoos unlikely (Murphy *et al.* 2007).

Our less conservative distribution reconstruction (MAXENT) may allow connection of Australia's Palm Cockatoo habitat to New Guinea's at the last glacial maximum, but it also supports continual connectivity provided a land-bridge persisted into the early/mid-Holocene. Other species that occupy rainforest and woodland also lack genetic structure between Australia and New Guinean populations, supporting existence of suitable rainforest habitat on the land-bridge (e.g. sooty owls Tyto tenebricosa, Norman *et al.* 2002). Refugial rainforest patches are also supported by sub-species level divergence among completely rainforest-reliant Australian and New Guinean bandicoots, *Echymipera rufescens* (Westerman *et al.* 2001), pademelons *Thylogale stigmatica* (Macqueen *et al.* 2010) and logrunners (Orthonyx spp.).

The persistence of Palm Cockatoos on western Cape York Peninsula, rather than a recent complete replenishment is weakly supported by our results with the fast evolving mitochondrial ND2 region which show some very low, two base pair (bp) divergence and no haplotype sharing between New Guinea and Cape York Peninsula populations. We cannot completely distinguish between recent colonisation or ongoing connectivity based on our ND2 results because of a possible founder effect (Provine 2004), if brief replenishment resulted in only one haplotype carrying over to Cape York Peninsula from New Guinea. Sequencing the ND2 region of a greater number of New Guinea individuals is a suitable next step for confirming whether the Cape York haplotype evolved in situ with persistence, or is a result of a founder effect with replenishment.

Genetic distinctiveness of Iron Range

We found structure in nuclear SNP genomic data and a slightly divergent mitochondrial ND2 haplotype in Palm Cockatoos from the Iron Range. These findings are consistent with the unique mitochondrial control region haplotypes found by Murphy *et al.* (2007) and in conjunction with the more conservative historical distribution model support longer occupation of Palm Cockatoos at Iron Range than elsewhere on Cape York Peninsula.

Our BIOCLIM distribution model shows the Iron Range as the only area with Palm Cockatoosuitable climate for Palm Cockatoo habitat (i.e. woodland with patches of rainforest) on Cape York Peninsula in the mid-Holocene, and that there was no suitable area at all on the Peninsula during the last glacial maximum. However rainforest pockets were probably preserved at the very least at topographic refugia (e.g. the escarpment of the Great Dividing Range) due to reliable orographic rainfall. Enough rainforest for Palm Cockatoos was probably maintained at the Iron and McIlwraith ranges given the persistence of other large rainforest dependent vertebrates that have disappeared from rainforests elsewhere in Australia (eclectus parrots Eclectus roratus, Legge *et al.* 2004; green pythons Morelia viridis, Wilson and Heinsohn 2007). Evolution of a unique vocal dialect at Iron Range may have occurred in isolation in the refugial population there, similar to isolation-recombination dynamics creating dialect boundaries in other Australian parrots (e.g. ring-necked parrot Platycercus zonarius, Baker 2008; crimson rosella Platycercus elegans, Ribot *et al.* 2009; Ribot *et al.* 2012).

We consider it unlikely that Iron Range samples cluster separately as an artefact of differential DNA degradation. Although the Iron Range samples were collected within the last 18 years and were of better quality than skin and feather tissue from specimens up to 102 years beforehand, the maximum sampling gap among specimens from within Cape York Peninsula is also 102 years and there is no concomitant differentiation. It is also unlikely that our structure reflects drift as a result of sampling different generations; firstly because Palm Cockatoos breed exceedingly slowly (about one successful offspring every 10 years, Murphy *et al.* 2003), and secondly because we again see no such generation gap among Cape York Peninsula samples.

Contemporary population connectivity

Australian and New Guinean Palm Cockatoos represent separate management units due to their reluctance to cross Torres Strait (Murphy *et al.* 2007). The way variation in nuclear loci clusters separately for Australian Palm Cockatoos from Iron Range compared to elsewhere on Cape York Peninsula despite occupying the same landmass suggests a further division may be necessary.

Some connectivity between Iron Range and the rest of Cape York Peninsula is supported by admixed individuals in the Central Cape York area. Palm Cockatoos are closely associated with the gallery-forest of river corridors (Murphy *et al.* 2003), and we found individuals along the Wenlock River on Cape York Peninsula show the greatest admixture with Iron Range, strongly suggesting that this river corridor in particular is important for Palm Cockatoo movement between differentiated populations. The northern section of the Great Dividing Range may separate the Iron Range population from the other areas on Cape York Peninsula due to association with catchments that flow in opposite directions. The small distance (3km) between the Wenlock (west-flowing) and Pascoe (east-flowing) rivers at one point north of Iron Range may allow sufficient dispersal for the admixture we found. The Great Dividing Range (824m at McIlwraith Range) itself is also a plausible barrier to dispersal as mountains explain population structure in other large parrot species (e.g., scarlet macaws Ara macao, Olah *et al.*), and Palm Cockatoos occur most commonly below 750m in New Guinea (see Murphy *et al.* 2007 and references therein). A modelling approach based on hypotheses about contemporary connectivity may provide the extra information required for assessments of future population viability (Keighley *et al.* in prep).

Despite differentiation representing separate populations, the divergence we found in nuclear SNPs was low compared to sub-species level structure in rainforest restricted birds of the region (e.g., logrunners Norman *et al.* 2002; black butcherbirds Cracticus quoyi Kearns *et al.* 2013). Low heterozygosity (θ) and nucleotide diversity (π) within-populations outlines two possibilities, that low divergence between the two populations reflects either small effective population size in the ancestral population, or gene flow. Although heterozygosity estimates can be calculated, parameter estimation of effective population size proves to be unreliable when derived from ddRAD SNP data such as this (Shafer et al. 2016). The results of our admixture analysis provide evidence that some two-way gene flow may have ameliorated divergence of the Iron Range population; which combined with the extremely slow life history strategy of Palm Cockatoos (Murphy *et al.* 2003), and the recency of population split could explain shallow divergence. The prevalence of the Cape York Peninsula ND2 haplotype at Iron Range suggests more recent introgression than between Cape York Peninsula and New Guinea which don’t share haplotypes in this fast-evolving region of the genome.

There is a small possibility that emigration from Iron Range is less prominent since we do not find the unique ND2 (or CO2, Murphy *et al.* 2007) haplotype from Iron Range elsewhere despite greater sampling effort representing the broader Cape York Peninsula population. If so, this restriction may only apply to females who transmit mitochondrial DNA (Marais 2007). Furthermore, the slope of the Great Dividing Range escarpment is more gentle west-to-east (Figure 1a) creating an interesting possibility that one-way dispersal into Iron Range could result from topographical gradients in a similar way to small scale weather dynamics influencing sea-bird movements (Schneider 1991). We consider it more likely though, that any bias to dispersal into Iron Range would result from a disproportionately slow reproductive rate creating a population ‘sink’ there (Heinsohn *et al.* 2009).

Culture and connectivity

Connectivity restrictions may also result from behavioural differences. Parrot vocalisations have social functions (Bradbury and Balsby 2016) and cross-dialect dispersers might experience greater difficulty establishing a territory, acquiring a mate or admission into social groups (Marler and Tamura 1962; Nottebohm 1969; Slabbekoorn and Smith 2002). Vocalisations and drumming behaviour feature significantly in Palm Cockatoo courtship displays (Zdenek *et al.* 2015) and drumming may be sexually selected (Heinsohn *et al.* 2017). Iron Range Palm Cockatoos have unique vocal dialects (Keighley *et al.* 2016) and may drum more frequently (personal observations). Immigrating males that drum less and are vocally different might have lower reproductive fitness and impeded social interaction (e.g., yellow-naped amazons, Salinas-Melgoza and Wright 2012) which might be maintaining the genetic divergence we find in the Iron Range population (see also Irwin 2000; Ribot *et al.* 2012).

Alternatively, vocal learning can preserve dialects without impeding gene flow (e.g. Wright *et al.* 2005; Baker 2008; Salinas-Melgoza and Wright 2012). However dialect preservation can reflect processes that limit cross-population movement such as short distance dispersal and high philopatry (e.g. Yellow-naped Amazons *Amazona auropalliata*, Salinas-Melgoza and Wright 2012). High philopatry is a known characteristic of Palm Cockatoos (Murphy *et al.* 2003) and could contribute to maintenance of their vocal dialects through limited dispersal.

Conclusion

Our data provide evidence for considerable connectivity between resident Australian and New Guinean Palm Cockatoo populations prior to geographic separation, but also show prominent genetic differentiation within Australian populations that align with vocal dialect boundaries. We show that genetic differentiation within Australia could have evolved in historical climatic refugia, which probably coincided with evolution of a unique vocal dialect there. Genetic mixing among Australian populations suggests some connectivity among vocally distinct populations, and that the distinct dialects are maintained through learning by immigrant individuals (as in Wright *et al.* 2005; Baker 2008). Our data also suggest the possibility that Palm Cockatoo dispersal into Iron Range outweighs dispersal out of the region, which alongside local declines characterize it as a ‘sink’ population (Heinsohn *et al.* 2009). Our results represent the only genetic study of Palm Cockatoos at the population scale. Although divergence is shallow compared to sub-species level structure in other species, preservation of unique vocal dialects, tool use behavior and the little remaining genetic diversity between the distinct sub-populations is a primary concern for future conservation management in this species. The unique characteristics of the Iron Range population make it key for future conservation effort.

Acknowledgements

We would like to thank Sam Banks, Leo Joseph and Kerensa McElroy for advice and direction, George Olah and Todd Cross for advice on feather examples, Sonal Singhal for advice on using the Rainbow assembler and Matteo Fumagalli for assistance with ngsTool. For valuable assistance and companionship in the field we thank Chris Sanderson, Maddie Castles, Zoe Reynolds, Claudia Benham, Richie Southerton and Andrew Neilen. We thank Dejan Stojanovic for assistance with grant applications, Xenia Weber and one anonymous reviewer for feedback on the manuscript, Julie Brokenbrow, Eridani Mulder and Kristy Philliskirk for providing feathers.

Author contributions

The idea for this study was conceived by R.H. who alongside N.E.L. contributed substantial resources, funding and edits the manuscript. The molecular and modelling methods were developed, conducted and written by J.V.P. alongside the results. The remaining manuscript was written with genetic samples collected and collated by M.V.K. and S.A.M extracted additional DNA from bloods and tissue and commented on the manuscript.

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Supplementary methods section

DNA sequencing

We used a modified version of the hyRAD protocol to screen the nuclear genome for anonymous SNPs (Suchan *et al.* 2016). The hyRAD protocol uses double-digest restriction digest (ddRAD) sequencing libraries as probes for a sequence capture to screen for thousands of SNPs (Peterson *et al.* 2012; Suchan *et al.* 2016). As the hyRAD protocol has been described in detail by Suchan et al. (2016), we focus on the modifications. We used the Iron Range samples for probe design as those samples had the highest quality DNA. A standard ddRAD library preparation protocol was carried out using the restriction enzymes *PstI* and *EcoRI* (Peterson *et al.* 2012). After the adapter ligation step, all five samples were pooled together and we used a LabChip XT to select for a size range of 345-407 bp. Half of the output from the LabChip XT proceeded to a standard ddRAD library while the other half was converted into probes for hyRAD-like capture. For the subsample to be turned into probes, we amplified the libraries using IS7 (5’ ACACTCTTTCCCTACACGAC 3’) and IS8 (5’ GTGACTGGAGTTCAGACGTGT 3’) to generate enough probe DNA. The probes were deadapterized with another restriction digest of *PstI* and *EcoRI*. Finally, we attached short biotinylated adapters, specifically designed to bind only to the restriction sites, using NEB Quick Ligase. The probes were stored in -20°C until the capture was ready.

To prepare shotgun genomic libraries, we used the protocol outlined by (Meyer and Kircher 2010). All samples except for those from the Iron Range were prepared as genomic libraries. The DNA quality was checked using an agarose gel. From the agarose results, only the feather samples needed additional shearing. The feather samples were sheared using a Diagenode BioRuptor on high for 6 cycles of 15 seconds on and 90 seconds off prior to library preparation. All samples underwent a double-ended bead size selection before and after the library preparation to reduce DNA fragments < 200bp and > 500bp. Samples from the different tissue type (toe-pads, and feathers) were pooled separately into three 2ug pools. Within each pool, the samples (5 toe-pad, 4 toe-pad, and 18 feather samples) were pooled equimolarly.

To prepare for the capture, the library pools were dried down completely and we added a hybridization mix similar to Peñalba *et al.* (2014). We added 25uL Agilent Hybridization Buffer, 5uL 10X Agilent blocking agent, 5uL Hybloc Chicken, 3uL of a blocking oligo mix, and 12uL containing 500ng of the biotinylated ddRAD probes. The reaction was incubated in 95°C for 10 minutes to denature the DNA and probes and incubated at 65°C for 48 hours to perform the hybridization. We cleaned 20uL of Streptavidin beads using 1X TEN buffer according the hyRAD protocol. We resuspended the cleaned Strepatividin beads with the 50uL hybridization mix and incubated for 30 min at 23°C to attach the biotin to the Streptavidin. We removed the supernatant and cleaned the beads using the SSC/SDS buffers according to the hyRAD specifications. To melt the libraries off the beads, we added 30uL of water to the cleaned beads and incubated the reaction in 95°C for 5 minutes. We used 15uL of this to amplify using IS5 (5' AATGATACGGCGACCACCGA 3') and IS6 (5' CAAGCAGAAGACGGCATACGA 3') for sequencing. Finally, we sequenced the hyRAD and ddRAD libraries using 47% and 6%, respectively, of a high-throughput NextSeq500 lane for 150bp, paired-end in the ACRF Biomolecular Resource Facility.

After confirming whole mitochondrial genome by-catch from the sequence capture, we sequenced an additional fragment of the mitochondrial ND2 (NADH dehydrogenase subunit 2) gene for the Iron Range samples, which were not included in the capture pools. We amplified ND2 using the primers L5204 (5’ TAACTAAGCTATCGGGCGCAT 3’) and H6312 (5’ CTTATTTAAGGCTTTGAAGGCC 3’) (Sorenson *et al.* 1999). We used this gene as it is proposed to be fast-evolving (Pacheco *et al.* 2011) and to use a different mitochondrial gene from previous studies (Murphy *et al.* 2007). Lastly, we sequenced the amplified fragments using an ABI 3100.

Data processing

The hyRAD and ddRAD-derived data sets were filtered differently as the ddRAD data is expected to have PCR duplicates. Since the hyRAD data is from a sequence capture, we utilized the first two scripts from the existing pipeline (https://github.com/MVZSEQ/SCPP) to filter the raw reads. For the ddRAD-derived data set, we used a custom python script to filter out low complexity reads common in NextSeq500 data. Finally, we utilized Trimmomatic to trim off low quality bases and the first 9 bp which contains the individual barcodes and restriction cut sites (Bolger *et al.* 2014). The resulting cleaned reads were used for remaining analyses.

The cleaned Iron Range ddRAD data were used to assemble the nuclear reference sequence set. We used the assembler Rainbow which is specifically designed to assemble paired-end ddRAD data sets for each sample (Chong *et al.* 2012). To finalize the reference contig set we used vsearch to cluster homologous contigs between the individual Rainbow assemblies (Rognes *et al.* 2016). The same reference contig set was used to map all the individuals. For the mitochondrial sequences, we performed a de novo assembly of the samples AMNH781401, AMNH619297, AMNH619295, AMNH425703, and AMNH425700 using SOAPdenovo (Luo *et al.* 2012) and the final assemblies script in (https://github.com/MVZSEQ/SCPP). We used BLAST in the assembled contig to find the mitochondrial genome and used the contig from AMNH781401 as a reference (Altschul *et al.* 1990). Finally, Bowtie2 was used to map the cleaned reads to the reference contig set (Langmead and Salzberg 2012).

For low-coverage data-sets, using genotype likelihoods performs better for calculating population genetic statistics compared to direct genotyping (Nielsen *et al.* 2011; Nielsen *et al.* 2012). ANGSD was used for SNP filtering and genotype likelihood calculations (Korneliussen *et al.* 2014). We employed multiple filters to obtain high quality SNPs for analyses. We only used contigs with a minimum coverage of 2x and maximum coverage of 40x per individual. For the population filter, at least 3 (out of 5) and 10 (out of 27) individuals within the Iron Range and Cape York Peninsula + Papua New Guinnea populations should pass the coverage filter, respectively. We used tools within ngsTools to find SNPs that overlapped between the two populations so the genetic distances are not biased to SNPs that are were only genotyped within a single population (Fumagalli *et al.* 2014). Lastly, we filtered against contigs with >5 SNPs which may be putative repeat or paralogous region (< 1% of the contigs). Only unlinked SNPs (one SNP per locus) were carried through to the population structure and all SNPs within all loci were carried through for the other population genetic statistics.

To recover the corresponding ND2 sequence from the mitochondrial genomes, we extracted a fasta file per mitochondrial genome alignment. Any bases that were suspected to be heterozygotes or had coverage lower than 10X were converted to ambiguous Ns. We used a local BLAST alignment to find the sequence fragment that corresponded to the Sanger sequenced ND2 sequence (Altschul *et al.* 1990). Finally, we aligned the samples using MAFFT (Katoh *et al.* 2002; Katoh and Standley 2013).

Population structure and statistics

We recovered the nuclear genome population structure using ngsDist in the ngsTools kit (Fumagalli *et al.* 2014; Vieira *et al.* 2016). We used the genotype likelihood output of ANGSD as input for ngsDist to incorporate the uncertainty in the distance measures. Finally we used the distance matrix produced by ngsDist to create a network in SplitsTree (Dress *et al.* 1996). Lastly, we used the getMDS.R in ngsTools to summarize the distance information using multidimensional scaling (MDS). For the ND2 population structure, we visualized the haplotype network using a minimum spanning network in PopArt (Leigh and Bryant 2015).

We then used ngsAdmix to try to detect additional population structure and estimate admixture between populations (Skotte *et al* 2013). A minor allele frequency cut-off of 0.01 was used in the admixture analyses. We ran ngsAdmix from K = 2 to K = 5 with 10 replicates for each K. We then used the standard deviation of the replicates within each K to select the best number of clusters. Finally, we used CLUMPP to combine the different replicates within K = 2 and K = 3 (Jakobsson & Rosenberg 2007).

We used the allele frequencies from ANGSD to calculate population genetics summary statistics. We used F_{ST} (Reynolds *et al.* 1983) to estimate population differentiation between the Iron Range population and the Cape York Peninsula + Papua New Guinea population with ANGSD's realSFS. To calculate population divergence (d_{xy})

we used calcDxy.R in ngsTools. The calculation uses the allele frequencies from the genotype likelihoods and the following equation

$$d_{xy} = \sum(f_{A1} * (1 - f_{A2}) + (f_{A2} * (1 - f_{A1})) / n$$

where f_{A1} is the allele frequency in one population, f_{A2} is the allele frequency in the other population and n is the sequence length. Lastly, we calculated per site heterozygosity (θ) and per site nucleotide diversity (π) for each population using ngsTools and ANGSD. Since we didn't have an ancestral reference sequence, we used a folded site frequency spectrum to obtain θ. Lastly, we calculated divergence after population split (D_A) using the equation

$$D_A = D_{xy} – (\pi_1 + \pi_2) / 2.$$

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Not yet submitted

Chapter 5: Genetic and vocal data show that topography and restricted habitat corridors determine population connectivity in a large parrot.

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Abstract

In animal populations, landscape level processes such as dispersal are often difficult to observe in real time yet have serious consequences for the persistence of local populations and entire species. Dispersal is theoretically influenced by the spatial distribution of landscape features such as habitat and can be inferred from interaction patterns among populations, for example with landscape genetics approaches. However, elucidating how individual landscape features influence dispersal is difficult without tracking devices, which are rarely feasible for large birds that may be difficult-to-capture and are easily stressed. We predicted the extent of connection between palm cockatoo sub-populations through their range in north-eastern Australia using electrical circuit theory and hypothetical 'resistance' surfaces that represented the influence of habitat use and elevation. We tested predictions with genetic and behavioural data known to vary with landscape level interaction patterns. We used 1132 single nucleotide polymorphisms in 342 loci, partial vocal repertoires and vocal dialects. Genetic and acoustic variation in two vocalization types corresponded with resistance predictions based on landscape elevation and rainforest distribution. In contrast, variation in partial vocal repertoires did not correlate with resistance values from any of our model landscapes. Our results provide a rare demonstration of electrical circuit theory's utility for informing relationships among different data sources, and indicate that elevation and narrow rainforest corridors influence

landscape-scale movement in this large, difficult-to-capture parrot species, helping to identify particularly important areas for population connectivity.

Introduction

Small populations that have undergone population decline can suffer from altered sex and age class distributions, loss of genetic diversity and a higher risk of extinction (Frankham 2005). Local declines may not affect overall meta-population viability if numbers are replenished by dispersal, which 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 more detailed assessment beyond dispersal distance 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 may be logistically difficult for some species.

Non-invasive techniques for predicting dispersal through landscapes with heterogeneous resistance to movement has been improved by the use of electrical circuit theory (McRae 2006). This effectively models population connectivity by integrating multiple movement paths between populations through hypothetical resistance-to-flow (resistance) surfaces. These ‘model landscapes’ can integrate an animal’s range and theoretical movement capabilities with different hypotheses about the landscape’s resistance to animal movement. The models’ hypothetical connectivity estimates between pairs of locations can then be validated by comparing the predicted movement resistances to other kinds of population interaction data such as landscape genetics, or vocal dialects (McRae *et al.* 2008).

Genetics can be useful in assessing population connectivity by examining how diversity is differentiated among separate locations (Balkenhol *et al.* 2009). However, the ability to explicitly distinguish between connectivity hypotheses in heterogeneous landscapes can be greatly improved using alternative data sets, vocal dialects for example (Amos *et al.* 2012; Pavlova *et al.* 2012). 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). Fine-scale acoustic structure of avian vocalisations can theoretically reflect landscape-scale patterns of social interaction in this way (e.g. Irwin 2000; Ribot *et al.* 2012), and may complement genetics with information about meta-population processes on more recent time scales (Janik and Slater 2000; Laiolo and Tella 2005; Laiolo and Tella 2006; Laiolo and Tella 2007). Parrots are especially good vocal learners and have been shown to adjust their calls based on their territorial neighbours or social partners (Farabaugh *et al.* 1994; Hile *et al.* 2000; Walløe *et al.* 2015) leading to a high likelihood that vocal evolution aligns with landscape scale processes in parrots (e.g. Bradbury *et al.* 2001).

In this study we used variation in vocal behaviour and population genetics to determine the landscape features behind meta-population structure of 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 IUCN criteria (2012). Palm cockatoos have exceedingly slow reproduction as well as a specific association with rainforest within a larger matrix of woodland area (Murphy *et al.* 2003). In a previous contribution we show genetic structure among Australian palm cockatoos with some degree of gene flow between separate, vocally distinct populations (Keighley *et al*. in prep.), and immigration may be especially important for maintaining one of these populations that could otherwise be undergoing rapid decline (Heinsohn *et al.* 2009). Identification and preservation of landscape-scale movement corridors for dispersal are especially important for preventing local extinctions in this species.

We aim to identify the key landscape features that influence movement for palm cockatoos throughout their Australian range. Our hypotheses about palm cockatoo movement were represented in five model landscapes, which output resistance values (cumulative movement cost) between populations based on electrical circuit theory. Our hypotheses were (1) isolation by distance (null model), (2) dependence on rainforest, (4) impedance by elevation and (5) impedance by elevation alongside dependence on rainforest. We validated our hypotheses by comparing resistance distances among populations to pre-existing data about acoustic and genetic variation. Alongside important conclusions about the structure of the meta-population of Australian palm cockatoos, our use of two types of data (genetic and acoustic) provides an excellent demonstration of the value of electrical circuit theory for unravelling population structure in species that may otherwise be difficult to capture and observe moving through remote landscapes.

Methods

Study species

Palm cockatoos (*Probosciger aterrimus*) are large (up to 1kg), charismatic parrots which 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 containing multiple nesting hollows in the ecotone between open woodland and rainforest. The distribution of palm cockatoos in Australia has not had thorough bioclimatic investigation (but see Keighley *et al.* in prep.), however field studies have provided information about their habitat use (Murphy 2005). New Guinean palm cockatoos are found in the lowlands up to 1300m elevation though are most common below 750m (Juniper and Parr 1998).

Australian palm cockatoos occur in greatest density in woodland within 1km of rainforest (Wood 1984), especially where there are small patches of rainforest or linear corridors of gallery forest (Murphy 2005). Habitat contractions associated with aridification probably caused contractions in their distribution during arid periods in the Pleistocene (Keighley *et al.* in prep.) as in other rainforest dependent species (e.g. New Guinean bandicoots, *Echymipera rufescens*, Westerman *et al.* 2001, pademelons *Thylogale stigmatica*, Macqueeen *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). They occur at lower densities in continuous rainforest and do not cross open water (Igag 2002; Murphy *et al.* 2003). On Cape York Peninsula, the largest patch of rainforest extends along the eastern coast and includes the Iron and McIlwraith Ranges. This rainforest area supports what is thought to be one continuous palm cockatoo population, however this population is thought to be in severe decline unless supported by sufficient dispersal from populations elsewhere (Heinsohn *et al.* 2009).

Study sites

This study draws on acoustic and genetic data presented elsewhere for other purposes (Keighley et al 2016; Keighley et al in prep). Five major palm cockatoo populations on Cape York Peninsula, Australia were used for acoustic recordings in this study. Moulted feathers found at these and other locations were combined with blood and skin samples from museum collections for genetic analyses (see Keighley *et al.* in prep.; Figure 1). Piccaninny Plains Wildlife Sanctuary, Steve Irwin Wildlife Reserve and Moreton Telegraph Station are on major river systems inland on Cape York Peninsula, the free-hold lands around Bamaga are on the northern tip of Cape York Peninsula, and Iron Range National Park is on the eastern side of Cape York Peninsula (Figure 1). An additional site was used at the southernmost point of the species' recorded range near Port Stewart (Figure 1). The greatest geographic distance between populations was between 50km and 402km. Distances between sites ranged from 1.5 to 40.7km, and each site was visited at least once in the morning and once in the afternoon on a minimum of two occasions each year, with the exception of the Bamaga sites which were visited only in 2014. Data from Iron Range were collected by an experienced field researcher during the 2014 season, while the other populations were visited sequentially by MVK and volunteer research assistants in 2013 and 2014.

Recordings

Recordings of unmarked, wild palm cockatoos were made and analysed in Keighley *et al.* (2016), with a summary of the methods and results presented here. Recordings were

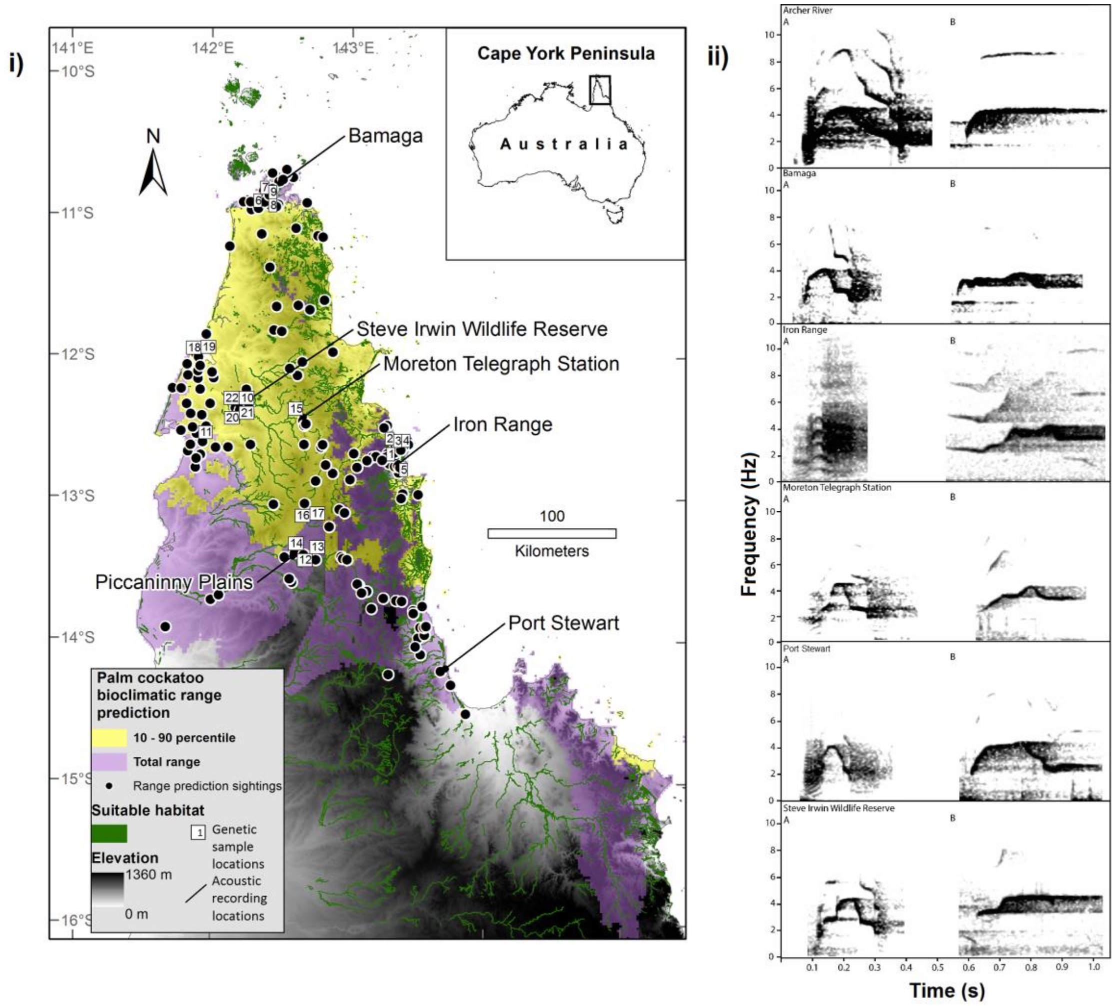


Figure 1. (i) The topography, suitable habitat and bioclimatic distribution prediction for palm cockatoos (*Probosciger aterrimus*) on Cape York Peninsula with genetic sampling locations and georeferenced sightings used for predicting the palm cockatoo distribution. (ii) Sectrograms of representative contact calls from six locations on Cape York Peninsula marked on the map. Note: 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).

collected between June-October 2013, and from July-November 2014. Spectrograms were created using RavenPro v. 1.5 (Charif *et al.* 2008), allowing acoustic measurements to be made which were used in statistical call analyses. The proportion of shared calls between each repertoire was assessed using pairwise discriminant function analyses (DFAs) quantified using Bray Curtis dissimilarity to produce a matrix of dissimilarity values (Keighley *et al.* 2016). The two most common and distinct varieties of the contact call (Bradbury 2003; Zdenek *et al.* 2015) from each population were also compared with DFA.

Mahalanobis distances between their multivariate means produced a dissimilarity matrix for each call type (Keighley *et al.* 2016).

Genetic structure

Nuclear single nucleotide polymorphisms (SNPs) at 342 loci were screened in Keighley *et al.* (in prep.), the methods and results used in this study are briefly summarized here. DNA from 27 palm cockatoo samples (5 blood, 9 skin and 13 moulted feathers) from Cape York Peninsula and southern New Guinea was extracted and the nuclear genome screened for anonymous SNPs (Suchan *et al.* 2016, Keighley et al. in prep). The resulting allele frequencies were used to calculate population genetics summary statistics (e.g. F_{ST}), and population divergence (D_{xy}) was calculated using calcDxy.R in ngsTools. Admixture between populations and any additional population structure was investigated with ngsAdmix (Skotte *et al.* 2013).

Based on genetic variation in the nuclear genome, Cape York Peninsula (CYP) samples were generally indistinguishable from Papua New Guinean (PNG) samples, but Iron Range (IR) samples were distinct (F_{ST} = 0.514). Absolute divergence was low (D_{xy} = 4.98e-3 per site, with equivalent relative divergence of D_A = 4.97e-3 per site) and so was per site heterozygosity (Watterson's θ) within each population (θ_{IR} = 5.42e-6 and $\theta_{CYP\&PNG}$ = 5.19e-6). The per site nucleotide diversity (π) was also low within each population (π_{IR} = 6.38e-6 and $\pi_{CYP\&PNG}$ = 8.39e-6). The admixture analyses shows support for K = 2 generally differentiating the Iron Range from the rest of the individuals with some two way gene flow (Keighley *et al.* manuscript in preparation-b).

Distribution prediction

BIOCLIM analysis

We used the ANUCLIM software package, specifically BIOCLIM (Hutchinson *et al.* 2009b), to predict the bioclimatic space occupied by palm cockatoos in Australia (Nix 1986; Hutchinson *et al.* 2009b). To derive the preferred climatic envelope of palm cockatoos we used an evenly spaced subsample of georeferenced sightings from our own records and Birdlife Australia (unpublished dataset), examined to remove any spurious location data (e.g. offshore). These locations were combined with elevation data from a recent digital elevation model (Hutchinson *et al.* 2009a) in BIOCLIM to calculate percentiles for six climatic parameters. Extreme values of each climatic parameter were hypothesized to limit palm cockatoo distribution: annual mean temperature, warmest period max temperature, coldest period min temperature, annual precipitation, warmest quarter precipitation and coldest quarter precipitation.

We derived two predicted distributions from the georeferenced sightings data; one representing the total range of the species based on minimum and maximum predicted bioclimatic values, and a more restrictive distribution given by the 10 – 90 percentile of the multivariate bioclimatic profile. The 10-90 percentile levels are considered to reasonably represent a species' 'core' distribution (e.g. Lindenmayer *et al.* 1991). Core area has the greatest conservation value and might act as refugia under changing climatic conditions. The total derived distribution of the species was used to constrain subsequent connectivity analysis.

Palm cockatoo preferred habitat

All georeferenced sightings were combined with maps of broad vegetation groups from the regional ecosystems classification scheme (Queensland Herbarium 2015) in *ArcGIS 10.4*

(ESRI 2011) to determine habitat preferences for palm cockatoos. 500m buffers were created around each waypoint forming a sample area of 217 km^2. We took the total area covered by 66 habitat types on Cape York Peninsula, and calculated the proportional area occupied by each habitat type within the predicted range of palm cockatoos. We then calculated the expected area of each habitat in our sample under no habitat preference by multiplying the proportion of each habitat in the predicted range by the total sample area. We tested if expected habitat area differed from our sampled area using a Chi Square test. Habitat types in our sample which covered at least double their expected area were considered preferred habitat, and were hypothesised to offer the least resistance to palm cockatoo movement subsequent connectivity models.

Landscape connectivity predictions

We constructed five model landscapes to represent each of five hypotheses about palm cockatoo population connectivity. Using electrical circuit theory and *Circuitscape (McRae 2006)* each model landscape produced resistance values in pairwise fashion between ‘sources’. Resistance values were then used as independent variables to test their effects on acoustic and genetic distance between source pairs. During comparison with acoustic data the sources were defined as the six populations and in contrast, during comparison of resistance values with genetic distance, sources were the 22 sampling locations (Figure 1).

We used spatial analysis techniques in *ArcGIS 10.4* (ESRI 2011) to create five landscape grid models of cell size 300m × 300m for the predicted range of palm cockatoos on Cape York Peninsula. Cell size of 300m was chosen as it is smaller than palm cockatoo range size (approx.1.5km^2) and is approximately the maximum distance from rainforest they choose to nest (Murphy *et al.* 2003). Model 1 represented the isolation by distance hypothesis (null model) and all cells were attributed a value of 1. In each subsequent model, grid cells had a numeric resistance value that reflected a hypothesized resistance to palm cockatoo movement based on vegetation type and elevation. Model 2 represented dependence on rainforest with resistance values reflecting continuous distance from rainforest (as per the “cost distance” function in the Spatial Analyst toolbox, *ArcGIS 10.4*; ESRI 2011) and was characterised by resistance values ranging from 0 to 58,870. Model 4 represented impedance by elevation using elevation data from the GEODATA 9 second digital elevation model version 3 and included resistance values ranging between 0 and 655 m above sea level (summarized in Figure 1) (Hutchinson *et al.* 2009a). Model 5 represented combined impedance by elevation and association with rainforest, with summed resistance values from the previous two grids (cost distance + elevation) including values ranging between 0 and 58,938.

To test for effects of landscape models on acoustic and genetic distances we used two different approaches; causal modelling with simple Mantel and partial Mantel tests (Samuel A. Cushman *et al.* 2006), and multiple regression modelling of distance matrices (MRDM) (Legendre *et al.* 1994). Both approaches were implemented in R (R Development Core Team 2016); causal modelling in the ‘vegan’, and MRDM in the ‘ecodist’ libraries. We began causal modelling with simple Mantel tests of the null model and each landscape resistance model with acoustic and genetic distance measures. We then used partial Mantel tests to assess the significance of any relationships ($P < 0.05$), given the spatial distance between our source locations. When there was a significant correlation in the first partial Mantel test, we used a second partial Mantel test to calculate the effect of geographic distance (the null model) on acoustic and genetic distances while controlling for the landscape resistance model. When the first partial Mantel test was significant but not the second, we inferred significant effects of the landscape resistance model on acoustic or genetic distance, beyond the effects of geographic distance (Samuel A. Cushman *et al.* 2006; Smith *et al.* 2014). For MRDM, we analysed the null model separately and then together with each landscape resistance model. Thus, these models included one predictor for IBD and a maximum of two predictor variables for all other models (Smith *et al.* 2016).

We generated cumulative current maps for every pair of samples with *Circuitscape* to identify areas which contribute most to connectivity between sample sites (McRae et al. 2013). Maps were visualized in *ArcGIS 10.4* (ESRI 2011).

Results

Range and habitat preferences

Bioclimatic distribution

BIOCLIM range predictions totaled 63,752 km^2 of climatically suitable area for palm cockatoos in two major areas separated by 37 km. The larger of the two areas (54,749 km^2) encompasses the whole of Cape York Peninsula north of Princess Charlotte Bay and includes approximately 26,928 km^2 of core area. The smaller area (8,829 km^2) includes Cape Melville and extends southwards to Port Douglas (Figure 1) and has only 345 km^2 of core area. However no sightings of wild palm cockatoos have been recorded within the second, more southerly area.

A small portion of core area (1413 km^2) near (but excluding) the Iron Range recording sites is separated from the major core area on Cape York Peninsula by the Great Dividing Range (incorporating Tozer, McIllwraith and Iron Ranges) which runs from north to south along the east coast of Cape York Peninsula (Figure 1). The mountain range is within the total distribution of palm cockatoos, yet is excluded as core habitat. Moreton Telegraph Station, Piccaninny Plains and the Steve Irwin Wildlife Reserve populations occur within the core area, whereas the population at Bamaga is just outside (Figure 1).

Defining habitat preferences

We identified seven broad vegetation groups (34e, 4b, 2d, 2c, 2b, 22c, 3a; Table 1) that were disproportionately represented within 500m of palm cockatoo sightings (χ^2 [1, N = 51] = 271.8, P = 0.05), their combined distribution is shown in Figure 1.

Table 1. Description of broad vegetation groups determined to be suitable palm cockatoo habitat.

Broad vegetation group	Area in range (km^2)	Area in sample (km^2) (OBS)	Expected area with sightings habitat (km^2) (EXP) *	Description
CYP total area	70067.8	217		
34e	0.8	0.4	< 0.1	Spring wetlands. Occurs on undeformed fine-grained sedimentary rock (limestone).
4b	1462.7	20.0	4.5	Semi deciduous mesophyll to notophyll vine forest which can include *Nauclea orientalis* (Leichhardt tree), *Bombax ceiba* var. *leiocarpum* (bombax), *Semecarpus australiensis* (tar tree), *Terminalia sericocarpa* (sovereignwood), *Canarium australianum* (scrub turpentine), *Gyrocarpus americanus* (helicopter tree), *Castanospermum australe* (black bean), *Aleurites moluccanus* (candlenut) (candlenut) and *Alstonia scholaris* (milky pine). Mainly occurs in catchments on loamy alluvia.
2d	153.9	5.3	0.5	Semi-deciduous notophyll to mesophyll vine forest commonly with *Cryptocarya* spp., *Buchanania arborescens* (native mango), *Bombax ceiba* var. *leiocarpum*, *Ficus albipila* var. *albipila* and *Terminalia sericocarpa* (Damsonwood). The evergreen *Alstonia scholaris* (milky pine) may occur as either a canopy or emergent tree. Occurs on basalt rises and cones.
2c	735.6	11.8	2.3	Simple evergreen notophyll vine forest with or without *Wodyetia bifurcata* on colluvium of granite ranges. Occurs only on the slopes and colluvial sediments of granite ranges.
2b	155	2.9	0.5	Semi-deciduous mesophyll to notophyll vine forest commonly including *Aleurites moluccanus* (candlenut), *Argyrodendron polyandrum* (brown tulip oak), *Alstonia scholaris* (milky pine), *Garuga floribunda* var. *floribunda*, *Bombax ceiba* var. *leiocarpum* and *Canarium australianum* (scrub turpentine). Occurs on granite slopes.
22c	640.03	5.6	2	Fringing woodland of Melaleuca leucadendra, Lophostemon grandiflorus, Eucalyptus camaldulensis and Livistona rigida. Corymbia aparrerinja and Lysiphyllum cunninghamii occur on sandier levees and Eucalyptus microtheca occurs on finer textured lower alluvial terraces on lower reaches.
3a	442.1	3.9	1.4	Evergreen to semi-evergreen notophyll vine forest dominated by *Syzygium forte* subsp. *forte*, *Terminalia muelleri* (Australian almond), *Mimusops elengi* (tanjong) and *Buchanania arborescens* (satinwood). Occurs on coastal dunes and beach ridges in dunefields.

CYP: Cape York Peninsula; * Habitat area in range / Total range area × Area in sample.

Testing landscape level connectivity

Vocal repertoire dissimilarity did not correlate with any of our resistance predictions. We found significant effects of elevation (Model 3) on short whistle similarity (r = 0.682, P = 0.014) and genetic distance (r = 0.594, P = 0.001), though only the effect on genetic distance was supported by our MRDM analysis (R^2 = 0.362, P = 0.001) (Table 2).

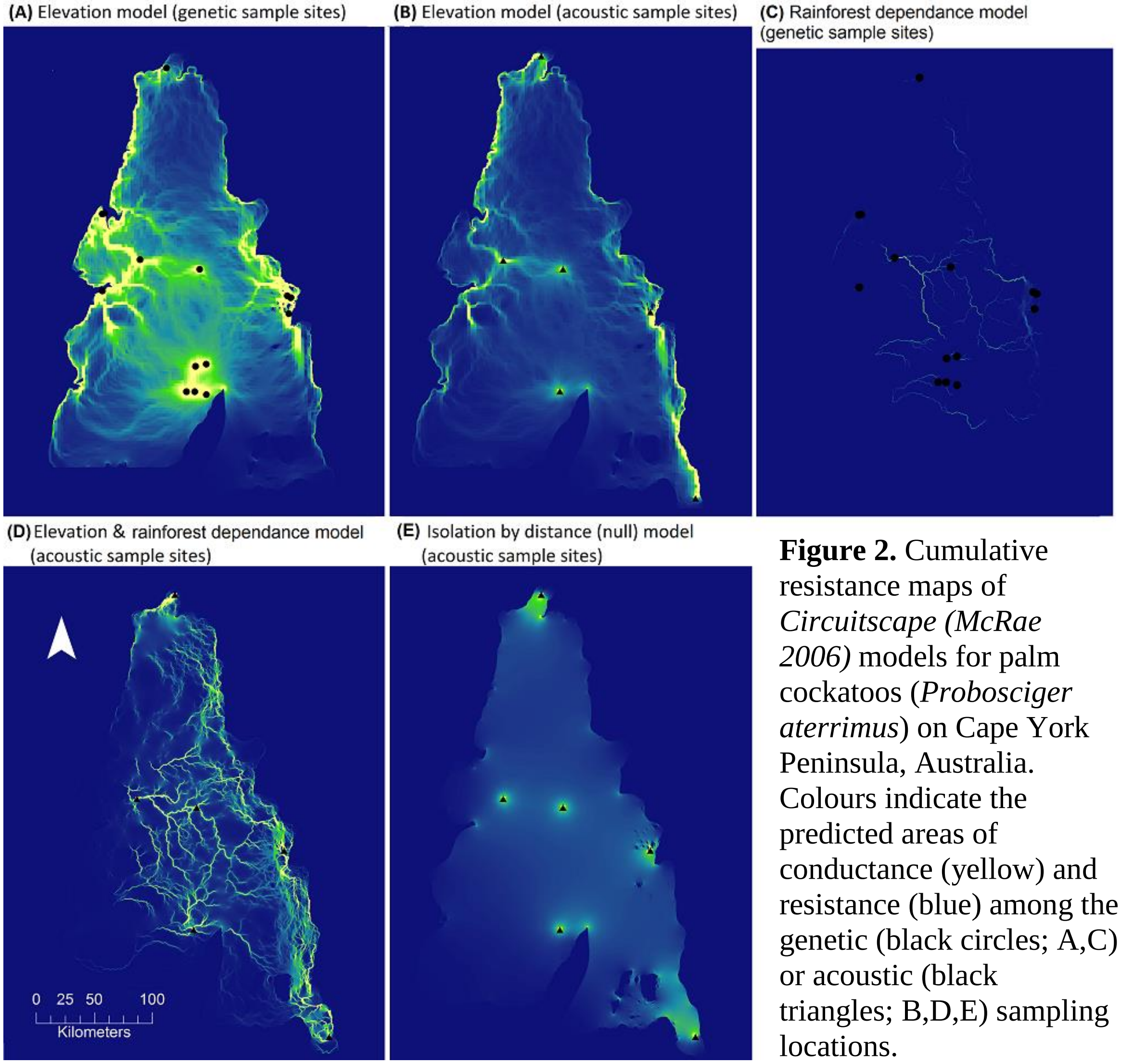
Table 2. The effects of geographic distance (Null) and landscape resistance models on several measures on vocal dissimilarity (partial repertoires and two contact call types) and genetic distance using causal modelling and multiple regression distance matrices (MRDM)

		Mantel test		Partial Mantel tests				MRDM	
		Distance measure × movement model		1) Distance measure × movement model (null partialled out)		2) Distance measure × null (movement model partialled out)		Accoustic distance ~ null ± other movement models	
Movement model (predictor)	Distance measure (independent variable)	*r*	*P*	*r*	*P*	*r*	*P*	R^2	*P*
1) Null, isolation by distance: Grid values = 1	Repertoire	0.200	0.385					0.040	0.782
	Short whistle	0.398	0.161					0.158	0.325
	Broadband contact call	-0.086	0.360					0.007	0.976
	Genetic divergence	0.125	0.117					0.016	0.259
2) Dependence on rainforest: Accumulating cost with distance from rainforest	Repertoire	0.336	0.149	0.285	0.299			0.258	0.624
	Short whistle	0.123	0.392	-0.039	0.436			0.168	0.686
	Broadband contact call	0.623	0.114	0.717	0.056			0.712	0.138
	Genetic divergence	-0.454	1	-0.445	1			**0.210**	0.015
3) Elevation impedance: Grid values = Elevation (0 – 655)	Repertoire	0.494	0.169	0.647	0.076			0.442	0.164
	Short whistle	**0.660**	0.022	**0.682**	0.014	-0.448	0.842	0.549	0.064
	Broadband contact call	0.127	0.260	0.397	0.176			0.164	0.624
	Genetic divergence	**0.574**	0.001	**0.594**	0.001	-0.224	0.964	**0.362**	0.001
4) Rainforest dependence and elevation impedance: (Model 2 + Model 4)	Repertoire	0.129	0.336	0.432	0.224			0.242	0.637
	Short whistle	0.352	0.215	0.009	0.490			0.167	0.680
	Broadband contact call	0.302	0.353	**0.778**	0.040	-0.640	0.839	0.700	0.140
	Genetic divergence	-0.243	0.975	-0.454	1			**0.218**	0.014

We also found a significant effect of rainforest dependence and elevation combined (Model 4) on broadband contact call variation (r = 0.788, P = 0.040). Our MRDM analysis did not support the relationship of this landscape model and acoustic distance either, but again supported an effect of rainforest dependence and elevation combined on genetic distance (R^2 = 0.218, P = 0.014) (Table 2). MRDM analysis revealed a significant effect of dependence on rainforest on genetic distance (R^2 = 0.362, P = 0.001) where Mantel tests did not (Table 2). The cumulative current map for Model 3 in Figure 2 reveal coastal regions are important for connectivity between populations. The maps output by Model 4 reveal rainforests, both coastal as well as inland are important for connectivity (Figure 2). These results support a role for topography and reliance on rainforest habitat in structuring genetic and acoustic variation at the landscape scale.

Discussion

Determining species range limits, important ‘core’ areas and relative strength of dispersal pathways or barriers in heterogeneous landscapes is valuable for understanding the conservation status and management requirements for threatened species (Lindenmayer *et al.* 1991; McRae *et al.* 2008). We provide a bioclimatic range estimation for palm cockatoos and tested predictions of population connectivity throughout their range using electrical circuit theory and genetic and vocal data. Our hypotheses that elevation impedes palm cockatoo movement, and therefore the extent of connections between major populations, was supported by both genetic data and variation in one contact call type. Another hypothesis that elevation and association with certain rainforest types constrain movement was supported by variation in the other contact call type, while the pattern of partial call repertoire similarity among populations did not correlate with any of our connectivity hypotheses. We discuss the utility of this detailed and multifaceted approach for identifying important habitat corridors and extent of population connection in species that may be difficult to capture and followed on an individual basis.


(A) Elevation model (genetic sample sites)

(B) Elevation model (acoustic sample sites)

(C) Rainforest dependance model (genetic sample sites)

(D) Elevation & rainforest dependance model (acoustic sample sites)

(E) Isolation by distance (null) model (acoustic sample sites)

Figure 2. Cumulative resistance maps of *Circuitscape (McRae 2006)* models for palm cockatoos (*Probosciger aterrimus*) on Cape York Peninsula, Australia. Colours indicate the predicted areas of conductance (yellow) and resistance (blue) among the genetic (black circles; A,C) or acoustic (black triangles; B,D,E) sampling locations.

Distribution and habitat

Our predictions of the bioclimatic distribution of palm cockatoos aligned closely with previous range estimates (Juniper and Parr 1998; Higgins 1999) except for the addition of potentially suitable habitat to the south, separated by the dry Laura basin. The contradiction between apparent climatic suitability and lack of sightings south of the Laura Basin supports this region as a persistent boundary to southward movement for many Cape York Peninsula species, including palm cockatoos (Bryant and Krosch 2016). As the Laura Basin is approximately only 30km wide, failure to cross could suggest their lack of tendency to disperse such distances is comparable to other sedentary cockatoo species (e.g. galah Eolophus roseicapillus, Rowley 1983b).

The core habitat prediction for palm cockatoos was concentrated at elevations below approximately 150m, and reflects the few sightings recorded above 200m elevation coinciding with the Great Dividing Range. The even coverage of sample points selected for this analysis ensured that any bias towards low elevation was representative of palm cockatoo land use in Australia, outlining a possibility that in Australia they are restricted to lower elevations than in New Guinea (Juniper and Parr 1998; Higgins 1999; Igag 2002). This supports the inclusion of elevation impedance in hypothetical resistance models in our study. This may indicate that palm cockatoos comprise different subspecies on either side of the Great Dividing Range, as has been detected bio-climatically in other species (Fischer *et al.* 2001) but similarity in their nuclear genomes makes this unlikely (Keighley *et al.* in prep.). Alternatively it is possible that the suitable vegetation communities are found at lower elevations in Cape York Peninsula than New Guinea (Rapoport's rule) mirroring the effect of increasing latitude (Stevens 1992). However the change in latitude from New Guinea to Cape York Peninsula is relatively small, making it more likely that other climatic factors (e.g. rainfall and seasonality) lower the elevation threshold for suitable palm cockatoo habitat in Australia. The separate core habitat at Iron Range supports historic periods of population separation during arid periods when their distribution retracted (Nix and Kalma 1972; Lindenmayer *et al.* 1991), pointing to a refugial explanation for evolution of different broadband contact calls and genetic differentiation there compared to elsewhere on Cape York Peninsula (Murphy *et al.* 2007; Keighley *et al.* 2016, Keighley et. al. in prep.).

Palm cockatoos nest in woodland trees but feed in both woodland and rainforest, they therefore reach their greatest density in savannah woodland close to rainforest patches or linear gallery forest corridors (Wood 1984; Murphy *et al.* 2003). Our method of habitat derivation relied on the proportion of habitat types in our sample relative to Cape York Peninsula overall and identified seven broad rainforest types disproportionately associated with palm cockatoo occupation. This approach may have preferentially identified habitat types with relatively small extent on Cape York Peninsula, despite habitat types with large extents also being important for palm cockatoos. However the approach is suitable for discriminating which habitats with small extent (e.g. rainforest types) palm cockatoos show the greatest association with.

Landscape level connectivity

Given the evidence from our landscape connectivity analysis, impedence of palm cockatoos by elevated terrain and restriction to patchy rainforest habitat are plausible explanations for genetic and vocal variation patterns. Resistance predictions based on elevation correlated with genetic and short whistle differences in Australian palm cockatoos. This corresponds with the effects of elevation barriers on vocal and genetic evolution found in other species (e.g. greenish warbler Phylloscopus trochiloides, Irwin 2000; burrowing parrot Cyanoliseus patagonus, Masello *et al.* 2011; scarlet macaw Ara macao, Olah *et al.* 2016b). The genetic and acoustic correlation with resistance predictions for elevation is concordant with the Great Dividing Range as a persistent barrier to movement. However an alternative explanation is that genetic and vocal differentiation could have evolved in periods palm cockatoos were restricted to separate mountainous regions in New Guinea and Australia, the only climatically suitable areas for rainforest during arid periods (e.g. the last glacial maximum until mid-Holocene) (Nix and Kalma 1972; Webb and Tracey 1981). The climate refugia explanation with recent connectivity is supported by distribution models based on climate data for the mid-Holocene (Keighley *et al.* in prep.), and that individuals from the broader Cape York Peninsula population display genetic admixture close to the interface between the two populations (Keighley *et al.* in prep.).

We observed an indirect spatial relationship between genetic variation and short whistle variation. Whilst indirect (i.e. effected by elevation similarly) this suggests that short whistle evolution may follow genetic evolution closely as in some other parrot species (Ribot *et al.* 2012), and could be used as an approximation for gene flow (Laiolo 2010). Furthermore, short whistles are primarily given during courtship and territorial displays (Zdenek *et al.* 2015; Keighley *et al.* 2016) and the indirect relationship with genetic variation supports a role for vocal learning in reproductive success. Our genetic and vocal sample distributions were spatially different and so could be directly compared using mantel tests; however alternative data (e.g. genetic samples) from Port Stevens would help validate this relationship.

Geographic patterns in vocal structure vary with call type (Keighley *et al.* 2016) and likely reflect different biological functions (Bradbury 2003). Unlike short whistles, impedance by elevation did not explain variation in broadband-contact calls. This discrepancy likely reflects insufficient call similarity between Iron Range and Port Stevens, compared to low resistance between them in this model. Despite correlating with elevation resistance when restriction to rainforest habitat was included, Port Stevens broadband contact calls were more similar to populations on the other side (west) of the Great Dividing Range. Untangling this discrepancy could also be achieved with alternative data (e.g. genetic samples) from Port Stevens.

Fine scale habitat distribution can affect animal movement and therefore population connectivity (e.g. Robertson and Radford 2009). The results of our landscape connectivity simulations support a relationship between rainforest distribution and landscape scale interaction patterns through its influence on broadband contact call structure in palm cockatoos (Models 4 and 5). However this relationship was only significant in combination with elevation inhibiting movement (Model 5). Resistance values resulting from an effect of elevation may fit better due to Iron Range having greater broadband contact call differences and being placed on the opposite side of the mountains from most other populations. However, broadband contact call structure at the southern extent of the cockatoo's range at Port Stevens is more similar to western and northern populations, despite being on the eastern side of the Great Dividing Range as is Iron Range. Therefore Model 5's fit to broadband contact call variation may rely on an accumulation of resistance from habitat gaps over the considerable distance between Port Stevens and Iron Range. Again, further comparison of alternative (e.g. genetic) data from Port Stevens with other Cape York Peninsula populations would help to elucidate the effect of vegetation gaps in more detail.

This modelling method elucidates specific areas of importance for population connectivity. The cumulative current map for Model 4 shows that although many ‘corridors’ of rainforest habitat west of the Iron range could provide some connectivity to the declining population there, the area to the north of Iron Range appears to carry the most flow, probably because this path circumvents the Great Dividing Range which functions as a barrier in this model. Palm cockatoos from the Iron Range (and Port Stevens) use gallery forest associated with east-flowing river systems of Cape York Peninsula, whereas other populations use forest associated with west-flowing rivers. The western and eastern river systems are separated by the northern section of the Great Dividing Range with only 3km at their closest point to the north of the mountain range, which may explain the greater flow north of Iron Range.

Our results demonstrate the effectiveness of a multifaceted, model validation approach for elucidating landscape scale processes via their influence on interaction patterns among populations. We show with palm cockatoos on Cape York Peninsula that both topography and rainforest habitat could plausibly have shaped vocal and genetic variation. We identified particular rainforest corridors that are important for population connectivity given that the Great Dividing Range is a plausible dispersal barrier. Our results raise concerns for the more isolated and declining population at Iron Range which may depend on dispersal through very specific corridors. Furthermore, we indirectly discovered a relationship between genetic and vocal variation in one call type, identifying a useful alternative data source for future non-invasive assessments of interpopulation interaction.

Acknowledgements

This research is supported by an Australian Government Research Training Program Scholarship. We would like to thank the Hermon Slade Foundation, the National Geographic Society and Birdlife Australia for funding field work. We wish to thank Michael Hutchinson and Tingbao Xu for help with BIOCLIM, John Stein for helpful comments on the manuscript as well as help with *ArcGIS* analyses for which we also thank Janet Stein and Nélida Villaseñor. We also wish to thank George Olah for valuable discussion.

Author contributions

M.V.K. conducted fieldwork, analyses and wrote the manuscript. N.E.L. assisted with comments on the manuscript and sought funding. R.H. conceived the idea for the project, sought funding, guided the project and commented on the manuscript.

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Not yet submitted

Chapter 6: Slow breeding rates and low meta-population connectivity indicate low population viability for Australian Palm Cockatoos

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Abstract

Dispersal dynamics can determine whether populations of animals recover or become extinct following decline or disturbance, especially for species with slow life-histories that cannot replenish quickly. Palm cockatoos (*Probosciger aterrimus*) have one of the slowest reproductive rates for any parrot, and likely face steep decline in at least one of four major populations on Cape York Peninsula (CYP), north-eastern Australia. Here we calculated minimum population size estimates and demographic rates with data from field surveys and population genetics, and use population viability analysis (PVA) to determine independent trajectories of four plausibly interconnected populations on CYP together with the trajectory of the meta-population. We incorporate likely dispersal between populations based on effects of topographical barriers and non-uniform habitat distribution. Females in our models breed depending on the fluctuating availability of nest-hollows. Our models suggest that while dispersal between populations can reduce the rate of local declines, the reduction is not substantial enough to buffer the steep decline predicted for the population, on the east coast of CYP. We also found that dispersal from more robust source populations into locations with lower reproductive success (sinks) could reduce overall meta-population viability. Both findings highlight managing local threats as a priority for

conservation in palm cockatoos. Our research supports a change of conservation status for the Australian palm cockatoos from vulnerable to ’Endangered’ under IUCN criteria.

Introduction

Natural or human-induced fragmentation of species distributions cre[4 ates separate, small populations that are vulnerable to decline from local threats or stochastic fluctuations in numbers (Frankham 2005). Population declines can cause loss of genetic and cultural diversity resulting in lower adaptability to change, which can increase species’ vulnerability to extinction even further (Frankham 2005). However, local declines can be buffered by replenishment from connected populations which convey the benefits of increased effective population sizes and lower extinction vulnerability in small populations (Frankham 2005; Sunnucks 2011). These dynamics are important in determining which species or populations of species recover or disappear following dramatic changes in distribution due to climate or disturbance (e.g. Saunders 1990).

Habitat loss and fragmentation is the main process behind the disproportionate number of species in the order Psittaciformes (hereafter parrots) that are threatened with extinction (Olah *et al.* 2016a). Of the 398 parrot species, 28% are threatened with extinction (‘critically endangered’, ‘endangered’ or ‘vulnerable’ according to IUCN criteria, IUCN 2012); a greater proportion than in the three largest avian groups *Passeriformes* (5913 spp., 10%), *Caprimulgiformes* (593 spp., 9%), and *Piciformes* (484 spp., 7%). At most risk, are those with large body size, slow reproduction, dependence on forest and small historical distributions (Toft and Wright 2015; Olah *et al.* 2016a). Many cockatoo species (family Cacatuinae) fit this description, over half of which are threatened with extinction (Juniper and Parr 1998; Snyder *et al.* 2000).

Field studies on wild cockatoos have assessed population size, breeding activity and dispersal (Rowley 1983a; Rowley and Chapman 1991; Walker *et al.* 2005; Cahill *et al.* 2006), and palm cockatoos (*Probosciger aterrimus*) are a charismatic example of a species that has been studied in some detail. Palm cockatoos are the largest in the cockatoo family and are sedentary canopy dwellers. Pairs defend territories containing multiple nesting hollows in the ecotone between open woodland and rainforest. Their global distribution includes lowland New Guinea, the Aru Islands, and Cape York Peninsula north of the Laura Basin (14.5˚S) on mainland Australia. The conservation status of palm cockatoos worldwide is ‘least concern’ but they are potentially threatened by vegetation clearing, poor fire management, hunting for subsistence and the pet trade (IUCN 2012).

Within Australia the palm cockatoo is listed as ‘vulnerable’ under IUCN criteria (Garnett *et al.* 2011) largely due to exceedingly slow reproduction discovered by a field study on the population at Kutini-Payamu National Park (Iron Range National Park, also connected to McIllwraith Range to the south, hereafter referred to as the Iron/McIllwraith Ranges population), eastern Cape York Peninsula (Murphy *et al.* 2003). Large scale vegetation clearing associated with mining operations within their range increases their vulnerability further (Gould 2011). During the three-year study of the Iron/McIwriath Ranges population, females laid a single egg every 2.2 years on average, which alongside predation and a low fledging rate, resulted in 0.11 offspring per female each year (Murphy *et al.* 2003). Subsequent analyses forecast rapid decline for this population unless some individuals live longer than 100 years; an unlikely scenario (Heinsohn *et al.* 2009). While it is possible that dispersal from adjacent populations helps to maintain numbers at the Iron/McIllwraith Ranges, genetic evidence suggests restricted connectivity to the

Iron/McIllwraith Ranges population (Keighley *et al.* in prep.b). Genetic differentiation and distinct vocal dialects of palm cockatoos at Iron/McIllwraith Ranges compared to elsewhere on Cape York Peninsula have been explained by landscape resistance models that incorporate elevated terrain as a barrier to interpopulation interaction (Keighley *et al.* 2016, Keighley *et al.* in prep.*a*,*b*). Australian palm cockatoos also have low genetic diversity (Keighley *et al.* in prep.b), a possible result of historic population bottlenecks that coincided with habitat contraction in arid periods of the Pleistocene (Nix and Kalma 1972; Legge *et al.* 2004). While good ecological and demographic data exist for the Iron/McIlwraith Ranges (Murphy *et al.* 2003), neither population trajectories nor abundance are known for the other populations comprising the Australian meta-population.

Understanding the viability of the Australian palm cockatoo meta-population is becoming more important in the face of disturbance of their habitat due to bauxite mining activity in the western part of their CYP range. Mining lease covers approximately 5,300 km^2, much of which is potential palm cockatoo habitat. Western Cape York Peninsula contains the world's largest deposits of bauxite (over 11,000 km^2) which supports substantial mining operations (Taylor *et al.* 2008). The bauxite deposits are just below the surface, and extraction requires complete removal of surface vegetation. Thus far palm cockatoos have not been reported to use rehabilitated mining sites within 23 years, perhaps because of the great deal of time required for natural processes (termite action and cyclones) to result in suitable tree hollows for their nests (Murphy and Legge 2007; Gould 2011).

We explore the connectivity and demographic conditions that would be required for palm cockatoos on Cape York Peninsula to be stable enough to prevent both local and overall extinction. As neither population trajectories or abundance are known for Australian palm cockatoos outside of the Iron/McIlwraith Ranges, we first estimated population sizes at three other locations on Cape York Peninsula using field surveys combined with habitat maps. We then determine the individual and collective population trajectories and population viability of Iron/McIlwraith Ranges and other geographically separate populations on Cape York Peninsula using known demographic rates and connectivity information from genetics, vocal dialects and landscape resistance modelling in population viability analysis (PVA) models. We conclude by using the predicted population trajectories to assess whether the current conservation status of palm cockatoos (‘Vulnerable’) is adequate.

Methods

Study species

The distribution of palm cockatoos in Australia has not had thorough bioclimatic investigation (but see Keighley *et al.* in prep.a,b), though they are known to occur only in limited areas on Cape York Peninsula north of 14.5 ˚ S. Field studies have, however, provided detailed information about their habitat use (Murphy 2005). Palm cockatoos are cavity nesters, and in Australia prefer large hollows in woodland tree species, although sometimes rainforest species are chosen (Murphy *et al.* 2003). Palm cockatoos feed on the seeds of rainforest species (e.g. *Canarium australiana*, *Cryptocarya exfpliata*, *Buchanania arborescens*), as well as woodland species (e.g. *Terminalia microcarpa catappa*, *Parinari nonda*, *Eucalyptus tetradonta*, *Corymbia nesophyla*, *Corymbia clarksonia*) (Wood 1988; R.D. Pillans, C.N. Zdenek pers. com.; pers. obs). Therefore they occur in greatest density in woodland within 1km of rainforest (Wood 1984) and appear to prefer to nest in hollows within 300m of rainforest, 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 open water (Igag 2002; Murphy *et al.* 2003). On Cape York Peninsula, the largest area of rainforest extends along the eastern coast and includes the Iron and McIlwraith Ranges (Figure 1). This rainforest area supports what is thought to be one continuous palm cockatoo population which was featured in a previous population viability assessment of the species (Heinsohn *et al.* 2009).

Aside from slow reproduction (Murphy et al 2003), palm cockatoos face additional threatening processes throughout their range. They compete with sulphur-crested cockatoos for nests (Heinsohn *et al.* 2009), and suffer nest predation by varanid lizards (*Varanus* spp.), giant white-tailed rats (*Uromys caudimaculatus*), black butcherbirds (*Cracticus quoyi*) and amethyst pythons (*Morelia amethistina*) (Murphy *et al.* 2003). Mining for bauxite around Weipa in western Cape York Peninsula (Figure 1) involves complete vegetation clearing, and palm cockatoos fail to re-inhabit mine-sites at least 23 years post rehabilitation (Gould 2011). Altered fire regimes affect recruitment and persistence of nest-trees (Murphy *et al.* 2003; Murphy and Legge 2007). Increasing numbers of sulphur-crested cockatoos and land clearing around Weipa may be a local decline in that area (Gould, cited in Garnett *et al.* 2011, Heinsohn et al. 2009).

Field sites and data sources

We used detailed demographic data from a three year study of palm cockatoos at Iron/McIllwraith Ranges on Cape York Peninsula Australia (Murphy *et al.* 2003), together with genetic and vocalization data describing the extent of population connectivity (see below), to run computer simulations of long-term population viability. The Iron/McIllwraith Ranges population is considered to be one contiguous population, though connectivity with other populations north and west of the Great Dividing Range appears to be restricted (Figure 1). Connectivity may occur between the Iron/McIllwraith population and other populations via the populated gallery forest corridors that occur along major rivers to the west of the mountain ranges and gallery forest on the wetter eastern side of the peninsula. However, given genetic dissimilarities between Iron/McIlwraith Ranges palm cockatoos and those elsewhere on CYP, limited connectivity due to a mountain range barrier is a likely scenario. We use information about connectivity from a study on their genetic population structure (Keighley *et al.* in prep.b) and landscape 'resistance' modelling (Keighley *et al.* in prep.a) to simulate the influence of different connectivity regimes on viability of individual populations.

As no complete palm cockatoo census has yet been conducted, we used a combination of methods to attain abundance estimates for four major populations on CYP (see *Estimating abundance* below). For the population at Iron/McIllwraith Ranges to the east we used the same estimate as Heinsohn *et al.* (2009) of 1000 individuals (500 males, 500 females). We used our own observations from a previous study on their acoustic behaviour to estimate the size of a second population located centrally and a third to the north Cape York Peninsula. To estimate the size of a fourth population on the west coast for which we had no survey data and appeared to have a lower density of certain habitat requirements, we used data from the central population. Data for the central peninsula population came from surveys at Piccaninny Plains Wildlife Sanctuary, Steve Irwin Wildlife Reserve and Moreton Telegraph Station which are all on major inland river systems. Data for the northern population came from surveying the free-hold lands around Bamaga on the tip of the Peninsula (Figure 1). Survey sites were chosen based on accessibility of suitable habitat (Murphy *et al.* 2003) and occupation by palm cockatoos, and were visited by MVK or volunteer research assistants at least once in the morning and once in the afternoon on a minimum of two occasions each year, with the exception of the Bamaga sites which were visited only in 2014. Survey walks within sites were conducted on foot and routes were not necessarily constrained to repeated paths as observers deviated often to obtain audio-visual recordings. Surveys lasted from 13 to 420 minutes, and ranged from stationary to 8.16km in distance travelled. Observers recorded their paths using GPS devices (Garmin e-trex 10) and recorded waypoints when hearing palm cockatoo calls and if followed, once again upon seeing the bird. The second waypoint was used to verify detection distance in a later step. The number of cockatoos seen or heard during the entire walk was recorded. From these counts, palm cockatoo density in the central and northern populations was estimated using generalized linear modeling (see next section). Population abundances were estimated by extrapolating these densities to suitable habitat within each.

Population size modelling

Our modelling approach to estimating palm cockatoo abundance in the central and northern populations was based on our counts and the abundance of habitat within reserve boundaries, and in the case of the northern population an arbitrary boundary encompassing the study area (Figure 1).

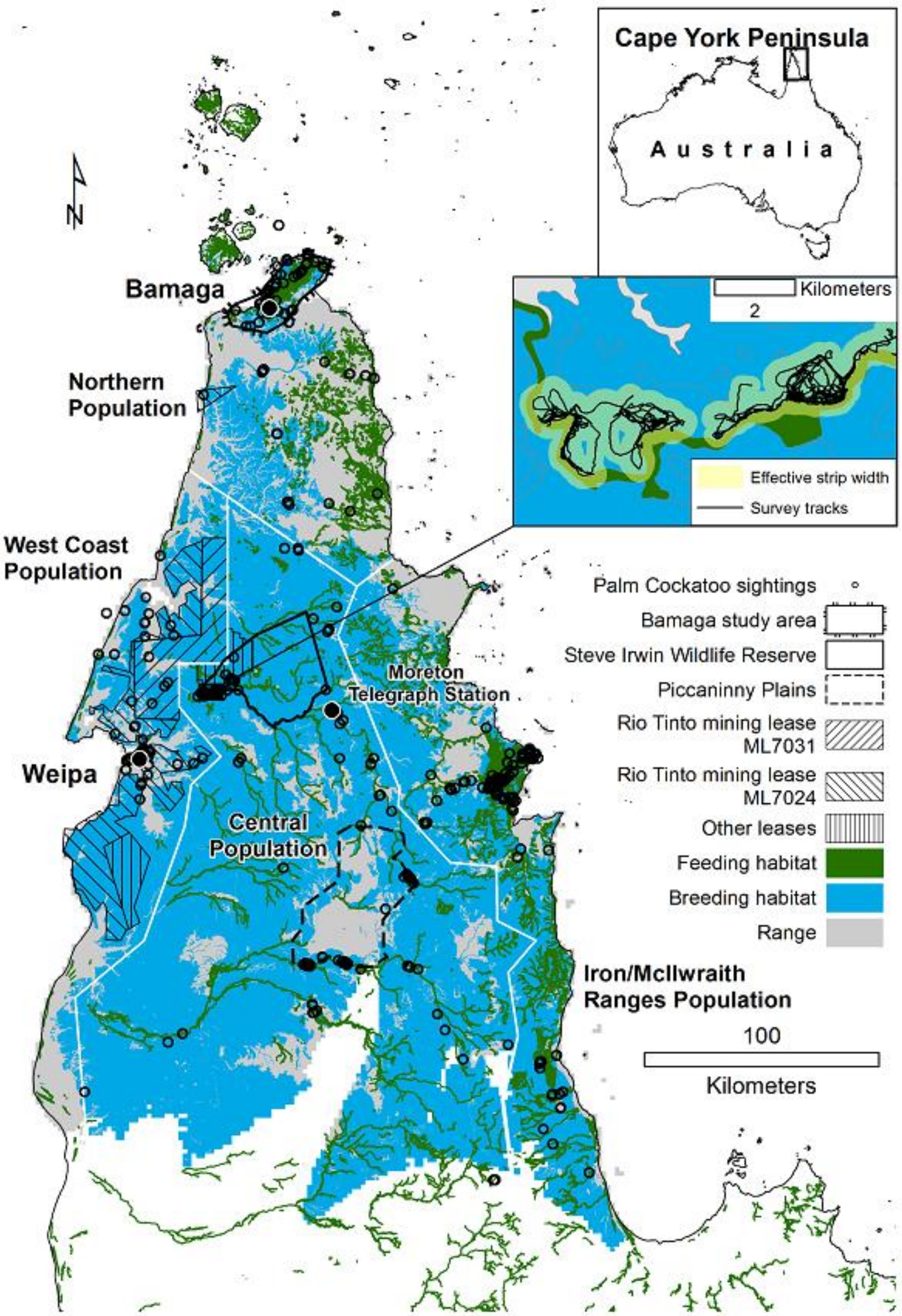

Figure 1. Map showing palm cockatoo sightings from our data and Birdlife Australia, their bioclimatic range, and potential feeding and breeding habitat. Also shown are mining lease boundaries, our study area and population boundaries. Inset shows an example of survey tracks (black lines) with area sampled under each observer's effective strip width (pale green).

Detection probability and effective area sampled.

To estimate the actual number of birds per unit area on each search in addition to those we detected, we calculated the probability of detecting palm cockatoos if they were present. For this we specifically used verified detection distances from a subset of observations (N = 46) which ranged between 14m and 448m. Therefore, we fitted a range of detection functions all truncated to 450m, with and without covariates, and ranked their appropriateness for the data based on Akaike's information criterion (AIC). The uniform, half normal and hazard-rate functions were assessed with and without 2^{nd} order cosine and Hermite adjustments, and month and observer co-variates were tested with the half-normal detection function. The detection function choice was found to have an insignificant effect on abundance estimates in downstream analyses, nevertheless the half-normal function scaled by observer had the lowest AIC value so it was used to calculate effective strip widths (ESW) (the equivalent distance at which detection probability is 1). The ESWs were calculated using the *Rdistance* package in R (R Development Core Team 2016) for three of five observers for which detection distance data were available, and were used to calculate an effective area sampled by each search when considering observer specific detection probabilities. This was done by applying a round ended buffer corresponding to the observer's ESW to search tracks in a geographic information system (ArcGIS 10.4; ESRI 2011).

Suitable habitat

To ensure the most realistic possible upscaling of our density estimate to suitable habitat within reserve boundaries we used a definition of required feeding habitat calculated in

Keighley *et al.* (in prep.a) and breeding habitat based on Murphy *et al.* (2003). To determine which rainforest types were required as feeding habitat, georeferenced palm cockatoo sightings from our data and Birdlife Australia (unpublished dataset) were combined with maps of broad vegetation groups from the regional ecosystems classification scheme (Queensland Herbarium 2015) in ArcGIS (ESRI 2011). 500m buffers were created around each waypoint forming a sample area of 217 km^2. The proportional area occupied by each of 66 broad vegetation groups was calculated within palm cockatoos' predicted range (Figure 1) as well as within the sample area. The area of each vegetation group *expected* to be in the sample (under no preference) was calculated by multiplying the proportion of each vegetation group in their range by the total sample area. We tested if *expected* vegetation group area differed from the sample using a Chi Square test, and vegetation groups in the sample which covered at least double their expected area were considered required habitat. This approach identified seven broad vegetation groups as *feeding* habitat (34e, 4b, 2d, 2c, 2b, 22c, 3a; Table 1a) that were disproportionately represented within 500m of palm cockatoo sightings (χ^2 [1, 51] = 271.8, $P < 0.05$), their combined distribution is shown in Figure 1.

Due to the large area of woodland on Cape York Peninsula this method was not appropriate for identifying disproportionately important types. We therefore separately extracted as breeding habitat any broad vegetation groups from the above sampled area that included open woodland or forest in their description (excluding low or closed forest) (Queensland Herbarium 2015) because of the requirement for large woodland trees for breeding outlined by Murphy *et al.* (2003). This approach identified eleven broad vegetation groups as breeding habitat (14a, 14b, 14d, 16b, 16c, 21a, 22b, 5d, 9b, 9c, 9e; Table 1b).

Estimating abundance

To calculate a basic palm cockatoo density for each sampled population we used a quasi Poisson model with bird count as the dependent variable and fixed effects of 1) the effective area of each search (m2), 2) the area of each search within three distance bands retreating from required (rainforest) habitat (0 - 200m, 200m – 1km and < 1km) and 3) survey location to account for multiple visits. The quasi Poisson distribution was used to account for over-dispersion. The three distance bands were considered to adequately represent the declination in palm cockatoo occurrence with distance away from rainforest based on a subjective assessment of palm cockatoo observation data provided by Birdlife

Table 1a. Description of broad vegetation groups determined to be suitable palm cockatoo feeding habitat.

	Area in range (km^2)	Area in sample (km^2)	Expected area with sightings habitat (km^2)*	Description
CYP total area	70067.8	217		
Broad Vegetation Group				
34e	0.8	0.4	< 0.1	Spring wetlands. Occurs on undeformed fine-grained sedimentary rock (limestone).
4b	1462.7	20.0	4.5	Semi deciduous mesophyll to notophyll vine forest which can include *Nauclea orientalis* (Leichhardt tree), *Bombax ceiba* var. *leiocarpum* (bombax), *Semecarpus australiensis* (tar tree), *Terminalia sericocarpa* (sovereignwood), *Canarium australianum* (scrub turpentine), *Gyrocarpus americanus* (helicopter tree), *Castanospermum australe* (black bean), *Aleurites moluccanus* (candlenut) (candlenut) and *Alstonia scholaris* (milky pine). Mainly occurs in catchments on loamy alluvia.
2d	153.9	5.3	0.5	Semi-deciduous notophyll to mesophyll vine forest commonly with *Cryptocarya* spp., *Buchanania arborescens* (native mango), *Bombax ceiba* var. *leiocarpum*, *Ficus albipila* var. *albipila* and *Terminalia sericocarpa* (Damsonwood). The evergreen *Alstonia scholaris* (milky pine) may occur as either a canopy or emergent tree. Occurs on basalt rises and cones.
2c	735.6	11.8	2.3	Simple evergreen notophyll vine forest with or without *Wodyetia bifurcata* on colluvium of granite ranges. Occurs only on the slopes and colluvial sediments of granite ranges.
2b	155	2.9	0.5	Semi-deciduous mesophyll to notophyll vine forest commonly including *Aleurites moluccanus* (candlenut), *Argyrodendron polyandrum* (brown tulip oak), *Alstonia scholaris* (milky pine), *Garuga floribunda* var. *floribunda*, *Bombax ceiba* var. *leiocarpum* and *Canarium australianum* (scrub turpentine). Occurs on granite slopes.
22c	640.03	5.6	2	Fringing woodland of Melaleuca leucadendra, Lophostemon grandiflorus, Eucalyptus camaldulensis and Livistona rigida. Corymbia aparrerinja and Lysiphyllum cunninghamii occur on sandier levees and Eucalyptus microtheca occurs on finer textured lower alluvial terraces on lower reaches.
3a	442.1	3.9	1.4	Evergreen to semi-evergreen notophyll vine forest dominated by *Syzygium forte* subsp. *forte*, *Terminalia muelleri* (Australian almond), *Mimusops elengi* (tanjong) and *Buchanania arborescens* (satinwood). Occurs on coastal dunes and beach ridges in dunefields.

CYP: Cape York Peninsula; * Habitat area in range / Total range area × Area in sample.

Table 1b. Description of broad vegetation groups determined to be suitable palm cockatoo breeding habitat.

Broad Vegetation Group	Description
14a	*Eucalyptus tetrodonta* (Darwin stringybark) predominates forming a distinct but discontinuous canopy (18-34m tall). Occurs on deeply weathered plateaus and remnants.
14b	A diverse group of species dominate a dense, even canopy (18-25m tall). Occurs as small patches on plateaus.
14d	Woodland to sometimes open forest of *Eucalyptus tetrodonta* (Darwin stringybark). Occurs on sandstone plateaus.
16b	*Eucalyptus leptophleba* and/or *E. chlorophylla* w./w.o. *Corymbia dallachiana* woodland on river levees and terraces.
16c	*Eucalyptus platyphylla* woodland on depressions in Tertiary plains.
21a	*Melaleuca viridiflora* and/or *M. citrolens* low woodland ± *Corymbia spp*. emergents on alluvial deposits.
22b	*Melaleuca dealbata* w./w.o. *Acacia crassicarpa* open forest in dune swales on the west coast.
5d	*Acacia mangium* and/or *A. celsa* and/or *A. polystachya* closed forest on alluvial plains.
9b	*Eucalyptus leptophleba, Corymbia clarksoniana* open forest to woodland, on alluvium, in near-coastal areas with moderate rainfall.
9c	*Eucalyptus tereticornis, Corymbia intermedia* and *E. reducta woodland* to open forest of uplands on weathered soils of a remnant surface.
9e	*Corymbia tessellaris* w./w.o. *Acacia leptocarpa* w./w.o. *Allocasuarina littoralis* w./w.o. *Banksia integrifolia* w./w.o. rainforest species open forest on parallel dunes.

Australia (Figure 2). We used sampling locations corresponding to each population to extrapolate out to any breeding habitat within their relevant reserve boundaries (A). To do this we divided the *breeding* habitat areas according to the distance bands retreating from rainforest (A_δ), and estimated abundance for each (γ_δ) as the combined product of their areas, exponents for the model intercept (β) as well as coefficients for effective search area (α) and the corresponding distance band (δ) summarized in the following formula. Model coefficients can be found in Appendix 1; Table 6.

$$\gamma_\delta = e^{\beta + \delta + A\delta \times \alpha}$$

Standard errors for study area abundance estimates (*s.e.*) were calculated by accumulating the products of; variance of γ_δ and the square of A_δ's proportion of A, then finding the square root of the sum and multiplying it by A. We calculated the standard error of γ_δ as the product of α's standard error and γ, and calculated variance by squaring the standard error.

For whole population abundances, relevant study area abundances were divided by their total area, and the resulting density applied to suitable habitat within 1km of rainforest within overall population boundaries (Figure 1). Whereas the Bamaga study area density was used for the northern population, we used the average density (and *s.e.* taken as the square root of average variance) thus calculated from the two central study areas (Steve Irwin Wildlife Reserve and Piccaninny Plains Wildlife Sanctuary) to calculate abundance in both the central and west coast populations. The standard error of population abundance values represent the same proportion of error in study area estimates. Our whole population abundances should be treated with caution as our approach assumes similar abundance in un-sampled areas to 'average' sampled areas and could be overestimated.

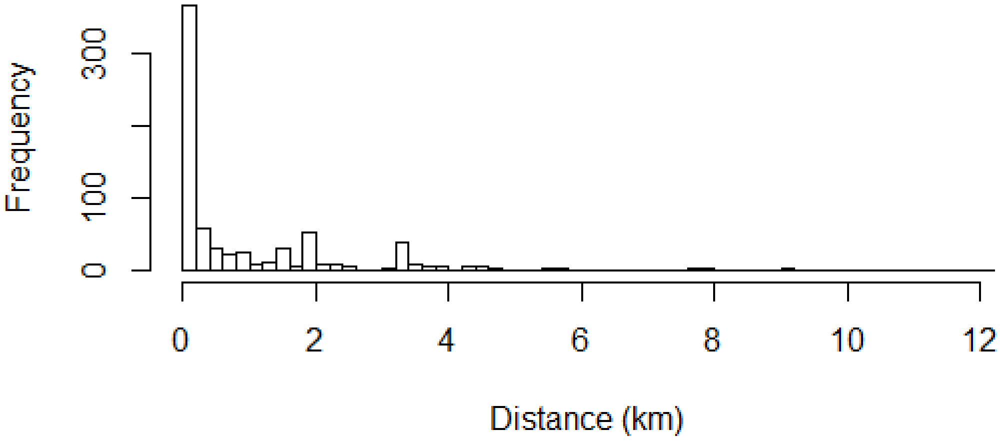

Figure 2. Distance from rainforest feeding habitat at which palm cockatoo sightings were recorded (unpublished data, Birdlife Australia).

Population viability assessment

Modelling approach and parameters

We used the software VORTEX to model population trajectories from individuals' sequential life history events (e.g. birth, death, reproductive success, dispersal) based on data from field studies. Where good quality data were not available for certain parameters, we made conservative assumptions (informed by good quality data from similar species where possible) so that output trajectories reflected the 'best case' scenarios for our study system. VORTEX is an individual-based simulation of the deterministic and stochastic forces that effect the persistence of small populations, and can provide insight into the relative importance of different parameters, events or treatments. These forces are modelled as constants or as random variables following specified distributions, and since random events can strongly influence population outcomes, models are typically repeated many times (e.g. 1000) revealing a distribution of outcomes given their set of parameters. Catastrophes that affect survival and reproduction can also be included in the model, as well as transmission of genes to incorporate the effect of inbreeding depression on population viability. Model outputs summarize population growth, extinction probability over the simulated time period, time until extinction as well as the average size and genetic variation in extant populations.

VORTEX simulations were run 1000 times and extinction was taken as occurring when only one sex remained. Simulations were run with a timeframe of 100 years with results after three generations (54 years)(Garnett *et al.* 2011) being of primary interest given the IUCN criteria for threatened species listings (IUCN, 2012). VORTEX models require an estimate of the level of concordance between reproductive success and mortality. We assumed low concordance, as field observations suggest that though palm cockatoos may fail to breed this has no apparent effect on their survival. We allowed our population size to fluctuate freely according to our model parameters by using carrying capacities in each population of twice their initial numbers.

Reproductive success, sexual maturity and mating system.

We used the same parameters for palm cockatoo reproductive success, sexual maturity, and mating system as used by Heinsohn *et al.* (2009) which are explained in detail there and in Appendix 2 of this manuscript. We used generation time (17.7 years) and age at first breeding (4 years) based on expert elicitation (Garnett *et al.* 2011). Given the lack of mortality data for palm cockatoos, we derived a conservative baseline per annum mortality rate from generation time and age at first breeding according to the formula:

$$G = b + 1/m$$

Where G = generation time, b = age at first reproduction, and m = annual adult mortality rate.

Mortality rates based on this calculation were adjusted to be in proportion to those applied to sex and age-classes in PVA simulations of Heinsohn *et al.* (2009) (see *Mortality* below). Other parameters used here are based on high quality data from Murphy *et al.* (2003) and Igag (2002). We also used the same method as reported in Heinsohn et al (2009) to model the effect of gradual loss of nest hollows and their creation by cyclones every 20 years on average. We did not incorporate inbreeding in our models, because it had little effect on population viability simulated for the population of 1000 individuals at Iron/McIllwraith Ranges (Heinsohn *et al.* 2009). It is unknown whether reproductive success is similar at Iron/McIllwraith Ranges compared to elsewhere on CYP. We therefore used the reproductive rate calculated for Iron/McIllwraith Ranges by Heinsohn *et al.* (2009) (single egg clutch every 2.2 years and 25% fledging, giving 0.11 ± 0.02 offspring per year overall) as a base for all our simulated Australian populations in Models 1 to 5. Reproductive success at Crater Mountain, New Guinea is higher (40%), though exact rates are uncertain (Igag 2002). In Models 6 to 9 we catered for the possibility that reproductive success in populations outside of Iron/McIllwraith Ranges is not so poor by including scenarios in which they had two times the base reproductive success of Iron/McIllwraith Ranges (0.22 offspring per year) (Table 2) which could be interpreted either as higher success per attempt or a higher frequency of breeding attempts (i.e. one breeding attempt every 1.1 years).

Mortality

No age-specific mortality data exists for palm cockatoos. However, previous simulations by Heinsohn *et al*. (2009) inferred the mortality schedule necessary to maintain a stable population at the Iron/McIlwraith Ranges. These were based on mortality data from similar species, carnaby's black-cockatoos (*Calyptorhynchus latirostrus*) from Saunders (1982), the most extensive available for any cockatoo species. Heinsohn adapted Saunders' data by removing deaths from un-natural causes (e.g. vehicle collisions) to establish background mortality rates, and maintained differences between adults and juveniles as well as higher female mortality, as female palm cockatoos incubate at night and are more vulnerable to nest predators. However, as discussed by Saunders, even the baseline figures may be unnaturally severe due to increased mortality associated with study subjects being wing-tagged. Therefore we used a less severe background adult mortality rate (m) which we derived using generation time (17.7 years) = $1/m$ + age of maturity (4 years) which gave

Table 2. Demographic values used in models.

Italicised numbers indicate which of 13 models the adjusted parameters relate to.

Parameter	Value
Initial population size	2980 Central 170 West Coast 360 Northern 1000 Iron/McIlwraith Ranges (Eastern)
Carrying capacity	5960 Central 340 West Coast 780 Northern 2000 Eastern (Iron & McIlwraith Ranges)
Age of first reproduction by males	4
Age of first reproduction by females	4
Maximum age	150
Mortality	See Table 3
Maximum progeny per year	1
Proportion males (sex-ratio) at hatching	0.5
Percentage adult females breeding	Limited by hollow availability
No. of offspring per female per year	0.11 ± 0.02 Iron/McIlwraith Ranges (*all models),* Other Cape York Peninsula populations (*1*, *2*, *3 & 4*) 0.22 ± 0.04 Other Cape York Peninsula populations (5, 6, 7 & 8)
Environmental variation (%)	10
Percentage of males in breeding population	100
Mating system	Long-term monogamy
Dispersal	(See table 4)

7.3% per annum. This method was shown to produce baseline mortality rates that were consistent with field observation of similar species by a previous study of another parrot species (Heinsohn *et al.* 2015). We assumed 7.3% was an average of the adult male and female rates and maintained the proportional differences among age/sex classes in Saunders' data (1982) (Table 3).

Table 3. Mortality rates (percentage mortality per year ± s.d.) for males and females over five age-classes

	Saunders (1982)	Calculated rate*
Female age (years)		
0-1	70.6 ± 14.1	16.6 ± 3.4
1-2	37.1 ± 7.4	8.8 ± 1.8
2-3	38.3 ± 7.7	9 ± 1.8
3-4	36.4 ± 7.0	8.6 ± 1.65
4+	36.4 ± 7.0	8.6 ± 1.65
Male age (years)		
0-1	70.6 ± 14.1	16.6 ± 3.4
1-2	37.1 ± 7.4	8.8 ± 1.8
2-3	38.3 ± 7.7	9 ± 1.8
3-4	25.7 ± 5.1	6 ± 1.65
4+	25.7 ± 5.1	6 ± 1.65

*Calculated using generation time = 1/m + age of maturity giving 7.3% mortality on average for adult males and females, then made proportional to Saunders (1982) for each age/sex class.

Dispersal between populations

VORTEX does not provide a full model of dispersal across complex landscapes, but instead models movements among discrete populations, with the user specifying the rate of movement between each pair of populations. Current evidence suggests that palm cockatoos are philopatric using the same territories from year to year (Murphy *et al*. 2003). However it is unknown at what age or how far from their natal area individuals first establish their territories. Genetically admixed individuals occur adjacent to genetically admixed populations indicating some movement of individuals among palm cockatoo populations from different areas on Cape York Peninsula (Keighley *et al.* in prep.b). In lieu of more detailed information about gene-flow, we tested three dispersal scenarios. Our first model was based on information from other cockatoo species, the second adapted the first model's connectivity by encompassing data from landscape resistance modelling, landscape scale genomic variation and vocal dialects in palm cockatoos, and the third was a hypothetical situation in which there is high connectivity between all populations.

Detailed information from Major Mitchel's cockatoos (*Cacatua leadbeateri*) shows roughly 7.5% of individuals between two and four years old disperse further than 20km, and a similar pattern is shown by galahs (*Cacatua galerita*) (Rowley 1983a; Rowley and Chapman 1991). We assume that this proportion of long distance travellers is similar for palm cockatoos and represent the proportion of individuals that cross into different breeding populations each year. In our first simulation we therefore designate 7.5% of two to four year olds switching populations every year in total, spread evenly over population pairs without any restriction (2.5% to each, Table 4: Model 1). We maintained the age of dispersal as from 2 to 4 years in each model, and although palm cockatoo mortality is high pre-fledging (81%), we assume complete survival of dispersing individuals to ensure the best case result for the study species.

There is data suggesting restriction of connectivity to the Iron Range, for example genomic and mitochondrial single nucleotide polymorphisms (Keighley *et al*. in prep.b) and acoustic geographic variation in contact calls (Keighley *et al.* 2016). The Australian palm cockatoos likely form two distinct units, Iron/McIlwraith Ranges birds being different genetically and acoustically to other populations on Cape York Peninsula. Connectivity patterns are likely affected by impedence due to the steep elevation change westwards from Iron/McIlwraith Ranges and to some extent the pattern of suitable habitat existing as discreet rainforest corridors Keighley *et al.* (in prep.a) . We emulated an elevation and habitat dependent pattern of dispersal in our simulations by using figures from the connectivity models in Keighley *et al.* (in prep.a) to modify the above dispersal parameters derived from Major Mitchel's cockatoos. For this we took the average 'resistance' values between populations from those models, divided by their maximum value and subtracted the result from 1 giving a value between 0 and 1 'connectivity' meaning low and high connectivity respectively. We adjusted the Major Mitchel's derived dispersal percentage by multiplying by this value for each population pair, so high connectivity values remained close to the original dispersal percentage and low values had reduced dispersal (Table 4: Model 2).

In addition, the presence of unique mitochondrial haplotypes at the Iron/McIllwraith Ranges that have not been spread elsewhere (see also Murphy *et al*. 2007) outlines the possibility of one-way dispersal into Iron/McIllwraith Ranges. We therefore conducted the same simulations without any dispersal out of Iron/McIllwraith Ranges (Table 4: Model 3). To highlight effects on population viability specific to dispersal, our fourth model tested the hypothetical situation of 50% individuals between the ages of two and four years old dispersing evenly to other populations (Table 4: Model 4).

Results

Population size estimate

Our models output approximately 2980 ± 75*s.e.* individuals (1490 males, 1490 females) for the central population (6,795 km^2 breeding habitat < 1km from feeding habitat) and 170 ± 4*s.e.* individuals (75 males, 75 females) for the west coast population (380 km^2 breeding habitat < 1km from feeding habitat) based on estimates of 440 ± 11*s.e.* individuals at Steve Irwin Wildlife Reserve (1,417 km^2) and 1090 ± 0*s.e.* at Piccaninny Plains (1,922 km^2). We estimated 360 ± 64*s.e.* individuals (180 males, 180females) for the northern population

(1,633, km^2 breeding habitat < 1km from feeding habitat) based on an estimate of 140 ± 25 in the Bamaga study area (701 km^2). In total (including 1000 individuals from Iron Range; 500 males, 500 females; Heinsohn *et al.*, 2009) we estimate the entire CYP meta-population to be 4510 ± 97 individuals. As our extrapolation approach was based on a subset of locations known to contain palm cockatoos, we consider that these estimates represent the upper limits of possible abundance.

Table 4. Proportion dispersal for two to four year old palm cockatoos between populations.

Model 1	Iron/McIlwraith Ranges	Bamaga	West coast	Central
Iron/McIlwraith Ranges		0.025	0.025	0.025
Bamaga	0.025		0.025	0.025
West coast	0.025	0.025		0.025
Central	0.025	0.025	0.025	
Model 2				
Iron/McIlwraith Ranges		0.007	0.02	0.007
Bamaga	0.007		0.025	0.011
West coast	0.02	0.025		0.022
Central	0.007	0.011	0.022	
Model 3				
Iron/McIlwraith Ranges		-	-	-
Bamaga	0.007		-	-
West coast	0.02	0.025		-
Central	0.007	0.011	0.022	
Model 4				
Iron/McIlwraith Ranges		0.17	0.17	0.17
Bamaga	0.17		0.17	0.17
West coast	0.17	0.17		0.17
Central	0.17	0.17	0.17	

Model 1: Palm cockatoo dispersal based on data from Major Mitchels cockatoos (*Cacatua leadbeateri*) and galahs (*Cacatua roseicapella*) showing 7.5% of 2 – 4 year olds dispersing to each of three other populations. Model 2: dispersal adjusted for landscape permeability based on elevation and habitat from Keighley *et al.(* 2017 in prep *b*). Model 3: one way dispersal into Iron/McIlwraith Ranges based on Keighley *et al.* (2017 in prep *a*). Model 4: hypothetically unrestricted dispersal, 50% of 2 - 4 year olds dispersing evenly between populations. Dispersal is from populations in rows to populations in columns.

Population viability assessment

Our simulations predict severe declines in the meta and sub-population respectively between 62.3-92.1% and 87.3–92.2% for models with restricted connectivity among populations (Figures 3 and 4, Table 1). The probability of complete extinction $P(E)$ was < 1 in all of our models but this finding is not emphasised here because our simulations are conservative and aimed at deterministic rates of decline to address specifically IUCN criteria regarding the extent of estimated population decline over three generations (see discussion).

We suggest the most appropriate model to use for assessment of conservation status is Model 6 because it uses dispersal based on habitat distribution and topographic influences on movement (determined via correlation with genetic and vocal variation, Keighley *et al.* in prep.a), and conservatively assumes that populations outside Iron/McIlwraith Ranges have twice the reproductive success determined from reliable data (greater even than the only other reliable data source from New Guinea which shows better reproductive success, Igag 2002). In spite of presenting an optimistic scenario based on high reproduction elsewhere, Model 6 predicts a 62.3% meta-population decline and an 87.3% decline in the Iron/McIlwraith Ranges population within three generations.

To indicate an average trajectory for all simulations, we took the mean number of remaining individuals after three generations. This gave an average predicted meta-population decline of 82.5%, and an 87% decline at Iron/McIlwraith Ranges. Furthermore, the models that represent the best case scenarios for palm cockatoo viability predict 62.3% (Model 2) and 70.6% (Model 4) declines in the meta-population and Iron/McIlwraith Ranges sub-population respectively over the same three generation time span. The specific results of our scenarios with respect to decline rates, probability of extinction, time until extinction and population extant after 100 years are presented in Table 5. In general, we found that altering the dispersal scenario affected population trajectories only slightly, while the rate of meta-population decline was reduced by experimentally increasing reproductive success for populations outside of the Iron/McIllwraith Ranges. The trajectory of the Iron/McIllwraith Ranges population was similarly unaffected by changing dispersal scenario, unless values for reproductive success in other populations were increased; in which case the scenario of liberal dispersal (Model 8) improved that sub-population's prospects the most followed by the scenario of equal, but more limited, dispersal among populations (Model 5).

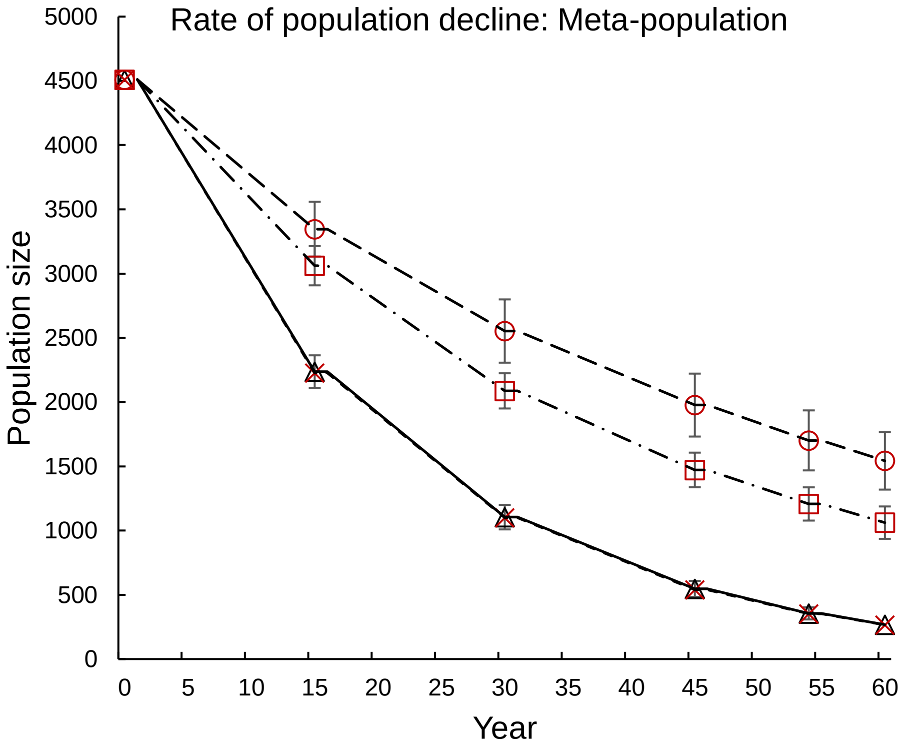

Figure 3. A selection of the simulated population trajectories for the meta-population. The graph shows trajectories under the two reproductive success scenarios outlined in Table 2, and two of the dispersal scenarios outlined in Table 4, Model 2 = triangles, Model 4 = crosses, Model 6 = circles and Model 8 = squares.

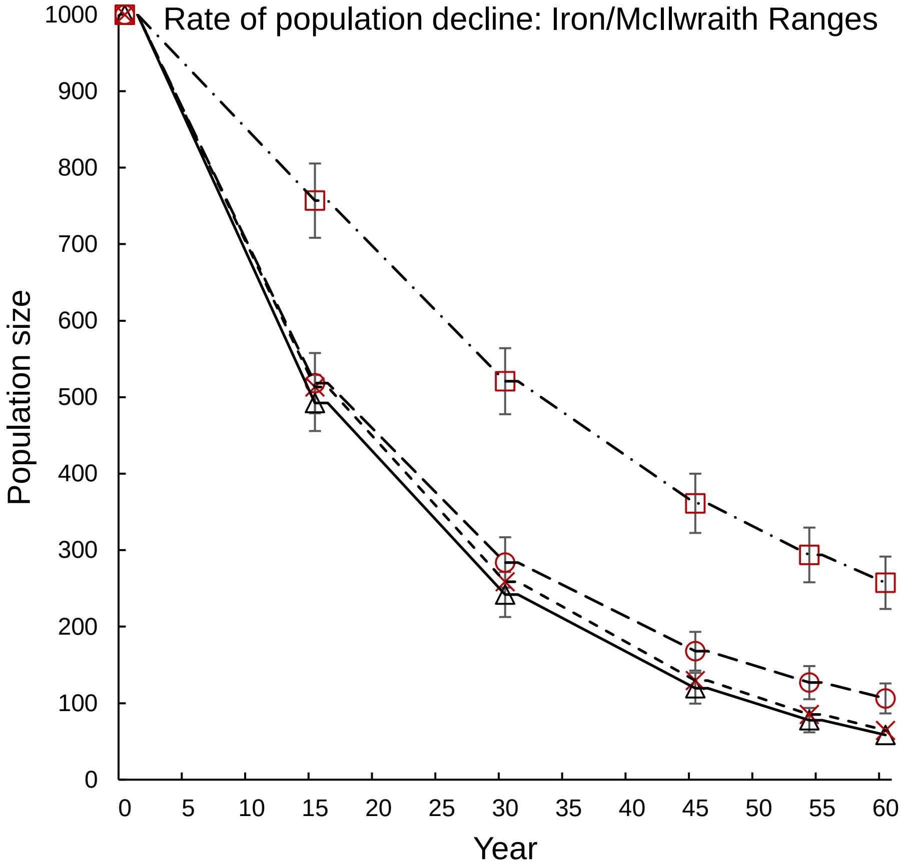

Figure 4. A selection of the simulated population trajectories for the Iron/McIlwraith Ranges population. The graph shows trajectories under the two reproductive success scenarios outlined Table 2, and two of the dispersal scenarios outlined in Table 4, Model 2 = triangles, Model 4 = crosses, Model 6 = circles and Model 8 = squares.

Discussion

Our PVA models suggest that the conservation status of palm cockatoos in Australia is worse than previously supposed. When evaluated against the criteria provided by IUCN Red List and the Australian Government Environment Protection and Biodiversity Conservation Act, the > 50% meta-population decline in three generations predicted by all our models (mean across all models = 82.5%), as well as our preferred model predicting a best case scenario of 62.3% decline, strongly support a change in conservation status for Australian palm cockatoos from ‘Vulnerable’ to ‘Endangered’ according to Red List Criterion A3c (IUCN, 2012). Our models predict that even if populations have twice as much success reproducing than suggested by field data, and if loss of habitat from inappropriate fire regimes (Murphy and Legge 2007) and bauxite mining (Gould 2011) is ignored, we can expect severe meta-population decline within three generations (54 years) of this long lived species. Furthermore, the > 80% decline after three generations on average across all models suggest the status of Australian palm cockatoos could be ‘Critically Endangered’ under Criterion A3 (IUCN, 2012). To confirm the more severe category however, extra data is required to replace the many conservative assumptions we incorporated in our simulations which we discuss in more detail below (*Model assumptions*).

Palm cockatoos intrinsically have low reproductive success typical of large parrot species, but face additional processes that threaten to reduce availability of nesting hollows outlined above: fire, cyclones, land clearing and competition. Dependence on forest and small historical distribution are additional risk factors that face many parrot species (Olah 2016), including Australian palm cockatoos. Reliance on habitat with a restricted distribution also poses a problem for the meta-population because individual subpopulations are more vulnerable to extinction (Frankham 2005). Our preferred model showed that whilst allowing increased reproductive success outside Iron/McIlwraith Ranges, the dispersal scenario representative of landscape and habitat distribution results in a lower rate of decline for the Iron/McIlwraith Ranges population than predicted without dispersal (r = 0.032 compared to r = 0.05 from Heinsohn *et al.* 2009). However, this is only a minor improvement and insufficient to buffer the local decline there. Even with hypothetically liberal dispersal and increased reproduction elsewhere (representing the best case for the sub-population) we can expect an 70.6% decline after three generations, characteristic of ‘Endangered’ populations under IUCN Red List Criterion A3 (IUCN, 2012).

The way dispersal dynamics interact with population viability in Cape York Peninsula palm cockatoo populations could be characteristic of source-sink dynamics (Pulliam 1988). We found that increased dispersal, specifically under scenarios of meta-population wide poor reproductive success, only very slightly improves prospects for palm cockatoos overall. Among models with increased reproductive successes outside Iron/McIlwraith Ranges we generally see the lowest extant meta-population sizes with high dispersal, likely because the low reproductive success of birds there has a greater effect on the metapopulation in these models. Although we consider our highest dispersal scenario unrealistic, it demonstrates that increasing connectivity may not be as efficient as reducing local threats when attempting to ensure meta-population viability for this species.

Model assumptions

Despite ongoing debate about the accuracy of PVA population trajectories, it is broadly accepted that the trends they predict are reliable for formulating management strategies when good quality demographic data are available (Brook *et al.* 1997; Brook *et al.* 2000; Ball *et al.* 2003; Lindenmayer and Mccarthy 2006; Lahoz-Monfort *et al.* 2014), however the quality of the data and any assumptions require explicit evaluation (Coulson *et al.* 2001). We ensured assumptions in our simulations were conservative so that our population projections represent best case scenarios (i.e. actual trajectories are likely less optimistic), which adds confidence to the severity of decline we predicted in palm cockatoos. As our simulations naturally follow from those of Heinsohn *et al.* (2009), we used similar assumptions regarding longevity, reproductive senescence and age of first breeding because data are still insufficient for palm cockatoos. We outline seven assumptions unique to the current study, followed by a summary of those shared with the previous manuscript in the section below.

Firstly, our abundance estimation approach relies on a field study directed towards collecting behavioural data, and therefore areas known to contain the species were visited on repeated occasions. Although we only extrapolated numbers to arbitrary population boundaries, there may be residual upwards bias to our overall population size estimates because not all areas designated as suitable can be guaranteed to harbor palm cockatoos. Nonetheless we used generous carrying capacities (double initial population size) to allow population trends free fluctuation without an upper limit on numbers. This allowed our resulting population trends to reflect the influence of the modelled processes more accurately.

Secondly, the greatest proportion of palm cockatoo breeding hollows are in the woodland tree species *Eucalyptus tetradonta*, followed by *Corymbia clarksonia* (Murphy 2003, pers. obs.) though *Maleleuca*, *Alstonia* and *Ficus* may also be used (Wood 1988). For the purpose of density estimation, our survey areas followed rainforest edges but were not restricted to woodland with any particular dominant species. We therefore extrapolated our density estimates only to breeding habitat designated as tall open woodland, without specific requirement of *Eucalyptus* or *Corymbia* (according to their description in the regional ecosystems classification scheme Queensland Herbarium 2015). Overestimation of palm cockatoo abundance in our models is possible because the greater area counted as suitable breeding habitat does not reflect the species' documented preference for *Eucalyptus* or *Corymbia* when choosing nest hollows.

Thirdly, our initial scenario was based on robust data from other cockatoos from the open plains in south-west Australia, galahs and Major Mitchel's cockatoos (Rowley 1983a; Rowley and Chapman 1991). However, as a woodland species that requires rainforest, palm cockatoos' habitat requirements may influence their dispersal differently than to these open plains species, which is why we adjusted dispersal patterns depending on the limiting rainforest habitat distribution in a subsequent model. Species tend to disperse further in wet habitats, supposedly where habitat has a patchy distribution (Paradis *et al.* 1998), and palm cockatoos are not as limited to rainforest habitat as are strictly rainforest species (e.g. Legge *et al.* 2004; Moore *et al.* 2008) which potentially frees up a greater proportion of individuals to disperse further. The possibility of greater proportions of long distance dispersers was taken into account in our model which designated half the individuals of dispersing age as moving between populations.

Fourth, the age of dispersing individuals logically plays a role in determining the overall proportion of individuals moving between populations. However we consider that modifying the overall proportion of two to four year olds moving between populations gives an adequate picture of how dispersal dynamics shape populations' viability so we did not experimentally manipulate the age bracket for dispersal.

Fifth, our models also assume that once individuals of dispersal age have dispersed to another population they do not disperse again, because palm cockatoos appear to be philopatric (Murphy *et al.* 2003). Sixth, we assumed complete survival of dispersing individuals and no reduced breeding success. However, cultural differences such as vocal dialects have been shown to influence social integration in wild parrots (Salinas-Melgoza and Wright 2012). With regards to success of dispersing individuals, we did not take into account the different vocal dialects of Iron/McIlwraith Ranges palm cockatoos which may reduce reproductive success of dispersers (at least initially) to/from this population in relation to resident birds. We also assumed no sex specific dispersal though known to occur in other species e.g. (Wright *et al.* 2005) because there is limited evidence to suggest this occurs in palm cockatoos (but see Keighley *et al.* in prep.a).

Seventh, although demographic data collected about the Iron/McIlwraith Ranges population was of uncommonly good quality, we had no such data for other populations apart from anecdotal accounts of decline of the population at Weipa (Gould, cited in Garnett *et al.* 2011, Heinsohn et al. 2009). Assuming that Iron/McIlwraith Ranges represents a 'sink' population, we tested scenarios in which the constraint imposed by low reproductive success at Iron/McIllwraith Ranges was relaxed in other populations.

The average adult mortality rate we derived (using generation time and age at first breeding; Gould, 2011) was lower than the most likely rate determined for palm cockatoos by Heinsohn *et al.*'s exploratory simulations (2009). We modified our rate according to differences among juvenile and adults observed in a study of wing tagged Carnaby's cockatoos during a seven year field study (Saunders 1982). Despite occupying a different habitat type, Carnaby's cockatoos have similar life-history traits to palm cockatoos in their small clutch size (two eggs, usually one survivor) and high rates of breeding failure, which however, as discussed by Saunders (1982) may be unnaturally elevated due to poor survival of wing-tagged birds. We retained only the proportional differences among age classes in mortality rate, so our rates should not reflect un-naturally elevated mortality. Furthermore, although the data we based our rates on were the most detailed for any cockatoo species, their true proportionality and variation may be different, and might also be different to that of palm cockatoos.

The following briefly discusses the assumptions we made regarding longevity, reproductive senescence and age of first breeding as well as the method of constraining breeding opportunities to a fluctuating supply of nesting hollows, all of which were described in more detail in Heinsohn *et al.* (2009). Our models assume palm cockatoos can live for over 100 years. Parrots are characteristically long lived, however the oldest official records for captive parrots come at least 30 years short of this: A Salmon-crested Cockatoo *Cacatua moluccensis* that died at 69, and a Major Mitchell's Cockatoo *Lophochroa leadeateri* lived to at least 63 at the time of review (Brouwer *et al.* 2000). Even though middle-aged birds tend to reproduce and survive better than either young or old birds (Newton 1989), our models assume that palm cockatoos show neither increased mortality nor reproductive senescence throughout life (as in Heinsohn *et al.* 2009). We also assumed palm cockatoos begin breeding by the age of four as supported by data from species of black-cockatoo (*Calyptoryhnchus*) (Saunders 1982, 1986), although some can breed even earlier Glossy Black-Cockatoo (*Calyptoryhnchus lathami*) (Garnett *et al*. 1999). Age of first breeding probably remains critically important given that shifting the breeding age of palm cockatoos by one year to age five could decrease population growth rate considerably (Heinsohn *et al.* 2009). Nesting hollows are a limiting resource for palm cockatoos, and the apparent cause for much inter-specific (Igag 2002; Murphy *et al*. 2003), as well as intra-specific (Heinsohn *et al*. 2009) conflict and possibly interference with breeding attempts. Our models flexibly limit the number of breeding females to the total number of breeding opportunities depending on either availability of hollows or breeding males. Hollow availability fluctuates with destruction by fire, wind and rot, and episodic creation by cyclones (Murphy and Legge 2007) which results in a variable resource that interacts with competition and reproductive success. When hollows are abundant, interference competition (not captured by our approach) may relax alongside an increase in reproductive success, however it is unlikely that this could ever compensate for the high rate of egg and nestling predation and therefore overall reproductive success (Heinsohn *et al.* 2009).

Conclusion

The PVA presented here provides a strong indication of the long term deterministic effects that slow reproduction and poor success in at least one population have on the Australian meta-population of palm cockatoos under different scenarios of interpopulation connectivity. Our results should be interpreted as confirmation that palm cockatoos are threatened with extinction throughout their Australian range. When our results are reviewed in the framework of the IUCN Red List and the Australian Government Environment Protection and Biodiversity Conservation Act criteria, clearly the current listing of palm cockatoos as ‘vulnerable’ is not representative of the meta-population status as well as the genetically and vocally distinct Iron/McIlwraith Ranges sub-population. The > 50% population decline within the next three generations predicted by all of our models (inclusive of our best case scenarios) supports a change in status to ‘endangered’ for the Australian meta-population of palm cockatoos and the Iron/McIlwraith Ranges sub-population under Criterion A3 (IUCN, 2012). The more serious declines we predict in this sub-population suggest that dispersal is highly unlikely to buffer local declines and highlights the importance of further investigating and relieving local threatening processes. Our data and analyses provide an important demonstration of how PVA can be used to assess the influence of complex meta-population scale processes on the trajectory of species and populations of species that are challenging to monitor because capture and tracking are not feasible. When high quality demographic data are available PVA can be an effective tool for predicting severe population decline, and identifying the most effective conservation strategies.

Author contributions

M.V.K. conducted fieldwork, analyses and wrote the manuscript. N.E.L. assisted with comments on the manuscript and sought funding. S.H. provided detailed assistance with statistical methodology and commented on the manuscript. R.H. conceived the idea for the project, sought funding, guided the project and commented on the manuscript.

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Appendix 1: Palm cockatoo abundance model coefficients

Table 6. Coefficients for generalized linear models of bird counts with observer and distance band away from required rainforest habitat as well as sampling locations from three regions within the a) northern and b) central populations using the quasi Poisson distribution.

a) Northern population	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	1.54E+00	3.86E-01	3.980	0.000
ESWSampHab_m	-4.62E-07	1.49E-07	-3.099	0.003
Gen.AreaARArcher_camp_west East	-4.63E-01	5.45E-01	-0.850	0.398
Gen.AreaARArcher_west(East)	-5.25E-01	4.53E-01	-1.159	0.250
Gen.AreaBAAirport_rd	-2.12E+00	8.55E-01	-2.485	0.015
Gen.AreaBAInjinoo_rd_inj	3.13E-01	4.36E-01	0.719	0.474
Gen.AreaBAInjinoo_rd_middle	7.65E-01	4.80E-01	1.592	0.116
Gen.AreaBAInjinoo_rd_Middle	3.82E-01	5.57E-01	0.685	0.496
Gen.AreaBAInjinooo_rd_int	-1.08E+00	7.45E-01	-1.447	0.152
Gen.AreaBAPunsand_bay_rd_South	-7.17E-01	6.93E-01	-1.035	0.304
Gen.AreaBAShortcut_rd_East	-2.98E-01	4.20E-01	-0.709	0.480
Gen.AreaBAShortcut_rd_West	6.83E-01	4.33E-01	1.579	0.119
Gen.AreaPCPalm_ck	1.91E-01	4.39E-01	0.435	0.665
Gen.AreaSIBoulder_bend	-2.69E-01	3.19E-01	-0.843	0.402
Gen.AreaSIJungle_camp	5.02E-03	6.54E-01	0.008	0.994
Gen.AreaSIRed_canyons North	-2.73E-01	5.64E-01	-0.484	0.630
Gen.AreaSIRiflebird_bend	-5.67E-01	2.99E-01	-1.893	0.062
Gen.AreaSIRiflebird_bend_south	-1.58E+00	1.15E+00	-1.376	0.173
Gen.AreaSISprings	-1.04E+00	2.99E-01	-3.490	0.001
Obs 2	3.70E-01	3.32E-01	1.114	0.269
Obs 3	5.51E-01	2.68E-01	2.059	0.043
Obs 4	-3.73E-01	3.39E-01	-1.100	0.275
Obs 5	4.78E-01	3.49E-01	1.369	0.175
Distance Band 0 - 200m	2.33E-07	1.88E-07	1.238	0.220
Distance Band 200m - 1km	-6.86E-09	1.44E-07	-0.048	0.962
Distance Band > 1km	4.63E-07	1.92E-07	2.413	0.018
b_1) Central population – Piccaninny plans				
(Intercept)	7.47E-01	4.62E-01	1.616	0.112
ESWSampHab_m	-2.02E-09	2.93E-07	-0.007	0.995
Gen.AreaARArcher_camp_west	-1.01E+00	3.35E-01	-3.002	0.004
Gen.AreaARArcher_camp_west East	-1.22E+00	5.67E-01	-2.155	0.036
Gen.AreaARArcher_East	-8.20E-01	2.57E-01	-3.192	0.002
Gen.AreaARArcher_scrubby_ck	-7.44E-01	5.36E-01	-1.388	0.171
Gen.AreaARArcher_tributary	-1.60E+00	3.70E-01	-4.338	0.000
Gen.AreaARArcher_west	-1.20E+00	3.41E-01	-3.520	0.001
Gen.AreaARArcher_west(East)	-8.83E-01	4.07E-01	-2.172	0.034
Gen.AreaARArcher_west_east	1.20E-01	4.62E-01	0.259	0.797
Gen.AreaARPicca_ck	-9.50E-01	5.77E-01	-1.648	0.105
Gen.AreaARPicca_ck_South	-1.92E+00	5.49E-01	-3.500	0.001
Gen.AreaARPicca_ck_West	-1.41E+00	7.86E-01	-1.798	0.078
Gen.AreaARPlain_ck	-4.19E-01	4.78E-01	-0.878	0.384
Obs 2	1.35E+00	4.32E-01	3.122	0.003
Obs 3	1.35E+00	4.22E-01	3.201	0.002

Obs 4	1.05E+00	4.15E-01	2.540	0.014
Distance Band 0 - 200m	-9.61E-08	2.17E-07	-0.442	0.660
Distance Band 200m - 1km	3.93E-07	3.54E-07	1.112	0.271
Distance Band > 1km	4.10E-07	2.78E-07	1.473	0.146
b_2) Central population – Steve Irwin Wildlife Reserve				
(Intercept)	7.02E-01	5.86E-01	1.198	0.234
ESWSampHab_m	-1.30E-07	2.20E-07	-0.591	0.556
Gen.AreaSICoolibah_area	-5.11E-01	2.58E-01	-1.983	0.050
Gen.AreaSIJungle_camp	2.20E-01	7.11E-01	0.310	0.757
Gen.AreaSIMaleleuca_arches	-3.65E-01	4.61E-01	-0.791	0.431
Gen.AreaSIRed_canyons	-5.39E-01	2.82E-01	-1.913	0.059
Gen.AreaSIRed_canyons North	1.16E-02	6.15E-01	0.019	0.985
Gen.AreaSIRiflebird_bend	-7.60E-02	2.77E-01	-0.274	0.784
Gen.AreaSIRiflebird_bend_south	-5.47E-01	1.31E+00	-0.416	0.678
Gen.AreaSISprings	-7.14E-01	2.80E-01	-2.550	0.012
Obs 2	8.78E-01	5.90E-01	1.489	0.140
Obs 3	1.19E+00	5.53E-01	2.146	0.034
Obs 4	1.75E+00	5.94E-01	2.945	0.004
Obs 5	1.04E+00	5.90E-01	1.757	0.082
Distance Band 0 - 200m	-8.25E-07	3.48E-07	-2.372	0.020
Distance Band 200m - 1km	2.88E-07	2.57E-07	1.120	0.266
Distance Band > 1km	-1.21E-06	7.57E-07	-1.597	0.114

Appendix 2: Population parameter details.

As the viability of one Australian population of palm cockatoos has already been thoroughly investigated in Heinsohn *et al.* (2009) we use the same population parameters summarized and explained below. These are based on data about reproductive rates and success outlined in Murphy *et al.* (2003). The data results from close monitoring of 28 active nests over 3 years at Iron/McIlwraith Ranges, and included 41 breeding attempts (Murphy *et al.* 2003). Females had at most one offspring per year, but apparently only attempted to breed every 2.2 years on average. Their single offspring has just a 0.22 percent chance of hatching and fledging, though some females attempt a second time within a season if at first unsuccessful giving a 0.25 percent chance success per season. The likelihood of attempting to breed combined with chance of success gives one figure of 0.11 offspring per year per female. Breeding success is slightly greater in the New Guinean population with probability of chicks fledging being 0.40, yet the overall reproductive rate is unclear (Igag 2002).

The age at which individuals begin to reproduce, and the maximum age of reproduction are unknown for wild palm cockatoos. In captivity they have not been observed to breed before 7 or 8 years old, one individual had their first offspring at age 40 suggesting captivity does not encourage early breeding (Brouwer *et al.* 2000). Black-cockatoos (Calyptorynchus sp.) reach sexual maturity earlier in the wild. For example, carnaby's black-cockatoos (C. latirostris) first attempt to breed at four years old (Saunders 1982, 1986). We use four years as the age of first breeding for palm cockatoos in our models. Heinsohn *et al.* (2009) use a generous maximum longevity of 150 years without reproductive senescence, which does not force long life but allows calculation of a range of mortality schedules that might be necessary for their persistence given such low reproductive rates.

For the mating system we used 'long-term monogamy' as DNA fingerprinting revealed monogamous breeding in Iron/McIlwraith Ranges palm cockatoos over multiple years (Murphy *et al.* 2003). In VORTEX this system involves pairs breeding with each other exclusively until one of them dies. There is no evidence that hatching sex ratios are unequal.

Chapter 7: Conclusion

In summary, this thesis concludes that cultural processes appear embedded enough in parrot communication that geographic cultural variation can indicate other population processes. Particularly detailed insights are possible when comparing cultural variation with other data that varies depending on interpopulation interaction. Focusing on palm cockatoos, cultural variation among geographically separate populations aligns with genetic variation. The interpopulation interaction patterns can be explained by particular importance of narrow corridors and hindrance due to elevated terrain. The declining population of palm cockatoos at Iron Range is highly unlikely to be buffered by connectivity, and we conclude overall that predicted decline rates for Australian palm cockatoos warrant change in conservation status from ‘Vulnerable’ to ‘Endangered’ (IUCN criteria, 2012).

The first aim of my thesis was to review conclusions about inter-population interaction drawn from cultural variation. In Chapter 2 I found that, especially in vocal communication, cultural processes appear more embedded in the communicative systems and ecology of parrots than other non-human animals. The large influence that social learning has on vocal expression makes them particularly suited for gaining insight into interaction dynamics among populations via analysis of cultural variation. Differences among species, for example in learning regime, life-history strategy, group size or stability make it difficult to generalise insights gained from detailed studies in a few species across all parrots. However with comparison to similar species and availability of alternative data, geographic variation in cultural behaviour among populations of a species can help fill important knowledge gaps about population level processes in difficult to study species.

This is evident in such data being increasingly considered in conservation management decisions (Laiolo 2010).

The other aims of this thesis were to investigate the interaction between cultural and genetic evolution among populations of Australian palm cockatoos at a relevant scale for conservation, and to interpret and use the resulting information for elucidating the species' management requirements and actual conservation status. Chapters 3 – 6 addressed these conservation aims with a case study of interaction among palm cockatoo populations on Cape York Peninsula, conducted in the context of local declines and the non-uniform distribution of habitat at the landscape scale. The key questions for their conservation management were:

4. What is the structure of the meta population?
5. What aspects of the landscape facilitate or prevent interpopulation movement?
6. Can connectivity buffer low reproductive success and prevent local declines?

Below I summarize the outcomes of this research with respect to these specific questions, as well as some additional insights about palm cockatoo biogeography, population size and a potential role of parrots as the most suitable model taxa for exploring the evolution of cultural processes among animals.

1) Population structure

In our assessment of vocal variation among populations (Chapter 3) we found that palm cockatoos from the east coast possess unique contact calls and have fewer call types in common with other locations on Cape York Peninsula. Coinciding with the vocal differentiation, genomic SNP data (Chapter 4) showed genetic differentiation separating east coast palm cockatoos at Iron Range from other Australian populations. The presence of admixed individuals suggests some connectivity among the otherwise distinct populations, and that the distinct dialects are most likely to be maintained by immigrant individuals learning the resident dialect. However, admixed individuals appear restricted to specific locations suggesting non-uniform dispersal. The unique mitochondrial ND2 gene haplotype found at Iron Range exists amongst the haplotype shared with the rest of Cape York Peninsula, which weakly suggests that palm cockatoo dispersal into Iron Range outweighs dispersal out of the region. I suggest dividing Australian populations into two distinct management units because genetic and behavioural diversity differentiate at the same location, and because of the combined possibilities of restricted, one-way or non-uniform dispersal between differentiated populations. However, more detailed information about landscape scale influences on movement are required to elucidate the optimal strategy for conservation management.

2) *Landscape level movement patterns*

Chapter 5 demonstrated the effectiveness of a multifaceted, model validation approach for elucidating landscape scale processes via their influence on genetic and vocal interaction patterns among populations of palm cockatoos. The results show that vocal distance in two call types, genetic variation and landscape ‘resistance’ values support hypotheses that both topography and rainforest habitat constrain landscape-scale interaction patterns. We identified that the Great Dividing Range is a plausible dispersal barrier, and that continuous rainforest corridors are important for population connectivity, specifically in the area north of Iron Range. Furthermore, we discovered an indirect relationship between genetic and vocal variation in one call type, identifying a useful alternative data source for future non-invasive assessments of interpopulation interaction.

3) *Meta-population viability*

The results of the population viability analysis in Chapter 6 showed severe declines for the metapopulation of palm cockatoos. Our simulations also showed that sufficient dispersal to buffer local declines predicted for the Iron/McIlwraith Ranges subpopulation is highly unlikely. We predicted declines of > 50% over three generations (54 years) (Garnett *et al.* 2011) under our best case scenario for the metapopulation (which assumed greater reproductive success outside Iron Range than data suggests, as well as dispersal representative of landscape and habitat distribution effects). Based on the magnitude of this predicted decline we recommend a change in conservation status for Australian palm cockatoos from ‘vulnerable’ to ‘endangered’ under IUCN criterion A3 (IUCN, 2012).

We predict that dispersal relieves local declines at the Iron/McIlwraith Ranges population, but not enough to avoid extinction risk. Our best case scenario for the Iron/McIlwraith Ranges subpopulation included liberal dispersal among populations and increased reproductive success outside Iron/McIlwraith Ranges. Another scenario in which connectivity was restricted also resulted in slower decline and reduced extinction probability compared to a no-dispersal scenario (Heinsohn *et al.* 2009). However, even under the best case scenario the sub-population’s viability improvement was only minor and insufficient to buffer local decline given the 87.3% decline within the next three generations predicted by our best case scenario.

Biogeographical insights

The BIOCLIM historical distribution models in Chapter 3 show the Iron Range as the only area with palm cockatoos, and therefore suitable habitat (i.e. woodland with patches of rainforest) on Cape York Peninsula in the mid-Holocene, and that there was no suitable area at all on the peninsula during the last glacial maximum. However, rainforest pockets were probably preserved throughout even the most arid periods at topographic refugia (e.g. the escarpment of the Great Dividing Range) due to reliable orographic rainfall. Enough rainforest for palm cockatoos was probably maintained at the Iron and McIlwraith Ranges given the persistence of other large rainforest dependent vertebrates that have disappeared from rainforests elsewhere in Australia (eclectus parrots *Eclectus roratus*). It is possible that isolation at this time allowed evolution of genomic differentiation and unique contact call dialect we found in Chapters 3 and 4 respectively.

The way dispersal dynamics interact with population viability in Cape York Peninsula palm cockatoo populations is characteristic of source-sink dynamics (Pulliam 1988). We found that increased dispersal, specifically under scenarios of meta-population wide poor reproductive success, only very slightly improves prospects for palm cocaktoos overall. Among models with increased reproductive successes (outside Iron Range) we generally see the lowest extant meta-population sizes in scenarios of high dispersal, which might be explained by the low reproductive success at Iron Range influencing a greater proportion of the metapopulation under increased dispersal.

Population size

In Chapter 6 I presented the first data based estimate of population size for palm cockatoos. Our estimate of 4510 individuals is based on combined density data from field surveys conducted as part of this study and field surveys from a previous study. The estimate represents extrapolation of densities measured in parts of their range that were known to contain palm cockatoos and should be regarded as an overestimate. Newer methods may make it possible to incorporate different data collected at different scales for more accurate abundance estimates relating to their entire range.

Parrot models for cultural evolution

Social learning of vocalisations in animal populations has been investigated in detail in songbirds fueled by curiosity about the evolutionary background of sophisticated, learned vocal communication such as human language. Producing learned vocalisations with reference to phenomena outside of the self is recognized as an important stepping stone identified in communication of dolphins, parrots and songbirds. Learned referential alarm calls have been shown in the wild in a songbird species, but vocal learning is more widespread among parrots and their use in a referential context has been shown in at least one captive individual. Elucidating the breadth of referential use for learned vocalisations, as well as how they benefit individuals in wild groups is an important next step, and parrots are perhaps the most promising focal taxa. The cultural repertoire of parrots also includes tool manufacture and use, and potentially instrumental music and visual gesture (if learned), and continued investigation of these capacities with regards to social learning and geographic variation among wild populations has potential to expand our insight about evolution of cultural processes in foraging, social and sexual ecology.

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