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Geographic variation in the vocalizations 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.

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Palm cockatoo; *Probosciger aterrimus*; vocal dialects; sound analysis; psittacine vocalizations; Cape York Peninsula

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 & Slater 1995). 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). In these groups, geographic variation in vocalizations can arise as a side effect or “epiphenomenon” of learning through the incorporation

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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 (Catchpole & 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 & 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 & Slater 1995; Farabaugh & Dooling 1996).

Many studies have explored differences in vocalizations between localities to understand how dialects are formed (reviewed by Podos & 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 & 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).

Methods

Study species

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 1 km 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

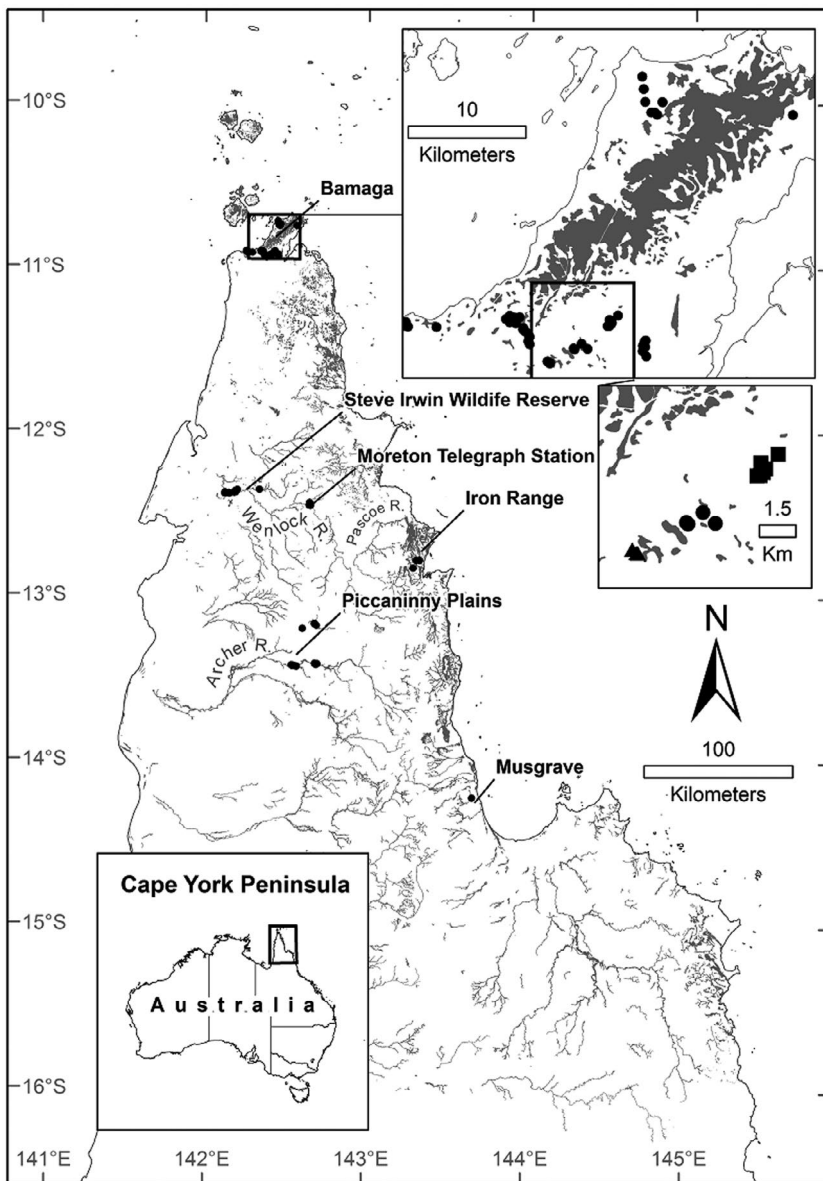


Figure 1. Palm cockatoo population study locations, showing distribution of rainforest and gallery forest corridors in grey.

Note: The Bamaga population is enlarged, with another inset illustrating three separate recording sites with different shapes.

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 sclerophyll woodland (Webb & 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 Zdenek et al. (2015) as “either a single element (continuous line on the spectrogram; Catchpole & 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 s 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.

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 50 and 402 km. 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 40.7 km, 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 ± 4.3 sd times, and we ceased visiting sites once we acquired approximately 15 min of calling behaviour, 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 h of non-continuous recordings from unmarked, wild palm cockatoos at a distance of 20–60 m. 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 1.5 km 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.

Recordings from the Iron Range were made with a Canon EOS 5D Mark III camera with a 400-mm EF 5.6L IS USM lens and a directional Rode VideoMic pro external microphone (with a windshield) set to 0 dB gain boost. All other recordings were made using a Canon 600D DSLR camera with 100–400-mm 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 15 dB. 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 \pm sd = 4 min 43 s \pm 3 min 14 s, totalling to means of 43 min 57 s \pm 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 analysed 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 vs. 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

Table 1. Acoustic parameters.

Measurement	Unit	Description (Raven Pro User Manual: Charif, <i>et al.</i> 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 analysing 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.

*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.

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 ± 2.81 sd 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 indicates 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 & Blumstein 2011) in the *vegan* package in R (R Development Core Team 2014) 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 & Blumstein 2011). Keeping a uniform recording number across populations was trialled by restricting all sites to six 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 (Figure 2).

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 2014; package: ade4). Geographic distance between populations was calculated using the great circle distance formula (Longley 2005):

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

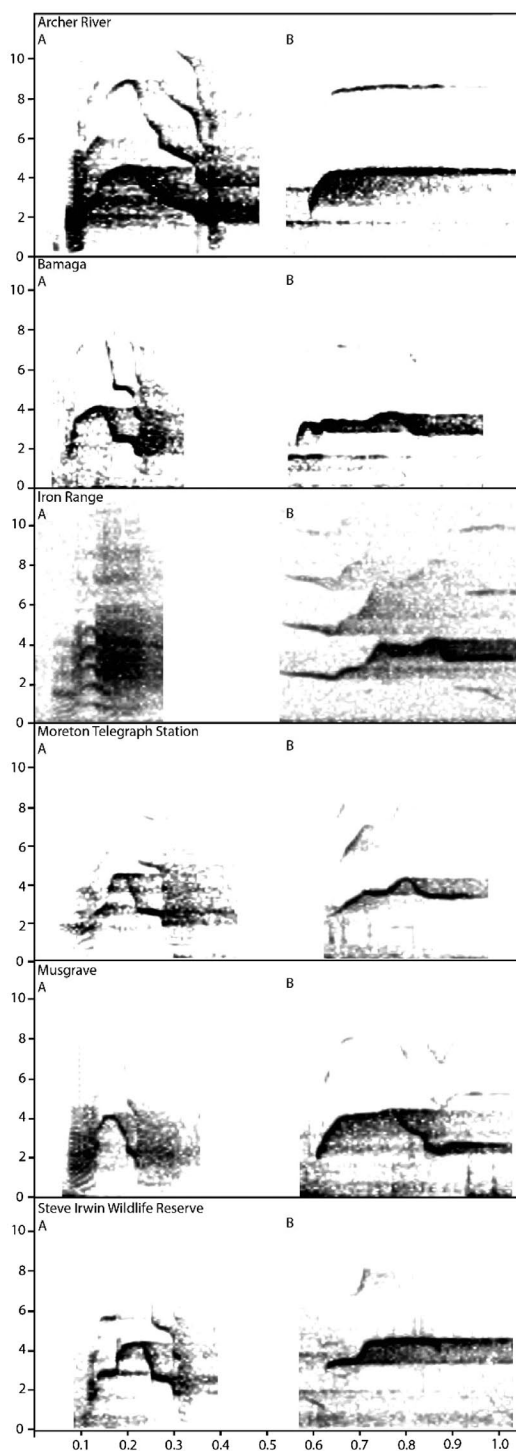


Figure 2. Representative spectrograms of the contact calls that were used in the structural comparison between populations, A = broadband contact calls, and B = short whistles.

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).

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

Population	Number of common call types and proportion of estimated repertoire size*	Estimated repertoire size*	Broadband contact calls		Short whistles	
			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 four populations; Archer River (AR), Bamaga (BA), Iron Range (IR) and Steve Irwin Wildlife Reserve (SI). Moreton Telegraph Station (MTS) only had 6 recordings with at least 20 calls and Musgrave (MU) had too few recordings for rarefaction.

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.

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 1.5-km 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 & 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 2014).

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 ± 2.80 sd 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 4 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 = 251 km). The site with the fewest shared calls, Iron Range (mean BC = 0.96), was relatively close to most of the other sites (mean distance = 143 km, Figure 1).

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. DFA on broadband contact calls from each site within the 4 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 (Table 5). 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).

DFA 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).

Between population scale analyses on contact calls

DFA 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 3(a)). 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.

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).

Table 4. Discriminant function loadings for site categories.

Discriminant function	Eigenvalue	Per cent variation	Effect size	P value
<i>Population comparison</i>				
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*
<i>Within population comparison</i>				
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

*P value <0.05, representing significant fit.

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 3(a)), despite its central position geographically. There was no significant correlation between acoustic distance and

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

Geographic scale		Acoustic distance measure	Mantel test	
			<i>r</i>	<i>P</i>
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	Short whistle	−0.404	0.997
	Wildlife reserve	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 analysed at within population scale due to their small geographic area.

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

Discussion

We found interesting 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.

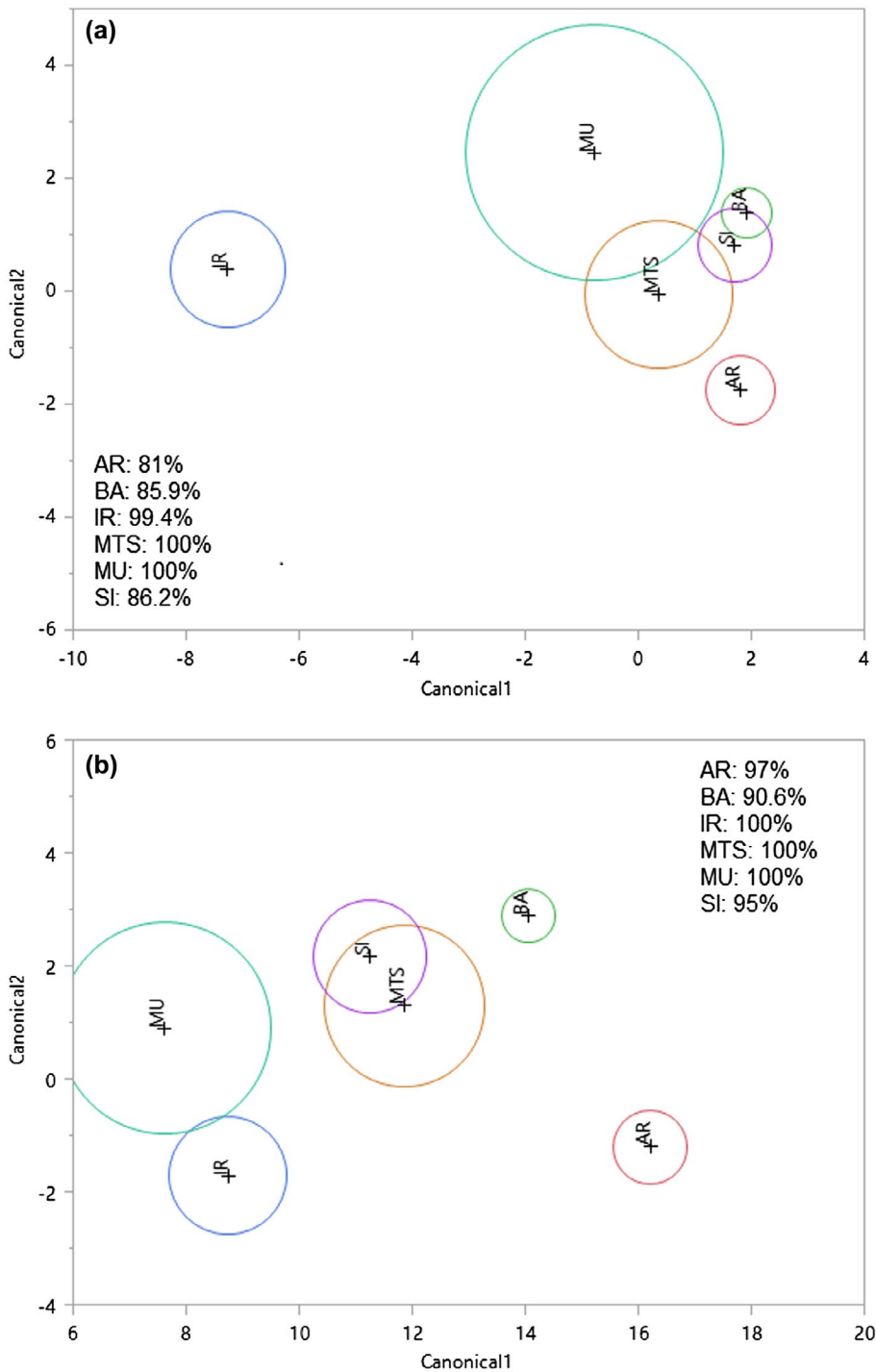


Figure 3. Discriminant function analysis based on the 22 acoustic parameters of (a) broadband contact calls and (b) short whistles from each of the 6 populations (AR: Archer River, BA: Bamaga, IR: Iron Range, MTS: Moreton Telegraph Station, MU: Musgrave, SI: Steve Irwin Wildlife Reserve).

Note: 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.

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 & 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 & 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 40.7 km). 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 occurs 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 & 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 & 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 & Kalma 1972; Webb & 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 (3 km) 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.

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References

- Andrew RJ. 1962. Evolution of Intelligence and Vocal Mimicking: studies of large-brained mammals promise to elucidate some problems of human evolution. *Science*. 137(3530):585–589.
- Baker MC. 2000. Cultural diversification in the flight call of the ringneck parrot in western australia. *Condor*. 102(4):905–910.
- Baker MC. 2003. Local similarity and geographic differences in a contact call of the Galah (*Cacatua roseicapilla assimilis*) in Western Australia. *Emu*. 103(3):233–237.
- Baker MC. 2008. Analysis of a cultural trait across an avian hybrid zone: geographic variation in plumage morphology and vocal traits in the Australian ringneck parrot (*Platycercus zonarius*). *Auk*. 125(3):651–662.
- Bioacoustics Research Program. 2014. Raven Pro: interactive sound analysis software (version 1.5) [Computer software]. Ithaca (NY): The Cornell Lab of Ornithology.
- Bond AB, Diamond J. 2005. Geographic and ontogenetic variation in the contact calls of the kea (*Nestor notabilis*). *Behaviour*. 142(1):1–20.
- Bradbury JW. 2003. Vocal communication in wild parrots. In: De Waal FBM, Tyack PL, editors. *Animal social complexity: intelligence, culture and individualized societies*. Cambridge (MA): Harvard University Press. p. 293–316.
- Bradbury JW, Cortopassi KA, Clemmons JR, Kroodsma D. 2001. Geographical variation in the contact calls of orange-fronted parakeets. *Auk*. 118(4):958–972.
- Catchpole C, Slater P. 1995. *Birdsong: biological themes and variations*. Cambridge (NY): Cambridge University Press.
- Charif R, Waack A, Strickman L. 2008. *Raven Pro 1.3 user's manual*. Ithaca (NY): Cornell Lab of Ornithology.
- Crisp MD, Laffan S, Linder HP, Monro A. 2001. Endemism in the Australian flora. *J Biogeogr*. 28(2):183–198.
- Dahlin CR, Young AM, Cordier B, Mundry R, Wright TF. 2014. A test of multiple hypotheses for the function of call sharing in female budgerigars, *Melopsittacus undulatus*. *Behav Ecol Sociobiol*. 68(1):145–161.
- Department of the Environment. 2015. *Probosciger aterrimus macgillivrayi*. Species profile and threats database, Department of the Environment, Canberra. [cited 2015 Dec 18]. Available from: <http://www.environment.gov.au/sprat>

- Farabaugh SM, Dooling RJ. 1996. Acoustic communication in parrots: laboratory and field studies of budgerigars, *Melopsittacus undulatus*. In: Kroodsma DE, Miller EH, editors. Ecology and evolution of acoustic communication in birds. Ithaca (NY): Cornell University Press. p. 97–117.
- Farabaugh SM, Linzenbold A, Dooling RJ. 1994. Vocal plasticity in budgerigars (*Melopsittacus undulatus*): evidence for social factors in the learning of contact calls. *J Comp Psychol*. 108(1):81–92.
- Farrar DE, Glauber RR. 1967. Multicollinearity in regression analysis: the problem revisited. *Rev Econ Stat*. 49(1):92–107.
- Friedman JH. 1989. Regularized discriminant analysis. *J Am Stat Assoc*. 84(405):165–175.
- Guerra JE, Cruz-Nieto J, Ortiz-Maciel SG, Wright TF. 2008. Limited geographic variation in the vocalizations of the endangered thick-billed parrot: implications for conservation strategies. *Condor*. 110(4):639–647.
- Heinsohn R, Zeriga T, Murphy S, Igag P, Legge S, Mack AL. 2009. Do Palm Cockatoos (*Probosciger aterrimus*) have long enough lifespans to support their low reproductive success? *Emu*. 109(3):183–191.
- Higgins P. 1999. Handbook of Australian, New Zealand and Antarctic birds. Volume 4: parrots to dollarbird. Melbourne: Oxford University Press.
- Hile AG, Plummer TK, Striedter GF. 2000. Male vocal imitation produces call convergence during pair bonding in budgerigars, *Melopsittacus undulatus*. *Anim Behav*. 59(6):1209–1218.
- Hile AG, Striedter GF. 2000. Call convergence within groups of female budgerigars (*Melopsittacus undulatus*). *Ethology*. 106(12):1105–1114.
- Irwin DE. 2000. Song variation in an avian ring species. *Evolution*. 54(3):998–1010.
- Jenkins PF. 1978. Cultural transmission of song patterns and dialect development in a free-living bird population. *Anim Behav*. 26:50–78.
- Krebs JR, Kroodsma DE. 1980. Repertoires and geographical variation in bird song. *Adv Stud Behav*. 11:143–177.
- Kroodsma DE. 1996. Ecology of passerine song development. In: Kroodsma DE, Miller EH, editors. Ecology and evolution of acoustic communication in birds. Ithaca (NY): Cornell University Press. p. 3–19.
- Laiolo P. 2010. The emerging significance of bioacoustics in animal species conservation. *Biol Conser*. 143(7):1635–1645.
- Legge S, Heinsohn R, Garnett S. 2004. Availability of nest hollows and breeding population size of eclectus parrots, *Eclectus roratus*, on Cape York Peninsula, Australia. *Wildlife Res*. 31(2):149–161.
- Longley P. 2005. Geographic information systems and science. Chichester (UK): Wiley.
- Murphy SA, Double MC, Legge SM. 2007. The phylogeography of palm cockatoos, *Probosciger aterrimus*, in the dynamic Australo-Papuan region. *J Biogeogr*. 34(9):1534–1545.
- Murphy S, Legge S, Heinsohn R. 2003. The breeding biology of palm cockatoos (*Probosciger aterrimus*): a case of a slow life history. *J Zool*. 261(4):327–339.
- Nix H, Kalma J. 1972. Climate as a dominant control in the biogeography of northern Australia and New Guinea. In: Walker D, editor. Bridge and Barrier: the natural and cultural history of Torres Strait. Proceedings of the Torres Strait Symposium; 1971; Canberra. ACT (AU): Australian National University.
- Pavlova A, Amos JN, Goretskaia MI, Beme IR, Buchanan KL, Takeuchi N, Radford JQ, Sunnucks P. 2012. Genes and song: genetic and social connections in fragmented habitat in a woodland bird with limited dispersal. *Ecology*. 93(7):1717–1727.
- Pepperberg IM, Neapolitan DM. 1988. Second language acquisition: a framework for studying the importance of input and interaction in exceptional song acquisition. *Ethology*. 77(2):150–168.
- Peshek KR, Blumstein DT. 2011. Can rarefaction be used to estimate song repertoire size in birds? *Curr Zool*. 57(3):300–306.
- Podos J, Warren PS. 2007. The evolution of geographic variation in birdsong. *Adv Stud Behav*. 37:403–458.
- R Development Core Team. 2014. R: a language and environment for statistical computing. Vienna: R Foundation for Statistical Computing.
- Ribot RF, Berg ML, Buchanan KL, Komdeur J, Joseph L, Bennett AT. 2009. Does the ring species concept predict vocal variation in the crimson rosella, *Platycercus elegans*, complex? *Anim Behav*. 77(3):581–593.

- Russell-Smith J, Stanton PJ, Edwards AC, Whitehead PJ. 2004. Rain forest invasion of eucalypt-dominated woodland savanna, Iron Range, north-eastern Australia: II. Rates of landscape change. *J Biogeogr.* 31(8):1305–1316.
- Salinas-Melgoza A, Wright TF. 2012. Evidence for vocal learning and limited dispersal as dual mechanisms for dialect maintenance in a parrot. *PLoS One.* 7(11):e48667.
- Sigler Ficken M, Rusch KM, Taylor SJ, Powers DR. 2000. Blue-throated hummingbird song: a pinnacle of nonoscine vocalizations. *Auk.* 117(1):120–128.
- Slater PJ. 1989. Bird song learning: causes and consequences. *Ethol Ecol Evol.* 1(1):19–46.
- Suchan T, Pitteloud C, Gerasimova N, Kostikova A, Arrigo N, Pajkovic M, Ronikier M, Alvarez N. 2015. Hybridization capture using RAD probes (hyRAD), a new tool for performing genomic analyses on museum collection specimens. *bioRxiv.* 025551.
- Thorpe WH. 1958. The learning of song patterns by birds, with especial reference to the song of the chaffinch *Fringilla coelebs*. *Ibis.* 100(4):535–570.
- Webb L, Tracey J. 1981. Australian rainforests: patterns and change. In: Keast A, editor. *Ecological biogeography of Australia*. The Hague: Dr. W. Junk. p. 605–694.
- Wood G. 1984. Tool use by the Palm Cockatoo *Probosciger aterrimus* during display. *Corella.* 8:94–95.
- Wright TF. 1996. Regional dialects in the contact call of a parrot. *Proc Biol Sci.* 263(1372):867–872.
- Wright TF, Rodriguez AM, Fleischer RC. 2005. Vocal dialects, sex-biased dispersal, and microsatellite population structure in the parrot *Amazona auropalliata*. *Mol Ecol.* 14(4):1197–1205.
- Zdenek C, Heinsohn R, Langmore N. 2015. Vocal complexity in the palm cockatoo (*Probosciger aterrimus*). *Bioacoustics.* 24(3):253–267.