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Vocal individuality, but not stability, in wild palm cockatoos (*Probosciger aterrimus*)

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ABSTRACT

The ability to identify individuals within a population is often essential for a detailed understanding of the ecology and conservation of a species. However, some species, including large parrots, are notoriously difficult to catch and mark for individual identification. Palm cockatoos (*Probosciger aterrimus*) are a large, poorly understood species of parrot which are likely in severe decline within the eastern part – and possibly the western part – of their range on Cape York Peninsula, Australia. Here, we investigated whether three different palm cockatoo call types are sufficiently individually distinctive to function as a non-invasive “marker” for identifying individuals over time. Using Discriminant Function Analysis, overall identification accuracy among 12 putative individuals for all call types was 81% (i.e. 148 out of 183 calls were assigned to the correct individual) on the basis of multiple temporal, energy (amplitude) and frequency measurements on the spectrogram. For three different call types, individual identification accuracy among males and females ranged from 69 to 95%. However, based on a limited sample sizes of five putative individuals between years, our data suggest that individual call structure, as quantified by call parameters, was not stable between years. We discuss the applicability of these results for future studies of palm cockatoos and other parrot species.

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Introduction

Identification of individuals is often essential for behavioural studies and to provide the life history data necessary for understanding population trends. Individual identification in birds is usually achieved by leg-bands or wing-tags, but this process can be problematic for both the study species and the researchers. Traditional capture techniques can be expensive and time-consuming, involve negative public perception (Mellor et al. 2004) and elicit multiple welfare issues for the study species. The latter can include injuries to the captured animals, avoidance of the capture area, suppressed immune responses and loss of reproductive success (Terry et al. 2005). Leg-bands and wing-tags can also cause physical

damage over time (Meyers 1994b), and marked individuals can experience increased predation (Saunders 1988) and mortality rates (Saraux et al. 2011).

Besides welfare issues, there can also be substantial logistical issues in the capture process due to the habitat and/or behaviour of some species. For example, leg-bands are difficult to see on nocturnal birds (e.g. Strigiformes) and some cryptic bird species like rails (Rallidae), which live among thick, tall reeds in wetlands. Some species are simply difficult to capture (e.g. Black-throated Divers *Gavia arctica*, Gilbert et al. 1994; Gebhardt et al. 2009; Meyers 1994a). Large parrots in general can also manipulate leg-bands with their strong beaks and mobile tongue (Meyers 1994b).

Vocal individuality (VI) is a common feature of vocal animals. Vocal signatures have been demonstrated across multiple species and taxa, including birds and mammals (Terry et al. 2005), dolphins (Tyack 2003) and amphibians (Feng et al. 2009). The aforementioned is perhaps unsurprising, considering the benefits for an individual to identify conspecifics. For example, the ability to identify neighbours may affect behavioural responses, depending on familiar (neighbour) or unfamiliar (stranger) conspecific vocalizations (Budka and Osiejuk 2013; Masco 2013). Being vocally individualistic also aids parent–offspring recognition in colonial species (e.g. penguins, Jouventin et al. 1999). Lastly, the ability to recognize a mate is particularly important for birds that share incubation duties (Curé et al. 2011).

Identifying individuals via their vocalizations offers a non-invasive alternative to traditional marking techniques. However, due to a range of biological and logistical factors, the usefulness and efficacy of this technique differ between species. A successful example is the European bittern (*Botaurus stellaris*); VI has been used for 10 years to increase the accuracy in routine population censuses (Gilbert et al. 2002). Similarly, by integrating the VI technique, there was an increased accuracy of population estimates of corncrake (*Crex crex*) in Scotland (Peake and McGregor 2001). In contrast, VI is less suitable for species with low rates of vocalization (e.g. Black-throated divers *Gavia immer*, Gilbert et al. 1994) and for species that lack stability of call structure over time (e.g. ground squirrel *Spermophilus fulvus*, Matrosova et al. 2010, fallow deer *Dama dama*, Briefer et al. 2010, e.g. Loons *G. immer*, Walcott et al. 2006, female white-throated magpie-jays *Calocitta formosa*, Ellis 2008).

Parrot vocalization studies have focused on vocal dialects (Baker 2003, 2008; Bond and Diamond 2005; Kleeman and Gilardi 2005; Buhrman-Deever et al. 2007; Rowe and Bell 2007; Guerra et al. 2008; Ribot et al. 2009), flock coordination (Balsby and Bradbury 2009), vocal learning (Pepperberg 1984; Pepperberg et al. 2000; Hile et al. 2005) and vocal behaviour (Venuto et al. 2000, 2001; Van Horik et al. 2007; Balsby and Bradbury 2009; Scarl and Bradbury 2009). Few studies have determined whether parrot calls are individualistic (Saunders 1983; Wanker and Fischer 2001). Saunders (1983) used observer volunteers to match printed spectrograms of wild Carnaby's cockatoo (*Calyptorhynchus carnabyi*) calls into groups (each representing a different individual) and qualitatively found an average of 87% of sonograms were correctly matched. Wanker and Fischer (2001) demonstrated that the calls of captive spectacled parrotlets (*Forpus conspicillatus*) were individualistic based on six call parameters.

Palm cockatoos (*Probosciger aterrimus*) are a large, non-flocking parrots that occur in Cape York Peninsula (north Queensland), as well as lowland New Guinea and some offshore

islands (Higgins 1999). Being large bodied, long-lived and having a limited geographical range are factors associated with extinction risk (Olah et al., 2016). In October 2015, their conservation status in Australia changed from “Near Threatened” to “Vulnerable” (EPBC ACT). Internationally, they are listed as “Least Concern” (<http://www.iucnredlist.org>). Recent studies suggest that Australian palm cockatoos are likely in decline due to changed ecology; a loss of habitat via rainforest encroaching into woodland (Russell-Smith et al. 2004); and low reproductive success (Heinsohn et al. 2009). Heinsohn et al. (2009) stressed that, in order to understand the viability of the meta-population of palm cockatoos on Cape York Peninsula, further research is urgently needed to determine unknown demographic parameters, particularly nest site fidelity, age at first reproduction and mortality rates of juveniles and adults.

While these demographic parameters require identification of individuals in the population, parrots can be difficult to capture and/or sensitive to handling. Palm cockatoos may be well suited for the VI technique because (1) both sexes vocalize and (2) males are highly vocal at known display trees. Using three common call types (*Whistle A*, *Whistle B* and *Hello*), we investigated the efficacy of VI as a non-invasive identification technique with which to progress research on this species.

Methods

Study area

We collected palm cockatoo vocal recordings from wild, unmarked birds in Iron Range National Park and surrounding aboriginal lands on Cape York Peninsula (north QLD, 12° 47'S, 143° 18'E) between June and December in 2009 and 2010. This tropical region is characterized by two main seasons, with the majority of the annual 2.1 m of rainfall (Bureau of Meteorology) occurring in the “wet season” from January to April and annual fires occurring in the “dry season” (May–December). The study area contains a mosaic of multiple habitat types, with frequent, distinct edges between the rainforest and savannah woodland.

Study species

Palm cockatoos are monogamous, obligate hollow-nesters that nest in savannah woodland adjacent to rainforest (Murphy et al. 2003). They invariably lay a single egg per nesting attempt, and breeding occurs every 2.2 years on average (Murphy et al. 2003). Limited data suggest that males defend and maintain an average of three to four potential nest sites (Murphy et al. 2003). Part of this maintenance involves males performing unique drumming displays on hollows, whereby they beat a stick (fashioned from a tree branch) on the edge of a hollow (“drumming,” Wood 1984) or on a tree branch. During such displays, they are vocally active and also use body language (e.g. bowing and calling into the hollow, wing-spreading, foot-stomping, crest erection and flushing of their naked crimson cheeks) (Murphy et al. 2003, pers. obs.). During these displays, males cycle through the majority of their vocal repertoire, which consists of at least 27 syllables (not including three chick/juvenile vocalizations), 19 of which are mixed and matched to make longer, more varied vocalizations (Zdenek et al. 2015).

Locating and recording individual palm cockatoos

To find palm cockatoos, we first used broad vegetation maps to locate the rainforest/savannah edge and then slowly approached calling birds to minimize disturbance. Birds were usually found in pairs, alone or (more rarely) in groups of three. Recording sites were located on the edge of the rainforest in open savannah woodland dominated by old growth *Eucalyptus tetrodonta*. We collected recordings on fine days (i.e. no rain and little wind), without the use of playback, when birds were within 75 m. Digital audio recordings were made using a Sennheiser ME K6 shotgun microphone (with a windscreen) connected to a solid-state Marantz PMD661 digital recorder, which was set to a sampling rate of 44.1 kHz. Automatic Level Control on the recorder was turned off; instead, manual level control was adjusted for distance. The recorder was set to mono-channel, with a recording format of PCM-16. Neither microphone attenuation (i.e. 0 dB) nor high or low audio filters were used.

Each individual was recorded once during a focal watch. Focal watches of individual birds lasted between 2 and 68 min (mean = 20 ± 1.66 s.e.) and each provided from 2 to 15 useable calls (i.e. one of the three call types analysed in this study). When birds were near a nest and appeared disturbed by the observer's presence, data collection ceased and the area was vacated so as to minimize impact. In total, 12 birds were identified. Although the birds were unmarked, males and females could be distinguished visually on the basis of bill length (Higgins 1999) and several individuals ($n = 6$, four females and two males) could be identified for the duration of a breeding attempt due to their parental behaviour at a nest containing young. An additional six males were considered different individuals because they performed regular displays on hollows separated by at least 1.5 km (mean = 6.1 km, range = 1.5–16.5 km). Because males display on multiple hollows (Murphy et al. 2003), we cannot be certain that these displaying males were indeed different individuals. However, unpublished data suggest that each displaying palm cockatoo on average occupies an area of 227 m² containing an average of 3.4 active and inactive nest trees (Murphy et al. 2003).

Although previous work by Murphy et al. (2003) showed that palm cockatoos reuse the same nest between breeding attempts (up to three years apart), changes in nest ownership between years were also documented. As such, for between-year analysis of call structure, we recorded three birds at the same nest hollows in 2010 as in 2009, but there is a possibility that these birds may not have been the same individual and so the between-year results are considered preliminary.

Sound analysis

Only call samples with high signal-to-noise ratio and no interference from other calling birds were used for analysis. Three different call types (the *Hello* call, *Whistle A* and *Whistle B*; see Figure 1) were sampled sufficiently often from three to six birds of each sex (except the *Hello* call in females) to be included in each analysis. The threshold for inclusion into the analysis was 6–10 samples of each call type per individual. The *Hello* call appears to be a territorial defence call (also used for simultaneous duets), and *Whistle A* is a contact call. *Whistle B* is not used to initiate contact, but it is frequently given throughout call-bouts. Recordings from adult females were less represented in our sample and analysis because

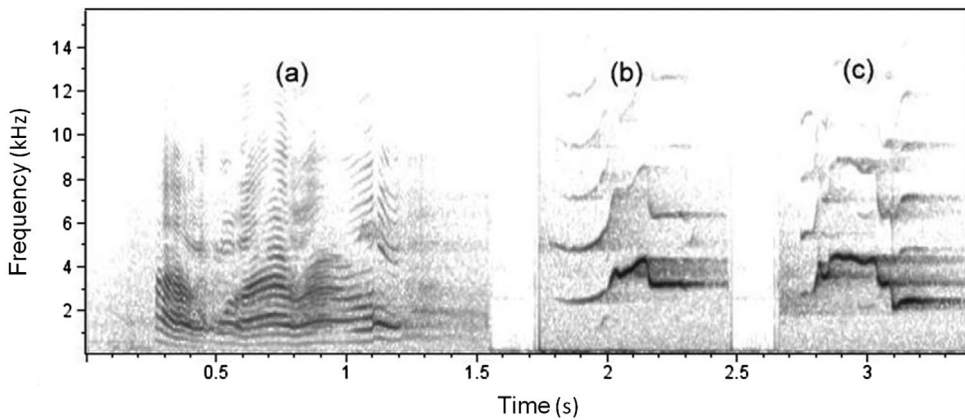


Figure 1. Spectrogram of three Palm Cockatoo calls. (a) *Hello*, (b) *Whistle A* and (c) *Whistle B*. Spectrograms were prepared using RavenPro v. 1.3 (Charif et al. 2010).

males were more vocal than females. Using 12 individuals in total, we analysed 32 *Hello* calls from four males, 46 and 32 *Whistle A* calls from six males and four females, respectively, and 30 and 20 *Whistle B* calls from four males and three females. Spectrograms were viewed in RavenPro v. 1.3 (Charif et al. 2010), using the following: 16-bit sample format, frame overlap = 50%, Hann Window, DFT = 512 and frequency resolution = 124 Hz.

In total, two manual and nine semi-automatic call parameter measurements were made. Due to broad structural differences between call types, different call parameters were applicable for different call types. All measurements were made on the fundamental frequency, except for *Hello*, where measurements were made on multiple finely stacked harmonics. Due to unclear high and low frequency bounds of the *Hello* call, we did not measure these frequencies for this call; we instead boxed the call using standardized high and low frequency bounds. To better account for individual differences in the spectrographic contour line of *Whistle A* (e.g. Figure 1 vs. Figure 2), we used the on-screen cursor in RavenPro to make two additional manual measurements: trough frequency (the frequency at the trough of the call) and ridge1 frequency (the frequency at the top of the first ridge of the call) (see Figure 2).

For semi-automatic measurements, manual selection boxes around individual calls were made using the on-screen cursor in RavenPro. Summary call parameter information was then automatically calculated for each selection box (call). To reduce the subjectivity of on-screen cursor measurements, we used the marked change in amplitude of the time-aligned waveforms to determine the start and end of each call.

Semi-automatic measurements are listed in Table 1. Centre time, inter-quartile bandwidth, inter-quartile duration and centre frequency are robust measurements in that they vary little in relation to placement of the on-screen cursor (RavenPro 1.3 User's Manual 2008). The centre time output from RavenPro was initially irrelevant, indicating where on the spectrogram (e.g. at 2.5 s; 1 min 24 s, etc.) the call is divided into two time intervals of equal energy. To get a meaningful measurement, we subtracted the centre time from end time of the call (the point in time on the recording where the manually boxed call ends) and used that corrected measurement for the analysis.

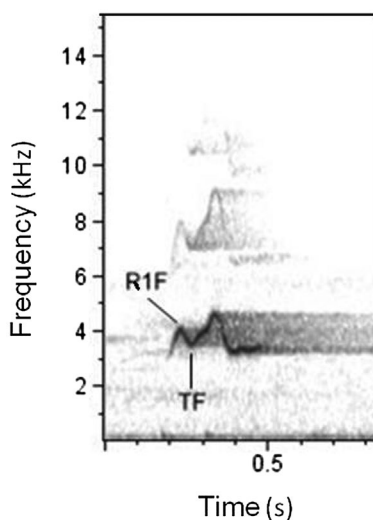


Figure 2. Two manual measurements made for *Whistle A* to account for the contour of the call. R1F: Ridge1 Frequency. TF: Trough Frequency.

Table 1. Call parameter definitions.

Call parameter	Definition
Length	The number of frames – comparable to milliseconds – in a call
High frequency	The highest frequency bound of the call
Low frequency	The lowest frequency bound of the call
Delta frequency	The difference between the upper and lower frequency limits of the call
Maximum frequency	The frequency at which the highest power occurs
Centre time	The point in time where the call is divided into two time intervals of equal energy
Inter-quartile bandwidth	The difference between the first and third Quartile Frequencies*
Inter-quartile duration	The difference between the first and third Quartile Times**
Centre frequency	The frequency that divides the call into two frequency intervals of equal energy

*First Quartile Frequency = The frequency that divides the selection into two frequency intervals containing 25 and 75% of the energy in the selection. Third Quartile Frequency = The frequency that divides the selection into two frequency intervals containing 75 and 25% of the energy in the selection; **First Quartile Time = The point in time that divides the selection into two time intervals containing 25 and 75% of the energy in the selection. Third Quartile Time = The point in time that divides the selection into two time intervals containing 75 and 25% of the energy in the selection. Definitions derived from Charif et al. (2010).

Statistical analysis

Vocal individuality test

We used discriminant function analysis (DFA) to determine whether a combination of call parameters could be used to discriminate between individuals (JMP 6.0, SAS Institute Inc.). Individuals used different call types at different rates, resulting in small sample sizes of comparable calls between individuals. As such, out of a total of 12 individuals recorded, only 3 to 6 could be included in each DFA analysis of each call type. Each individual was recorded once. Males and females were analysed separately because they can be distinguished morphologically. Rather than using a stepwise selection of variables for the DFA model, we included all variables in the model (regardless of their level of significance) because that increased our power to discriminate between individuals, and we were less concerned with determining which call parameters contributed most to individuality.

The probability that calls would be assigned to individuals by chance alone was calculated by taking the number of calls of each individual and dividing it by the number of total calls in the model. If this chance probability was below the percentage of calls correctly classified for that corresponding individual, then the model was considered to have classified calls correctly at a rate greater than chance alone for that individual. For example, if the calls from the “Conflict Hlw” male contributed to 10 out of 52 calls (19%) in the *Whistle A* call model, and 8 out of 10 (80%) of these calls were correctly classified, this was substantially higher than chance alone for that individual.

Vocal stability test

We use the term “vocal stability” to mean the consistency in measurable call parameters over time. To determine whether significant intra-individual variation in call structure occurred over time, we used multivariate (DFA) and univariate techniques (Mann–Whitney *U*-tests) across different calling events (either two or three calling events). Calling events were separated by between 3 and 12 months. For each individual test, the vocal recording used as the first calling event was the same recording used for the vocal individuality tests. Each calling event was treated as a different object or “individual” within an analysis. Each analysis consisted of single calling events from other putative individuals alongside multiple calling events from one putative individual whose vocal stability was being tested. A significant difference (i.e. no overlap in the 95% confidence circles) between two calling events by the same putative individual over time was interpreted as evidence that vocal stability was lacking for that individual. The size of the circle corresponds to a 95% confidence limit around each multivariate mean. Due to sample size constraints and the fact that individuals were unmarked, we consider this to be only a preliminary analysis of vocal stability for this species.

As an independent means of verifying the results of the DFA vocal stability analysis, we used Mann–Whitney *U*-tests to show which variables in particular were stable over time. Using only the most significant call parameters in DFA (as determined by the stepwise procedure of inclusion of variables into DFA), we independently compared each later call event with the first call event for each individual (Jones et al. 1993). Call events were separated by at least 3 months and a maximum of 12 months. Tests were performed on call parameter data from 6 to 10 calls of the same call type, recorded from the same individual in two or three different calling events. Using 129 calls from five birds in total, nine comparisons were made (five within-year comparisons; four between-year comparisons). To account for multiple pairwise comparisons and increased probability of making a Type I error, we calculated critical *p*-values for each individual within each call type using the Dunn–Sidak method. If there was a significant difference between call events for a call parameter, then that call parameter (for that call type) was not considered to be stable over time for that bird. We also report any significant differences at the standard level of $p < 0.05$.

The rate at which individuals used different call types differed across calling events and across individuals. As such, we analysed different call types for different individuals. To further increase the sample size, in one case, *Whistle B* calls from a nesting female (“Conflict Hlw” female) were pooled from four months to compare to the next breeding season.

Ethical Note: Permission for this study was sought and received from the traditional owners of the Uutaalnganu, Kanthanampu, and Kuuku Ya’u people. This work was approved by the QLD Department of Environment and Resource Management (permit

No.: WITK06171009) and received approval from the ANU Animal Ethics Committee (Protocol No. C.RE.62.09).

Results

Vocal individuality

Overall, DFA classified 81% (148/183) of all calls to the correct individual. Among females, 83–95% of all calls were correctly classified. Among males, 69–82% of all calls were correctly classified. These results compare to the considerably lower rates that would be expected by chance (range = 13–33%, see below). DFA could assign correct classifications in all cases to a percentage higher than would be expected by chance (Table 2).

Among four females, DFA classified 83% (35/42) of *Whistle A* calls to the correct individual (Figure 3(a)) (Wilks's Lambda = 0.011; Approx. $F = 5.1$; $p \leq 0.0001$), compared to the average rate of 26% that would be expected by chance (Table 2). Successful classification ranged from 67 to 90% among individuals. Among five males, DFA classified 81% (42/52) of *Whistle A* calls to the correct individual (Figure 3(b)) (Wilks's Lambda = 0.035; Approx. $F = 3.36$; $p \leq 0.0001$), compared to the average rate of 23% that would be expected by chance. Successful classifications ranged from 56 to 100% among individuals. Among three females, DFA classified 95% (19/20) of *Whistle B* calls to the correct individual (Wilks's Lambda = 0.017; Approx. $F = 6.73$; $p \leq 0.0001$), compared to the average rate of 33% that would be expected chance. Successful classification ranged from 86 to 100% among individuals. Among four males, DFA classified 82% (28/34) of *Whistle B* calls to the correct individual (Wilks's Lambda = 0.019; Approx. $F = 7.29$; $p \leq 0.0001$), compared to the average rate of 19% that would be expected by chance. Successful classification ranged from 63 to 100% among individuals. Among four males, DFA classified 69% (24/35) of *Hello* calls to

Table 2. Percentage expected by chances versus the percentage of correctly classified calls for each individual.

Sex of the bird	Bird ID	Whistle A		Whistle B		Hello	
		Expected by chance (%)	Correctly classified (%)	Expected by chance (%)	Correctly classified (%)	Expected by chance (%)	Correctly classified (%)
Females	Conflict Hlw	19	88	33	86	–	–
	Sewerage Pond	14	83	–	–	–	–
	Dbl Hlw	21	89	33	100	–	–
	Dunny Hlw	21	77	30	100	–	–
	Old Site Rd.	24	90	–	–	–	–
Average		–	83	–	95	–	–
Males	Conflict Hlw	19	80	21	70	29	60
	Sewerage Pond	13	71	–	–	–	–
	Old Site Rd.	–	–	–	–	17	67
	Hallelula Hlw	19	90	–	–	–	–
	Bushy Hlw	19	90	–	–	–	–
	Hypodermic Hlw	–	–	29	100	29	60
	Gadget Creek	12	100	18	100	–	–
	Muddy Water School	17	56	–	–	–	–
Average		–	81	–	82	–	69

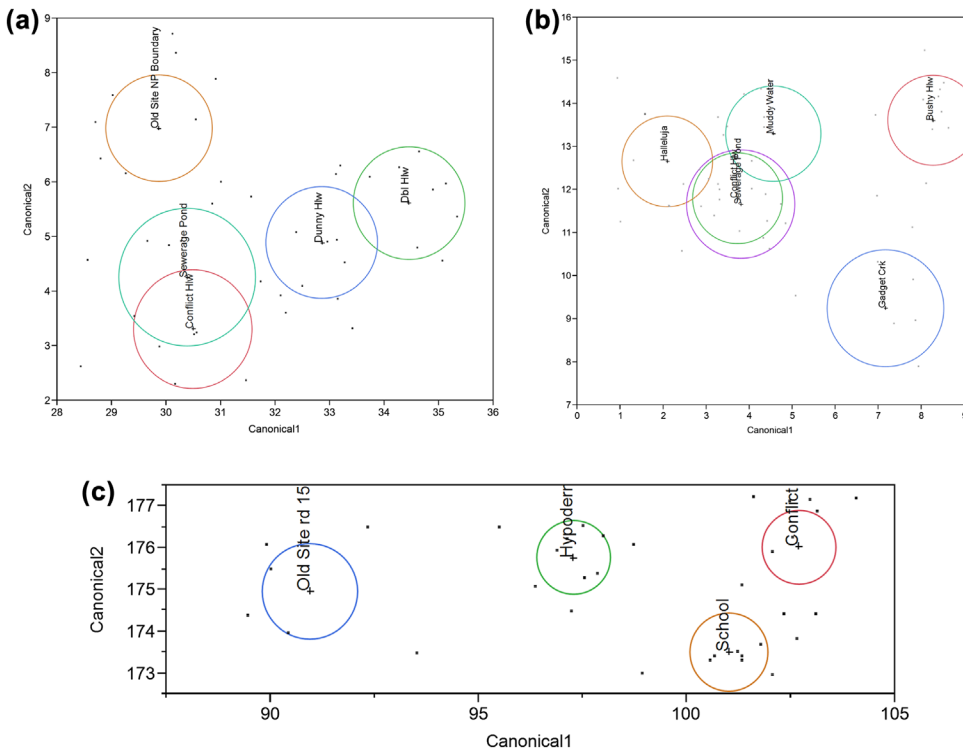


Figure 3. (a–c) Selected Discriminant Function Analysis results for vocal individuality tests of palm cockatoo calls: *Whistle A* (a, b) and *Hello* (c). Female calls: a. Male calls: b and c. The percent accuracy of identification of individuals for the figures is: a = 83%; b = 81%; c = 69%. The letters in the centre of each circle represent different individuals. Each dot represents one call. The size of the circle corresponds to a 95% confidence limit around each multivariate mean of 6 to 10 calls.

the correct individual (Figure 3(c)), compared to the average rate of 25% that would be expected by chance. Successful classifications for each individual ranged from 60 to 89%.

Vocal stability

For each call type, multiple calling events from a given individual over time were included in the DFA model against other individuals (see Figure 4(a) and (b) for selected outputs). Four out of 11 comparisons showed vocal stability: “Dbl Hlw” female, *Whistle A*, call event 1 and 2; “Dbl Hlw” female, *Whistle A*, call event 2 and 3; “Conflict Hlw” male, *Whistle A*, call event 1 and 2; “Hypodermic Hlw” male, *Hello*, call event 1 and 2.

Mann–Whitney *U*-tests indicated that most call parameters remained constant over time for all individuals but that different individuals were stable in different call parameters. The most significant variables, as determined by the stepwise procedure into DFA for each individual where vocal stability was tested, are included in Tables 3a–3c. For two females (“Dbl Hlw” female, *Whistle A*; “Conflict Hlw” female, *Whistle B*), no tested call parameters differed significantly between any call event, suggesting that these females had particularly stable call structure over time. Only one individual (“Hypodermic Hlw” male, *Hello* call) had more than one call parameter that was significantly different between call events.

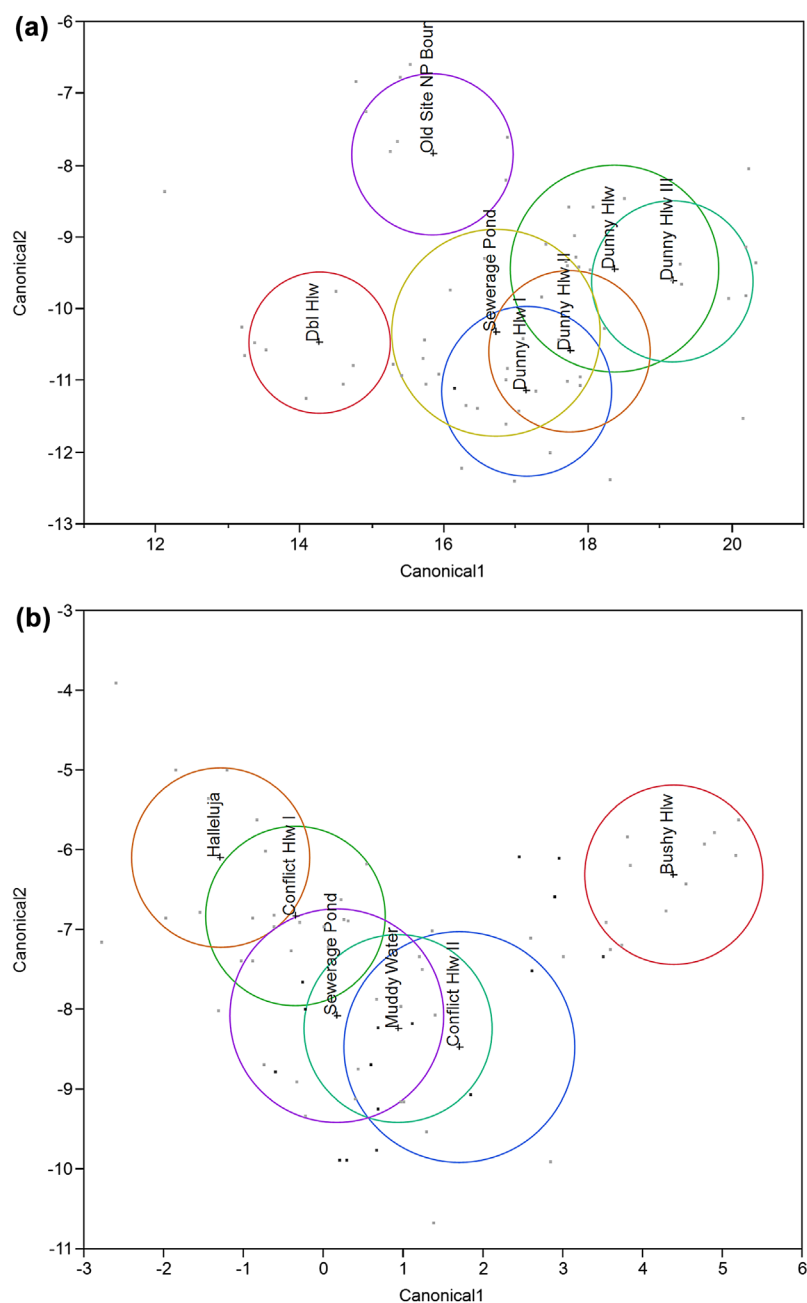


Figure 4. (a–b) Selected Discriminant Function Analysis results for vocal stability tests of palm cockatoo calls. Female Whistle A calls: a; male Whistle A calls: b. Sequential call events from the same individual are denoted by a I, II or III, following the name of the individual. Each dot represents one call. The size of the circle corresponds to a 95% confidence limit around each multivariate mean. The two canonical axes combined represent all call measurements.

Table 3a. Mean (\pm SE) call parameters for palm cockatoo *Hello* calls for each individual across call events[†].

Individual	Call event	<i>n</i>	Length	IQR BW	IQR Dur.
Conflict Hlw m	1	10	219.9 \pm 4.43	1050.83 \pm 84.98	0.35 \pm 0.02
	2 [‡]	8	217.88 \pm 6.95	807.5 \pm 98.6	0.48 \pm 0.04**
Hypodermic Hlw m	1	6	184 \pm 3.49	1033.6 \pm 20.29	0.47 \pm 0.03
	2	10	176.9 \pm 1.68	757.98 \pm 65.5**	0.33 \pm 0.02*
	3	10	182.1 \pm 4.16	1102.5 \pm 69.49	0.22 \pm 0.06

[†]Comparisons using Mann–Whitney U-test were made between events 1 and 2 (significant differences marked in the second call event); and events 2 and 3 (significant differences marked in the third call event). Call parameters included here were chosen based on the stepwise inclusion of the most significant variables into DFA.

[‡]Indicates a call event in 2010 (the second breeding season). All probabilities are for a two-tailed non-parametric test. IQR = Inter-quartile; BW = Bandwidth; Dur. = Duration; F = Frequency.

*Indicates standard significance ($p < 0.05$);

**Indicates significance at corrected critical value.

Table 3b. Mean (\pm SE) call parameters for palm cockatoo *Whistle A* calls for each individual across call events[†].

Individual	Call event	<i>n</i>	Length	Centre Time	IQR BW	Peak1 F.
Conflict Hlw m	1	10	79.6 \pm 1.34	0.16 \pm 0.01	473.72 \pm 71.78	3927.4 \pm 39.77
	2	6	64.67 \pm 3.85**	0.15 \pm 0.02	488.08 \pm 108.19	4010.83 \pm 60.43
Dbl Hlw f	1	10	–	–	574.22 \pm 45.39	3963.22 \pm 63.85
	2	10	–	–	602.94 \pm 57.42	3993.6 \pm 97.34
	3	10	–	–	654.62 \pm 44.85	3981.6 \pm 40.69
Dunny Hlw f	1	8	–	–	398.36 \pm 51.31	3832.75 \pm 34.1
	2 [‡]	6	–	–	459.38 \pm 114.85	4163.67 \pm 62.02**

[†]Comparisons using Mann–Whitney U-test were made between events 1 and 2 (significant differences marked in the second call event); and events 2 and 3 (significant differences marked in the third call event). Call parameters included here were chosen based on the stepwise inclusion of the most significant variables into DFA.

[‡]Indicates a call event in 2010 (the second breeding season). All probabilities are for a two-tailed non-parametric test. IQR = Inter-quartile; BW = Bandwidth; Dur. = Duration; F = Frequency.

**Indicates significance at corrected critical value.

Discussion

We set out to determine whether calls from individual palm cockatoos can be used to identify individuals. We demonstrated that VI can reliably be used to identify individuals of both sexes during a breeding season. However, our results based on limited repeated sampling of the same individuals over time failed to provide evidence that call structure is sufficiently stable to allow re-identification of individuals over multiple years. Thus, the vocal individuality (VI) technique described here may not be reliable to use for this species over multiple years; larger sample sizes are required to confirm this. Additionally, several aspects of palm cockatoo vocal behaviour and breeding system further impede the efficacy of VI for identifying individuals.

Each of the three call types used in this study had a similar identification accuracy to those found in other VI bird studies that used similar techniques (Hill and Lill 1998; Hoodless et al. 2008; Policht et al. 2009; Rognan et al. 2009). Among all call types, overall identification accuracy among males and females ranged from 69 to 95%. Inclusion of more individuals in the model resulted in a greater likelihood of overlap between some individuals in call structure (as indicated by the 95% confidence limits in the DFA). As such, the number of individuals in each call type model in this study has likely influenced the differing

Table 3c. Mean (\pm SE) call parameters for palm cockatoo *Whistle B* calls for each individual across call events[†].

Individual	Call event	<i>n</i>	Centre Time	IQR Dur	Low F.	High F.	Max. F.
Hypodermic Hlw m	1	10	0.14 \pm 0.01	–	–	4239.54 \pm 47.41	3186.9 \pm 100.28
	2	9	0.14 \pm 0.02	–	–	4117.13 \pm 69.55	2879.3 \pm 243.51
	3 [‡]	10	0.22 \pm 0.02**	–	–	4343.95 \pm 42	3178.3 \pm 154.83
Conflict Hlw f	1	7	–	0.16 \pm 0.03	1918.19 \pm 85.31	4378.56 \pm 64.24	–
	2 [‡]	7	–	0.16 \pm 0.03	1868.97 \pm 44.16	4578.8 \pm 26.48	–

[†]Comparisons using Mann–Whitney U-test were made between events 1 and 2 (significant differences marked in the second call event); and events 2 and 3 (significant differences marked in the third call event). Call parameters included here were chosen based on the stepwise inclusion of the most significant variables into DFA.

[‡]Indicates a call event in 2010 (the second breeding season). All probabilities are for a two-tailed non-parametric test. IQR = Inter-quartile; BW = Bandwidth; Dur. = Duration; F = Frequency.

**Indicates significance at corrected critical value.

identification accuracies between the call types. For example, the highest level of accuracy occurred in the model with the fewest number of individuals (*Whistle B*, three females, 95%). Combined with the fact that identification accuracies for different call types did not differ substantially, we therefore cannot confidently say which call type is most individually distinctive; rather, all three call types showed similar, high levels of individuality.

Whistle A was most useful to analyse for several reasons. Being the most widely used call type by individuals, sufficient samples of this call type were able to be obtained. Furthermore, this call type was visually easily distinguished among all other call types, plus it is given during most behavioural contexts (as a contact call). *Whistle B* also appears to be used as a contact call, but to a lesser extent than *Whistle A* and does not appear to be used to initiate contact (i.e. it rarely occurs at the start of a call-bout).

As with contact calls of most vocal animals, including other parrots (e.g. Berg et al. 2011), palm cockatoo pairs almost certainly use conspecific vocalizations as a means to identify each other at a distance. In particular, non-visual mate identification may be particularly important during nest-exchanges which occur twice daily during incubation (males incubate during the day; females at night). Murphy et al. (2003) found that 13.8% of unsuccessful breeding attempts failed because the chick or egg was crushed (but left uneaten), apparently by other palm cockatoos. As such, it could be particularly important for an incubating female to acoustically discriminate her mate – prior to arrival onto the hollow – from an intruder male interested in nest usurpation or destruction. The ability to identify each other acoustically is also likely to be important during dangerous territorial clashes, when visual identification is sometimes impeded by foliage.

Once VI has been established for a species, the consistency of the call parameters in individual vocalizations over time (vocal stability) must also be assessed. Without determining the efficacy of VI for that species in this way, calls recorded at a later date could be misattributed to the wrong individual. For example, the individual assignment accuracy of female begging calls of white-throated magpie-jays (*C. formosa*) decreased over time, rendering the VI technique unsuitable for monitoring that species over time (Ellis 2008). Similarly, when male loons (*G. immer*) changed territories, they changed their vocalizations to maximize differences between their yodels and those of their new neighbours (Walcott et al. 2006). In contrast, Lengagne (2001) found no significant differences in call parameters

across two years in five captive eagle owls (*Bubo bubo*), indicating vocal stability for those individuals.

Vocal stability was assessed for palm cockatoos, albeit only a small sample size was possible. DFA results indicated that vocalizations of individuals were not stable enough to be re-identified within a breeding season or between breeding seasons (Figure 4). Mann–Whitney *U*-tests further revealed that different individuals were stable in different call parameters (Tables 3a–3c), meaning that different individuals changed their calls in different ways over time. Given the unavoidable small sample sizes used in these analyses, there is a potential for single aberrant data points (e.g. distorted or low amplitude recordings) to skew the results towards significant differences.

Despite palm cockatoos being good candidates for the VI technique, we discovered that palm cockatoos have an extraordinarily large and complex vocal repertoire for a parrot (Zdenek et al. 2015). Consequently, it was difficult to record enough calls of each call type to compare across different birds. For example, although males are highly vocal during displays and may produce 35 or more calls in 15 min (unpublished data), during this behavioural context, they typically cycle through their repertoire. Some males favour different call types (unpublished data), making inter-male comparisons of the same call type further difficult. In contrast, birds that give calls in a series (i.e. repetitive calls in succession within a short time period) yield a higher sample size of comparable call types. Some examples are: “chattering” raptors (Falconiformes) (e.g. Eakle et al. 1989); “hooting” owls (Strigiformes) (e.g. Lengagne 2001; Rognan et al. 2009); or “booming” bitterns (Ciconiiformes) (e.g. Gilbert et al. 2002). Furthermore, whereas Wanker and Fischer (2001) collected 50 comparable calls per individual in another parrot, the spectacled parrotlet (*F. conspicillatus*), in this study, we often could only collect six comparable calls per individual.

A further problem we encountered in determining the efficacy of the VI technique for this species is their infrequent breeding (every 2.2 years on average) (Murphy et al. 2003). Birds recorded in 2009 were not seen nesting in 2010 (which was expected), and activity was either completely absent or very infrequent at the same nesting hollows in 2010. The birds that were found at the same hollows in 2010 as in 2009 were for the most part not vocal, probably because they were not leading up to breeding. This made it exceedingly difficult to acquire recordings of the same birds between seasons for the vocal stability part of this study. So although we recorded as many calls as possible from the same birds between breeding seasons, we only acquired enough calls from three birds for between-year vocal stability tests (Tables 3a–3c).

Overall, we found that VI functions to identify individual palm cockatoos in studies conducted within a single year. However, individuals do not appear to be sufficiently stable in their call structure to be re-identified over periods of time greater than one year. Furthermore, aspects of their vocal behaviour and breeding biology preclude the efficacy of applying the VI technique over multiple years. Future studies could trial the call-independent VI technique, where similarly structured call types – rather than exact same call types – are compared between individuals (Fox et al. 2008; Cheng et al. 2010).

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