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Vocal complexity in the palm cockatoo (*Prosbosciger aterrimus*)

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Parrots are renowned for their capacity for vocal learning and production of diverse sounds in captivity, yet little is known about why such advanced vocal capabilities have evolved. Here, we provide a detailed description and statistical classification of the vocal repertoire of wild palm cockatoos *Prosbosciger aterrimus* and investigate the behavioural contexts of vocalizations. We show that palm cockatoos produce vocalizations that conform to most of the common vocalizations described for wild parrots, but also produce a variety of additional syllables in a phonological syntactic manner in the contexts of display and vocal-exchange with neighbouring individuals. These additional syllables are mainly produced by males and are often combined to form long, complex sequences. Unlike most parrots, palm cockatoos defend large multipurpose territories and we speculate that the large vocal repertoire and vocal assemblages of palm cockatoos may function in territorial defense.

Keywords: palm cockatoo; *Prosbosciger aterrimus*; vocal repertoire; vocal duet; Psittacine vocalizations; phonological syntax

Introduction

Parrots exhibit a striking capacity for vocal learning and imitation (Bradbury 2003). Captive parrots can learn vocabularies of hundreds of sounds, comprehend meanings and interpret complex combinations of words (Pepperberg 1984; Bradbury 2003). Despite extensive research on the vocal capacities of captive parrots, relatively little is known about how they use vocalizations in the wild, or why they have evolved such advanced vocal capabilities (Bradbury 2003).

Studies of wild parrot and cockatoo vocalizations have revealed that vocal repertoires typically comprise 5–15 call types (e.g. Pidgeon 1981; Saunders 1983; Martella and Bucher 1990; Rowley 1990; Toyne et al. 1995; Fernández-Juricic and Martella 2000; Taylor and Perrin 2005; Cortopassi and Bradbury 2006; Van Horik et al. 2007) that are used primarily to manage social affiliations in fission–fusion societies (Bradbury 2003). Many parrots form foraging flocks, resting groups and communal night roosts, and vocalizations may provide an important mechanism for identifying other individuals and negotiating dominance hierarchies within these groups (Balsby and Bradbury 2009). Bradbury (2003) identified nine call types that are most widespread in parrot vocal repertoires: a loud contact call, a soft contact call, a pre-flight call, a juvenile begging call, pair duets, warbles, an agonistic protest, a distress call and an alarm call.

Here we describe the vocal repertoire of the palm cockatoo, a species which is a typical among parrots in that it does not form flocks and instead appears to defend large,

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year-round breeding territories that encompass multiple nesting and display trees (Murphy et al. 2003). In this aspect of social structure, the palm cockatoo more closely resembles territorial passerines than other parrots. Territorial passerine birds typically use a repertoire of complex songs to defend a large, multi-purpose territory (Catchpole and Slater 2008). Thus, palm cockatoos might be predicted to either possess larger vocal repertoires than other parrots to facilitate territorial defence, or smaller repertoires because they lack the high level of social interaction typical of flocking parrots. Moreover, the vocal repertoire might be expected to differ from those of other parrots, reflecting different contexts of use. To explore these possibilities, we quantify palm cockatoo repertoire size and compare the contexts of palm cockatoo vocalizations to the call types identified by Bradbury (2003).

Methods

Study species and study site

Out of 21 species of cockatoos (Cacatuidae) worldwide, palm cockatoos are the heaviest (650–1040 g) and one of the longest (Juniper and Parr 1998; Higgins 1999; Forshaw 2010). They are an elusive species of parrot that is restricted to Cape York Peninsula (north Queensland, Australia), New Guinea, and some offshore islands (Higgins 1999). In Australia they are a monogamous, non-flocking species that defends breeding territories incorporating multiple hollow trees that are used for nesting and displays (Murphy et al. 2003). Palm cockatoos have a slow life history with females only laying a single egg every 2.2 years on average. Pairs show nest-site fidelity between years, with one pair recorded to nest in the same hollow three years apart (Murphy et al. 2003). Palm cockatoos are also highly unusual among non-human species in their manufacture of sound-tools, which they use during "drumming" displays (Wood 1984).

Vocal recordings and behavioural data were acquired in Iron Range National Park and surrounding aboriginal free-hold lands on Cape York Peninsula (12° 47′S, 143° 18′E). This study took place from June–December 2009, corresponding with the months of most vocal activity (Murphy et al. 2003). A total of 12 individuals (seven males, three females and two juveniles) were recorded across 10 study sites, covering 71 km^2 with a maximum of 31.5 km and minimum of 2 km between sites. Study sites were visited at least once a fortnight. Because the activity level of several study sites fluctuated throughout the field season, these sites were only visited once a month during times of low vocal activity. Anecdotal evidence from two sites suggested the drop off of activity of sites occurred when formerly active, displaying birds commencing quiet nesting. Once the birds at a particular site began nesting, only the occasional conflict with an intruder pair elicited the otherwise quiet nesting pair to become vocally active in apparent territorial defence. Each of the 10 study sites had 1–2 dirt roads/tracks with infrequent vehicle traffic. Study sites were chosen based on vegetation-type (Murphy et al. 2003) and apparent use by palm cockatoos.

Recording individual bird vocalizations

We collected 210 h of non-continuous recordings from wild, unmarked palm cockatoos at a distance of 20–60 m. Although the birds were unmarked, males and females could be differentiated by beak size. Beak size ranges from 40 to 60 mm and is larger in males (Higgins 1999), and this distinction is obvious to trained observers. When there was any doubt in sexing a calling bird, the recordings were omitted from analysis. Juveniles can be

distinguished from adults morphologically (Higgins 1999). Eight individuals (three males, three females and two juveniles) could be identified for the duration of a breeding attempt due to nesting behaviour at active nests. The distances between these nest hollows ranged from 2.2 km to 28.6 km. A further four males could be distinguished based on their displays on hollows separated by at least 2 km (mean = 14.4 km, range 2.2–28.6 km). This distance was chosen because, since hollows are frequently defended against conspecific intruders, it is unlikely for a male to attempt to defend multiple hollows across this distance each morning and afternoon. However because males display on multiple hollows (Murphy et al. 2003), we cannot be certain that these displaying males were indeed different individuals, although we consider it unlikely.

All recordings were made using a Sennheiser ME66/K6 shotgun microphone (with a windshield) and a solid-state Marantz PMD661 digital recorder set to a sampling rate of 44.1 kHz. Automatic Level Control on the recorder was turned off; instead, manual level control was adjusted frequently during focal watches of calling birds, according to the distance to the birds. The recorder was set to mono-channel, with a recording format of PCM-16. Neither microphone attenuation (i.e. 0 dB) nor audio filters were used.

Fixed duration focal watches were not possible because focal birds could rarely be relocated following a flight. Instead, we followed a focal individual for as long as possible and watches lasted between 2 and 68 min ($\bar{x} \pm$ SE = 20 $\pm$ 1.66 min). 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. Recordings were made on fine days only (little wind and no rain) and when the distance to the birds was within 75 m. Spectrograms of syllables were viewed and analysed using the sound analysis computer program, RavenPro v. 1.3 (Charif et al. 2008).

Syllable classification

In studies of bird vocalizations, an "element" is generally defined as a continuous line on the spectrogram (Catchpole and Slater 2008). Here we define a syllable as either a single element, 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. Palm cockatoo vocalizations are harmonically rich, and the majority of energy occurs in the fundamental frequency (i.e. the lowest-frequency harmonic in the vertical series of harmonics, see Figures 1 and 2). The fundamental frequency of each syllable was measured in a standard, semi-automatic manner using RavenPro v. 1.3 (Charif et al. 2008) (16-bit sample format; frame overlap = 50%; Hann Window, DFT = 512; frequency resolution = 124 Hz). For semi-automatic measurements, a manual selection box was made on each vocalization using the on-screen cursor. Acoustic parameters were then automatically calculated for within the selection. To reduce the subjectivity of on-screen cursor measurements, the start and end of each vocalization were identified according to the marked change in amplitude of the time-aligned waveforms (energy versus time).

Syllables were initially classified by ear and by visual inspection of spectrograms produced in RavenPro. Using RavenPro, measurements were then taken of all vocalizations recorded. We measured seven variables from each syllable: Centre Time (the point in time at which the vocalization is divided into two time intervals of equal energy (sec)), Low Frequency (the lower frequency bound of the vocalization (Hz)), Inter-quartile Bandwidth (the difference between the 1st and 3rd Quartile Frequency, where the 1st Quartile Frequency is the frequency that divides the selection into two frequency intervals containing 25% and 75% of the energy in the selection, and the 3rd Quartile
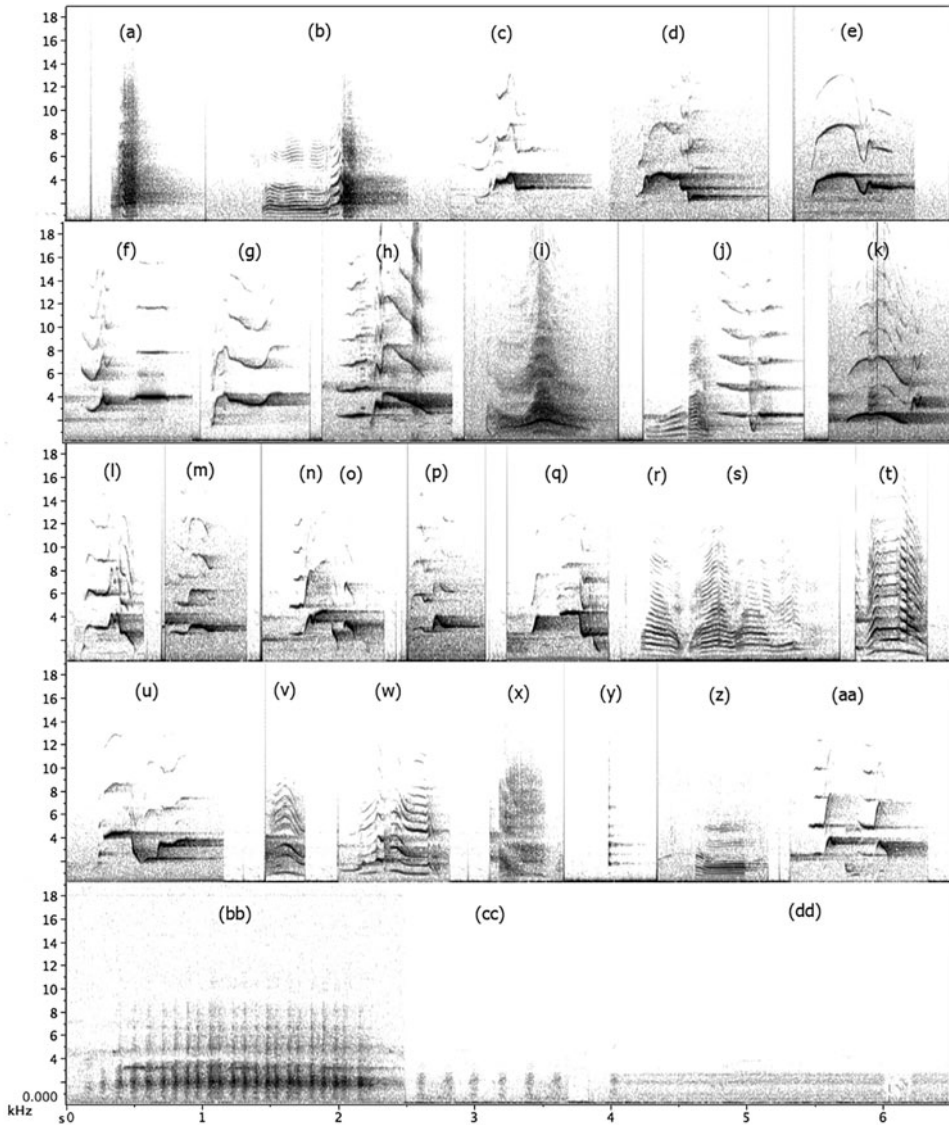
Figure 1.   Spectrograms of all discrete palm cockatoo syllables recorded from Iron Range and Lockhart regions in 2009. Notes: Out of the 27 adult vocalizations (rows 1–4), 19 were used for to make longer, more complex vocalizations (all except (e) and those in rows two and five). Row 5: Juvenile and chick vocalizations. (a) *Er-Crack*; (b) *Crack*; (d) *Whistle A*; (e) *Whistle C*; (f) *Ascending Ear-clencher*; (g) *Magnificent Riflebird Whistle*; (h) *Descending Whistle*; (i) *Pop-toy*; (j) *Rare Call*; (k) *Flight Whistle*; (l) *x*; (m) *Split Whistle b extended*; (n) *Split Whistle* a; (o) *Split Whistle b*; (p) *z*; (q) *Trisyllabic Whistle a*; (r) *Hello a*; (s) *Hello b*; (t) *Excited Whistle Slide*; (u) *w*; (v) *Slide Middle*; (w) *Slide Intro*; (x) *Growl*; (y) *Chuh Intro*; (z) *Donkey Intro*; (aa) *Double Whistle*; (bb) *Darter Staccato*; (cc) *Feeding*; (dd) *Begging Grate*. Of the 27 adult syllables, only six (Hello (*Hello a + Hello b*) and row 1: *Crack*, *Er-Crack*, *Whistle A*, and *Whistle B*) were previously illustrated (Higgins 1999). Spectrograms were prepared using RavenPro v. 1.3 (Charif et al. 2008).
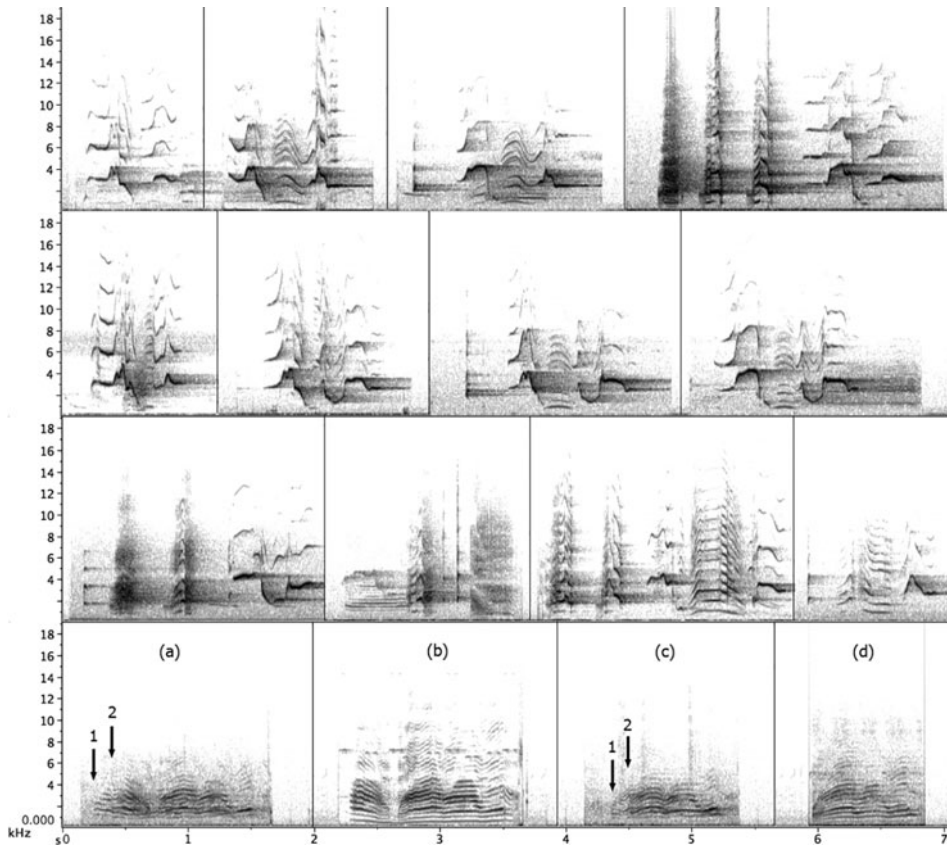
Figure 2. Examples of phonological syntax (rows 1–3) and simultaneous duet (row 4) by palm cockatoos. Notes: Row 4: (a) Simultaneous *Hello* duet by two birds; (b) *Hello* by one bird; (c) Simultaneous *Hello b* by two birds; (d) *Hello b* by one bird. Arrows indicate the start time of two different birds. In both examples, both duetting birds complete the duet at the same time. Spectrograms were prepared using RavenPro v. 1.3 (Charif et al. 2008).

Frequency is the frequency that divides the selection into two frequency intervals containing 75% and 25% of the energy in the selection (Hz)), Maximum Frequency (the frequency at which maximum energy of the vocalization occurs (Hz)), Length (the length of the vocalization, measured in frames, where the number of frames equals the number of individual spectra in the selection in one channel), Inter-quartile Duration (the difference between the 1st and 3rd Quartile Times, where the 1st Quartile Time is the point in time that divides the selection into two time intervals containing 25% and 75% of the energy in the selection, and the 3rd Quartile Time is the point in time that divides the selection into two time intervals containing 75% and 25% of the energy in the selection (sec), and Delta Frequency (the difference between the upper and lower frequency limits of the vocalization (Hz)). The Centre Time output from RavenPro was initially irrelevant, as it simply indicates 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 manually 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.

We used Discriminant Function Analysis (DFA) to test whether syllables were statistically distinct (JMP 6.0, SAS Institute, Inc.). We used a stepwise variable selection to determine which acoustic parameters were most influential in explaining the differences between calls. We incorporated only significant variables in the final model.

Our aim was to identify syllables that were representative of the population, rather than possible idiosyncratic variation on vocalizations produced by particular individuals. Therefore, we restricted this analysis to syllables that were recorded 5–10 times from a total of at least four different males from four different sites at least 2 km apart. Because individuals were represented with more than one syllable per syllable-type in the data-set, we calculated the means of all variables for each syllable from a single individual (rather than on independent data from each call) to avoid non-independent data (Mundry and Sommer 2007).

Eleven syllables were sufficiently widespread and common to be included in the analysis. A further 14 syllables were recorded, but had insufficient sample size (i.e. fewer than five replicate syllables from at least four individuals) to be included in the DFA of syllable types. DFA labels each multivariate mean with a circle. The size of the circle corresponds to a 95% confidence limit for the mean. Groups that are significantly different have non-intersecting circles. Overlap in the confidence limits indicates that the syllables are not significantly different. For the most part, syllables that were not significantly different (i.e. overlapped in canonical space in the DFA output) from one another were lumped and re-classified as a single syllable type.

Social context of syllables

Using log-linear modelling in Genstat (version 12.2; VSN International Ltd), we tested whether there was an association between syllable types and behavioural contexts. After each focal watch, recorded vocalizations were assigned to one of six behavioural categories: Flight, Display, Nesting, Vocal-exchange, Solo call-bout or Other (Table 1). A syllable was scored as occurring in a certain behavioural context (e.g. in Flight) if it was given one or more times in that context during a focal watch. Although vocalizations were

Table 1.   Definitions of five behavioural contexts.

Flight	When birds were in flight.
Display	Frequent calling by one focal bird, while performing at least two display activities[a] on or near a hollow. Male displays may also involve beating a fashioned stick on a hollow ("drumming," Wood 1984). These displays may have a territorial and/or mate-attraction function.
Nesting	When birds were involved in relieving each other at the nest during incubation or brooding, or approaching to feed a chick.
Vocal-exchange	When four or more birds were involved in a rapid exchange of vocalizations, sometimes including foot-stomping, wing-spreading and/or bowing when calling. These events always involved a degree of conflict, with one bird chasing another away (and calling consecutive *Cracks*) in apparent territorial dispute, often near a hollow. These vocal-exchanges may have resulted from non-resident pair intrusions.
Solo call-bout	When one bird calls from a perch for an extended period of time, with no other birds present or responding. This context is not accompanied by display activities and may serve to contact call a mate.
Other	All other behaviour.

[a] Display activities: foot-stomping, wing-spreading, wing-spread while grasping hollow edge with beak, bowing when calling, pirouetting, grinding edge of hollow loudly with beak.

Table 2. Focal watches of palm cockatoos in behavioural contexts.

Behavioural context[a]	# of Focal Watches (*m*)	# of Focal Watches (*f*)	$\chi^2 11$	*P*-value
Flight	18	17	157.6	<0.001
Display	46	5	163.5	<0.001
Nesting	5	11	95.7	<0.001
Vocal-exchange	33 (multiple birds)		65.1	<0.001
Solo call-bout	2	6	34.6	0.002

[a] See Table 1 for behavioural context descriptions. *m*, male; *f*, female.

recorded from 12 individuals (seven males, three females and two juveniles), each individual was not represented in each syllable-type for each behavioural context. The number of focal watches is reported in Table 2.

Ethical note

Permission for this study was sought and received from the traditional owners of the Uutaalnganu, Kanthanampu and Kuuku Ya'u language groups. This work was approved by the QLD Dept. 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 repertoire

Using visual inspection of sonograms, we initially identified at least 27 syllables in the vocal repertoire of adult palm cockatoos (Figure 1), and a further three chick/juvenile vocalizations. To test whether these syllables were structurally distinct, we performed DFA on 11 syllables which were recorded with sufficient frequency ($\geq$ four males, $\geq$ five recordings of each syllable per male) to include in the analysis. Eigenvalues one and two explained 91.2% of the variation. All acoustic parameters except Delta Frequency and Maximum Frequency contributed significantly to explaining the variation. The stepwise variable selection procedure resulted in 1 out of the 11 syllables being lumped and re-classified, leaving 10 syllables in the final DFA output (Figure 3). DFA eliminated "*Whistle B Flat*", as redundant to "*Whistle B*", so the former was not classified as a syllable in the repertoire, nor shown in the final DFA output (Figure 3). One case of call overlap in canonical space occurred: (1) "*Crack*" overlapped with "*Hello a*". Despite the statistical overlap, these two syllables were still considered to be separate syllables because they were visually distinct: *Crack* is a broad-spectrum syllable, and *Hello a* is made up of finely stacked harmonics (see Figure 1). All remaining syllables differed significantly from one another in structure, as indicated by non-overlapping confidence limits (Figure 3) and little (<15%) or no misclassification (Table 3) the DFA output. Most syllables were given by both sexes, but "*Excited Whistle*", "*Trisyllabic Whistle*" and "*Donkey Intro*" were recorded from males only (Table 3).

Vocal complexity

A syllable was considered to be a component of a complex vocalization if it was used in combination with at least two other syllables (e.g. $a + b$ and $a + c$) and if it was used in
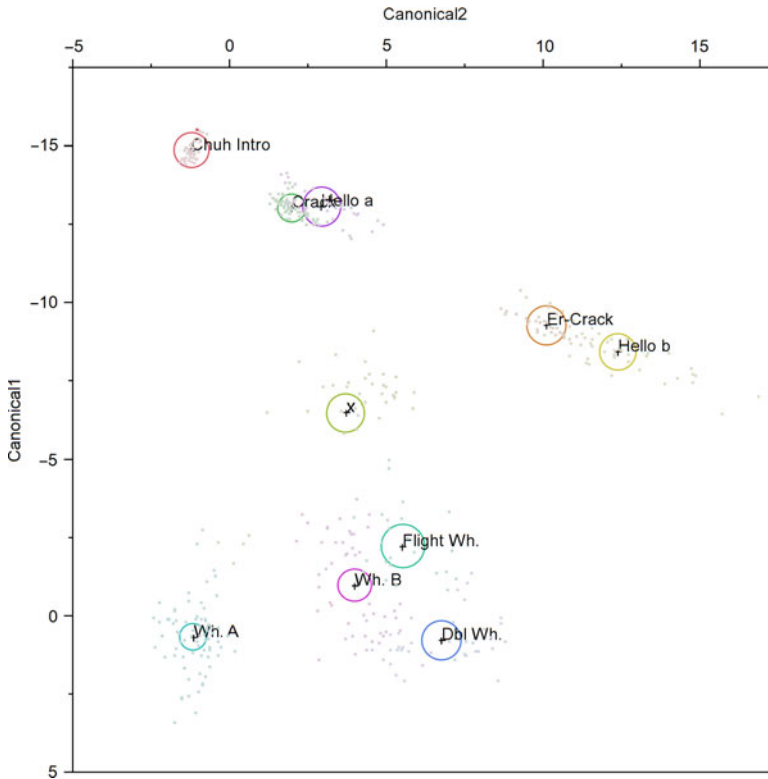
Figure 3.   DFA of a sub-set (10/27) of palm cockatoo syllables recorded from males in 2009. Notes: Syllables included in this anaysis were those with 5–10 replicates each from 4 to 7 males in the population. The size of the circle corresponds to a 95% confidence limit for the mean. Groups that are significantly different have non-intersecting circles. Dbl, Double; Wh., Whistle.

this manner by at least two birds. Of the 27 syllable types, 19 were used in combination to create more complex vocalizations (see Figure 2). Vocal complexity never exceeded seven syllables in succession and occurred almost exclusively during display and vocal-exchange (see "*Behavioural Contexts*" section).

Vocal duet

We recorded simultaneous *Hello* duets (Figure 2) given by the male and female of a pair. Direct observation, and subsequent spectrogram examination, confirmed vocal duets were produced on four occasions by four different pairs. On the spectrogram additional stacked harmonics (from the second bird) could be seen starting partway through the first bird's call. From these four occasions, it was unclear which sex initiated the duets and how the duets were initiated. *Hello* duets comprised either both parts of the hello call together (*Hello a* and *Hello b*) or only the second half of the hello call (*Hello b*). Duets always occurred during vocal-exchange and were not accompanied by coordinated visual displays.

Behavioural contexts

Vocalizations were used non-randomly by palm cockatoos in all five behavioural contexts (see Tables 1 and 2). During flight, the *Flight Whistle* was used almost exclusively

Table 3. The prevalence and possible function of palm cockatoo syllables across behavioural contexts and sexes.

Syllables	Behavioural categories[a]	# of individuals that gave the call	Given by both sexes?	# of syllables recorded[c]	% mis-classified by DFA	Possible functions
Crack	5/5	≥7	yes	281	5.8%	Contact call
Er-Crack	3/5: vocal-exchange, display, solo call-bout	≥6	yes	38	11.9%	Initiate a call-bout
Whistle A	5/5: only females used it in flight	≥7	yes	371	3.4%	Contact call
Whistle B	4/5: not in flight.	≥6	yes	175	10.5%	unk.
Whistle C	3/5: vocal-exchange, display, nesting	≥4	yes	28	–	Express excitement during display
Ascending Ear-clencher	2/5: vocal-exchange, display	≥2	yes	16	–	Express excitement during display
Magnificent Riflebird Whistle	3/5: vocal-exchange, display, solo call-bout	≥3	yes	9	–	Express excitement during display
Descending Whistle	3/5: vocal-exchange, display, solo call-bout	5/7	yes	9	–	unk.
Pop-Toy	2/5: flight, other behaviour (upon landing)	≥4	yes	4	–	Indicate landing (or sometimes flying)
Rare Call	2/5: vocal-exchange, display	≥3	unk.	12	–	Express excitement during display
Flight Whistle	1/5: flight	≥6	yes	35	0%	Indicate flight
X	2/5: vocal-exchange, display	≥5	yes	169	14.3%	Used for syntax to make more varied vocal repertoire
z	1/5: vocal-exchange	≥5	yes	7	–	Used for syntax to make more varied vocal repertoire
Split Whistle a	2/5: vocal-exchange, display	≥5	yes	65	–	Used for syntax to make more varied vocal repertoire
Split Whistle b	2/5: vocal-exchange, display	≥5	yes	68	– –	Used for syntax to make more varied vocal repertoire
Split Whistle b extended	1/5: vocal-exchange	≥5	yes	63	– –	Used for syntax to make more varied vocal repertoire
Trisyllabic Whistle a	2/5: vocal-exchange, display	≥2	m only	4	–	Express excitement during display

(*Continued*)

Table 3 – *continued*

Syllables	Behavioural categories[a]	# of individuals that gave the call	Given by both sexes?	# of syllables recorded[c]	% mis-classified by DFA	Possible functions
Hello a	3/5: vocal-exchange, display, solo call-bout	≥6	yes	170	21.6%	In the context of a vocal duet: Pair-bond maintenance and joint territorial defence
Hello b	3/5: vocal-exchange, display, solo call-bout	≥6	yes	214	0%	In the context of a vocal duet: Pair-bond maintenance and joint territorial defence
Excited Whistle slide	2/5: vocal-exchange, display	≥3	m only	38	–	Express excitement during display
W	2/5: vocal-exchange, display	≥2	yes	74	–	Express excitement during display
Slide middle	3/5: vocal-exchange, display	≥3	yes	34	–	Express excitement during display
Slide Intro	3/5: vocal-exchange, display	≥3	yes	11	–	Express excitement during display
Growl	2/5: vocal-exchange, display	≥3	yes	64	–	Indicate landing and territorial defence
Chuh Intro	5/5	≥7	yes	409	0%	Introduces vocalizations
Donkey Intro	4/5: all except flight	≥5	m only	5	–	Introduce calls during excited state
Double Whistle	2/5: vocal-exchange, display	≥5	m only	37	5.7%	Express excitement during display
Food Begging Call	1/5: nesting	≥2	yes	18[b]	–	Illicit food from parents
Feeding	1/5: nesting	≥2	yes	15[b]	–	Vocalization by juvenile while adult is regurgitating food
Darter Staccato	1/5: other	≥2	yes	7[b]	–	Initiate contact with parent after a period of separation

[a] Behavioural categories indicates which context the calls were given: Display, Nesting, Vocal-exchange, Solo call-bout or Other (see Table 1). All syllables are shown in Figure 1. The final three rows are non-adult vocalizations (i.e. from chick and juvenile).
[b] Number of call-bouts.
[c] The number of syllables reported as being recorded are from 34 recordings (out of 267 total) across all behavioural contexts.
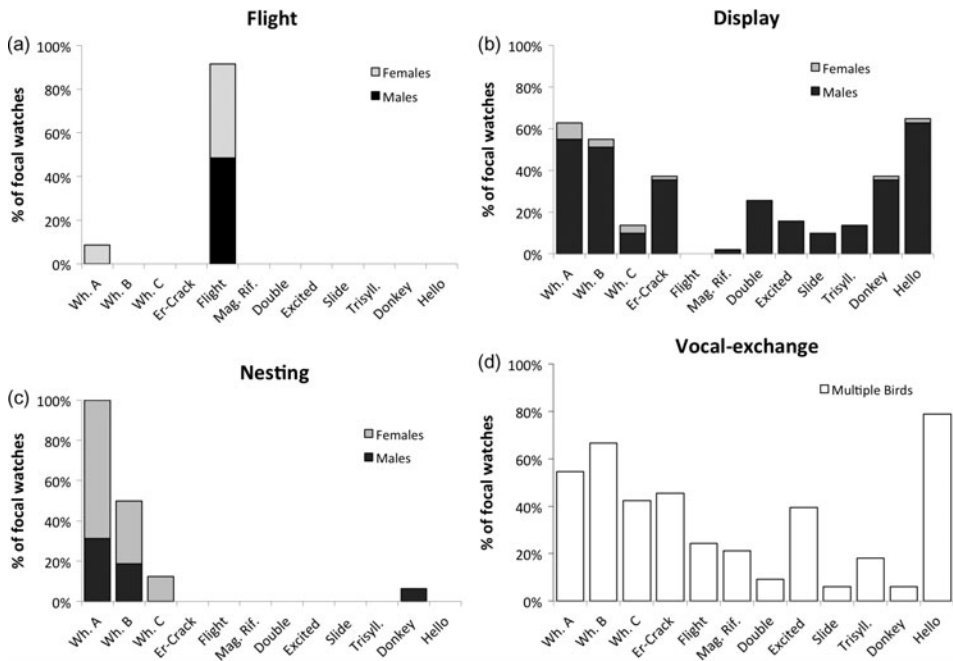
Figure 4. (a–d). Proportion of focal watches in which vocalizations were given across five behavioural categories. Notes: The final five vocalizations on the *x*-axis were used for phonological syntax. See Table 2 for sample sizes and statistical output. Wh., Whistle; Mag. Rifleb., Magnificent Riflebird Whistle; Trisyll., Trisyllabic Whistle).

(see Figure 4(a)–(d)). During display, *Whistle A*, *B* and *C* and *Hello* were particularly common. During nesting, only a few syllable types were used, with *Whistle A* as the most common. During vocal-exchange the entire repertoire was used, with the *Hello* call used most commonly. In all ($n = 143$) but four cases, sequences of multiple syllables (phonological syntax) were restricted to displays and vocal-exchange.

Males were more vocally active than females and were thus represented in more recordings (e.g. 46 male display focal watches; 5 for females). However, for solo call-bout, we recorded three times as many female focal watches than males. These discrepancies suggest that males give more displays than females, and females give more solo call-bouts than males. In contrast, both sexes were equally represented in the Flight context (males $= 18$; females $= 17$; see Table 2).

Discussion

The vocal repertoire of the palm cockatoo showed marked parallels with those of other parrot and cockatoo species but was more extensive and complex than most of those described previously (Table 3). We documented 27 syllables, of which only six (*Hello a* + *Hello b*, *Crack*, *Er-Crack*, *Whistle A* and *Whistle B*) have previously been illustrated (Higgins 1999). Eleven of these syllables were recorded sufficiently frequently to allow quantitative analysis. Of these 11, nine were structurally distinct, two could clearly be distinguished visually as well as acoustically (*Crack* and *Hello a*), and one (*Whistle B Flat*) was found to be a redundant classification (to *Whistle B*), following statistical analysis (Figure 3).

We documented overlapping (simultaneous) vocal duets in the *Hello* call. The term "avian duet" describes the act of two birds coordinating joint acoustic displays with a degree of temporal precision (Farabaugh 1982). One key feature of avian duets is a stereotyped call-structure that occurs repeatedly and predictably in time (Langmore 2002). Each of the vocal duets recorded had stereotypic finely stacked harmonics of *Hello*, each had a slight lag time (about 0.2 s) by the second bird joining the first bird, and both vocalizations ended simultaneously (Figure 2(a),(c)).

As in many other parrot species, palm cockatoo syllables were produced non-randomly with respect to context, age and sex. We identified syllables that conformed to most of the nine major classifications identified by Bradbury (2003):

(1) *Loud Contact Call*. These calls are typically given by parrots in vocal-exchange between two birds and while in flight and are often the loudest calls in the repertoire (Bradbury 2003). This definition fits with the attributes of the palm cockatoo's *Whistle A* and *Crack*. These syllables were used by palm cockatoos in all contexts and were more common than most other syllables in the contexts of display, when relieving a mate at the nest, solo call-bouts and in flight.

(2) *Soft Contact Call*. This call is typically used by parrots to coordinate the movements of flock members and tends to be low in amplitude and repeated regularly (Bradbury 2003). No palm cockatoo syllable fits this definition. This is perhaps unsurprising as they are not a flocking species. However, whilst perched, Palm Cockatoos sometimes give a solo *Chuh Intro*, which could be described as a soft click, but it is not repeated regularly.

(3) *Pre-flight Call*. This call is typically produced by parrots just prior to taking flight (Bradbury 2003). Palm cockatoos produced an analogous call specific to the context of flight, but it was produced during, rather than before, flight. Furthermore, although not strictly analogous to the *Pre-flight Call*, another call (*Pop-toy*) was produced almost exclusively upon landing (rarely during flight).

(4) *Begging Call*. This call is typically produced by parrot chicks and fledglings when soliciting food from their parents (Bradbury 2003). It corresponds to the *Begging Grate* of juvenile palm cockatoos at the nest (i.e. pre-fledging). Palm Cockatoo chicks also produce a *Feeding Call* whilst being fed (Murphy et al. 2003, this study). Post-fledging, there is also third non-adult call given by juveniles, termed here as the *Juvenile Call*. It is a "croaky, rattling call" (Murphy et al., 2003) (sounding similar to the most common call of the Australasian Darter). This call sometimes elicits feeding from a nearby adult. Whereas nests usually occur in the woodlands close to rainforest (Murphy et al. 2003), feeding of a juvenile by an adult was always observed in this study to occur in the dense vegetation of gallery forests ($n = 10$).

(5) *Pair Duet*. Among parrots, both members of a pair often vocalize simultaneously or antiphonally (Bradbury 2003). Such duets appear to function primarily for mediating agonistic conflict between pairs (Power 1966; Arrowood 1988; Bradbury 2003). The palm cockatoo *Hello* duet fits this definition, as simultaneous duets were produced exclusively in the vocal-exchange context.

(6) *Warble Songs*. Among parrots, these consist of long, rambling vocalizations with highly variable note types that are produced during rest periods, around nesting sites, or during late-afternoon staging (Bradbury 2003). Palm cockatoos combined multiple syllables to form more complex vocalizations (phonological syntax), but the context of these vocalizations appears to differ somewhat from that of other parrot warble songs. Palm cockatoo syntax occurred almost exclusively during

display and vocal-exchange. Both these contexts entail high amplitude, long-range communication, whereas warble songs appear to be directed towards individuals in close proximity or to no audience at all (Bradbury 2003).

(7) *Agonistic Protest*. Among parrots in general this is a loud "squawk" produced during fights (Bradbury 2003). Palm cockatoos produced consecutive *Cracks* (Figure 1(a)) during fights, but this syllable was also used non-consecutively in every other context as well, including for syntax.

(8) *Distress Call*. This is a call given by injured or threatened parrots (Bradbury 2003). Although not recorded in the wild, an injured (wild) palm cockatoo was observed in captivity during the course of this study. When initially being handled, this female bird made a "loud, high-pitched, distressing scream" that was also long in duration (pers. comm., K. Philliskirk).

(9) *Alarm Calls*. This is a call given by parrots when a predator is sighted, which usually elicits evasive action by listeners (Bradbury 2003). The *Crack* given in succession (termed *Consecutive Cracks*) is the only palm cockatoo syllable that fits this description. *Consecutive Cracks* were also used in flight, as well as for syntax (during display and vocal-exchange contexts).

As well as these vocalizations, palm cockatoos exhibited a wide variety of additional syllables (Figure 1), which were produced primarily by males, used mainly in the contexts of display and vocal-exchange (Figure 4), and routinely combined to form longer sequences (Figure 2). Both the warbles of many parrot species and the songs of passerine birds may comprise syllables that are combined in sequences to form more complex vocalizations (Bradbury 2003; Catchpole and Slater 2008). Palm cockatoos appeared to use numerous syllables in the vocal repertoire in an analogous manner, whereby a combination of syllables was organized in particular temporal arrangements. This vocal technique is called "phonological syntax" (Briefer et al. 2013).

A large vocal repertoire and phonological syntax are both attributes that are typical of territorial songbirds (Catchpole and Slater 2008). In these species, songs are usually long-range signals used for territorial defence and mate attraction (Catchpole and Slater 2008). Given that palm cockatoos are unusual amongst parrots in maintaining large, year-round territories, it is plausible that the large vocal repertoire and vocal syntax of palm cockatoos serve analogous functions to territorial song in songbirds. This possibility requires testing with playback experiments similar to those performed on songbirds (e.g. Krebs 1977; Stoddard et al. 1991).

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