Pair duets in the yellow-naped amazon (*Amazona auropalliata*): Phonology and syntax

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Summary

Pair duets are acoustically complex communication signals formed jointly by members of a mated pair. Duets may serve multiple communication functions; quantitative studies of the acoustic structure and organization of notes (or 'syntax') within duets are an important step in identifying these functions. This study examined duets of the yellow-naped amazon (*Amazona auropalliata*) at two sites in Costa Rica to determine the syntactical rules underlying duet variation. Duets were composed of contact calls and three other note types found only in duets. These latter note types were sex-specific, with one type performed by females and the other two types by males. Sex-specific notes were delivered antiphonally and in distinct pairs, with the male note following and often overlapping that of the female. Note types appeared in a strict sequential order in which each note could be repeated a variable number of times or omitted entirely, a pattern previously termed 'combinatorial syntax'. Additionally, there was considerable variation in acoustic parameters of notes within types. Many of these parameters varied significantly with note order within a duet. These syntactical features suggest a preliminary hypothesis that males and females encode different, and possibly multiple, messages in their respective contributions to duets.

Keywords: pair duet, combinatorial syntax, parrot, yellow-naped amazon.

Introduction

Quantitative descriptions of note structure and organization (or 'syntax') are fundamental to understanding the communication function of a complex

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acoustic signal (Marler, 1961; Bradbury & Vehrencamp, 1998). Descriptions of signal structure can both generate hypotheses for signal function and provide a baseline for informed tests of these hypotheses (Morton, 1977). Such tests include examining the correlations between structural variants and different social and behavioral conditions and contrasting behavioral responses to playbacks of signals with varied structures (Kroodsma & Byers, 1991). Quantitative descriptions also facilitate comparative studies of signal structure among populations within a species or across different species. Together, these approaches can lead to the formation of general design rules that relate the structure of signals to their function and evolution (Hockett & Altman, 1968; Bradbury & Vehrencamp, 1998).

Pair duets are one class of acoustic signals for which such quantitative descriptions may be particularly valuable (Kroosdma et al., 1996). Vocal duets performed by the members of a mated pair are widespread, particularly among tropical bird species (Farabaugh, 1982; Hall, 2004). These coordinated displays vary in form from a relatively simple call and response between pair members to duets composed of many different notes organized with a striking degree of acoustical complexity and temporal precision (Thorpe, 1963; Power, 1966; Payne & Skinner, 1970; Farabaugh, 1982; Horne & Short, 1988; Seddon, 2002; Grafe & Bitz, 2004; Grafe et al., 2004; Rogers, 2005). One explanation for the diversity of duet forms may be that they are produced by two individuals who potentially have different motivations for signaling and different intended receivers for their component of the duet. Potential receivers of duet messages include the other member of the pair producing the duet, members of other pairs, and unpaired individuals of either sex; these receivers may be intended or be part of a communication network (McGregor, 2005). Each duet may contain information relevant for several of these receivers, and each communication pathway within the network may exert distinct selective pressures on the syntax and acoustic structure of a duet. Thus the acoustical complexity of many pair duets could reflect their potential for conveying multiple messages and serving several functions simultaneously.

To date, hypotheses for the function of pair duets have largely emphasized different signal pathways (Hall, 2004). One class of hypotheses focuses on communication within the pair and suggests that duets serve to establish and maintain the pair bond (Thorpe & North, 1965; Wickler, 1980) or alert

mates to predators (Harcus, 1977). Other hypotheses focus on those pathways leading to other pairs and suggest that duets serve to defend jointly-held resources such as territories or nesting sites (Seibt & Wickler, 1977; Smith, 1994). These hypotheses all share the assumption that both members of a pair cooperate and jointly benefit from duet production. In contrast, other hypotheses have emphasized potential conflicts between pair members. The mate defense hypothesis suggests that duets may be a form of acoustic mate guarding in which one sex sings in tandem with the other to emphasize the mated status of its partner (Sonnenschein & Reyer, 1983; Levin, 1996a, b). In this case the duet elements of one sex are mainly directed towards extra-pair members of the same sex. The acoustic features of duets could potentially provide important information concerning their intended receivers and functions if these features are adapted for optimal transmission or perceptibility to certain receivers or designed to convey specific messages (Morton, 1977; Wiley & Richards, 1982; Rowe & Skelhorn, 2004). To date, however, there is relatively little baseline information on duets that can be used to relate structure to function in these complex signals.

The yellow-naped amazon, *Amazona auropalliata*, is a large (550 g) parrot that inhabits tropical dry forest habitat throughout the Pacific slope of Central America. Individuals sleep in large communal night roosts (50-300 birds) from which they disperse daily in smaller groups or pairs to forage widely for seeds, fruits and flowers. Mated adults form cohesive pair bonds that are maintained throughout the year. Pairs nest in pre-existing cavities in large, isolated trees; the same pair may use a successful nest site for several consecutive years (T. Wright, unpubl. data).

Yellow-naped amazons in northwestern Costa Rica produce complex and conspicuous pair duets. Mated pairs perch in close proximity (1-5 m apart) in the crowns of tall trees, often near their nest sites, and trade loud notes back and forth in long sequences. Variation in the length of duets and the acoustic features of the composite notes are clearly audible to the human ear. There is also considerable geographic variation in the acoustic form of pair duet notes; this variation follows the same dialect boundaries previously documented for contact calls (Wright, 1996) and pairs respond differently to playbacks of local duets than to foreign duets (Wright & Dorin, 2001).

The goal of this study was to describe the acoustic structure and syntax of pair duets in the yellow-naped amazon. We examined duets from pairs at two sites and quantified the phonology of notes, the variation in note structure

and the syntactical rules governing how notes are combined within duets. This study provides a basis for future experimental studies of duet function in this species and for comparative studies of duet syntax with other species.

Material and methods

Duet recording

Pair duets were observed as part of a long-term field study of the vocal behavior of the yellow-naped amazon in Guanacaste Province of Costa Rica. For this analysis we focused on pairs of adults that commonly performed duets at two sites, Pelon Altura and Horizontes, that are located 15 km apart within the 'North' vocal dialect (see Wright (1996) for map of sites and dialect boundaries). We recorded duets from the seven pairs between 28 September 1995 and 7 December 1995, a period prior to the nesting season, which begins in January. Each pair was unambiguously identified by unique feather markings and their use of habitual calling locations.

Pairs generally performed several duets in a series, which we term a 'session'. These sessions occur in the early morning or late evening as interludes between nighttime communal roosting and daytime foraging activity. Pairs begin calling shortly after arriving at their duet site and generally flew out of the immediate area shortly after duets ended. We recorded all duets in a session for each pair using a Cannon UCS5-A Hi-8 camera equipped with a Sennheiser MKH816-P48 external microphone powered by a Stewart BPS-1 phantom power source.

Analysis of duet note phonology

Pair duets in the Northern dialect of the yellow-naped amazon are composed of a limited number of different note types delivered repetitively by the members of the pair (Figure 1). One of these note types is the contact call, which is also used outside of pair duets in a variety of behavioral contexts and are the most common note type in this species' vocal repertoire (Wright, 1996, 1997). The three other notes types used in Northern dialect duets are observed only in the context of pair duets. Observations of nesting pairs (T. Wright, unpubl. data) have shown that use of these three note types is sex-specific, with the incubating female using a single note (termed the
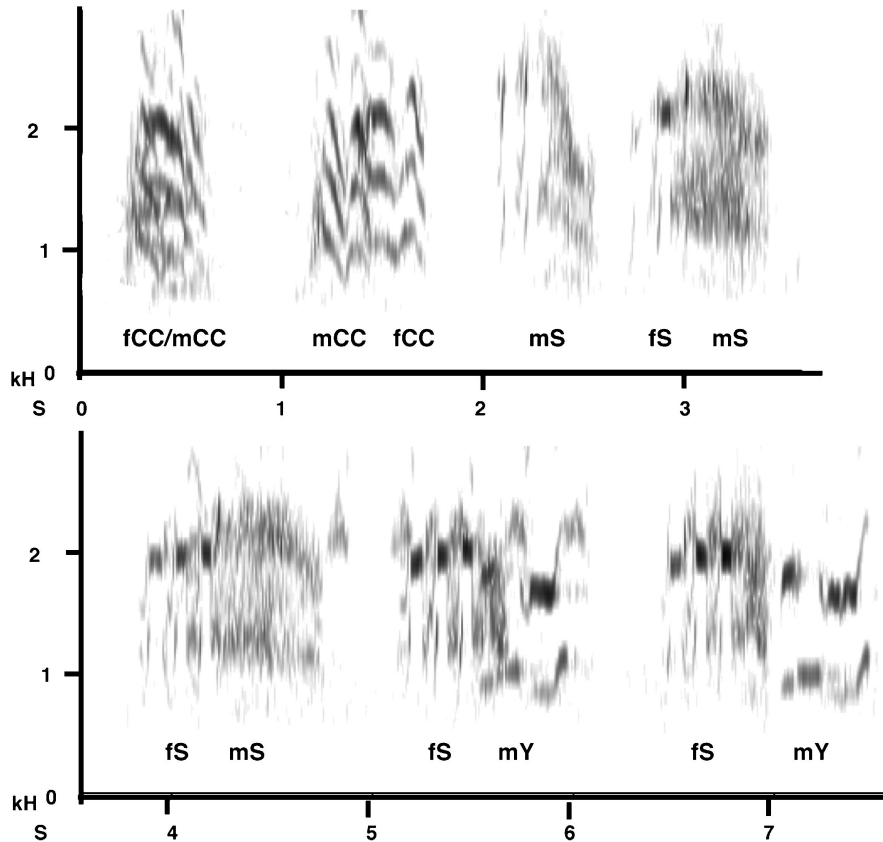
Figure 1. Spectrogram of a yellow-naped amazon duet recorded at Pelon Altura within the Northern dialect. The note type and sex of the caller are indicated below each note and are coded as follows: fCC = female contact call, mCC = male contact call, fS = female scree, mS = male scree, mY = male yoohoo. Several syntactical features characteristic of duets are visible, including sex-specific note use, alternation of male and female notes (antiphony), the overlapping of male notes on female notes to create note pairs, the repetition of note types, and the one-way transitions from contact calls to sex-specific notes and from male screes to male yoohoos. In addition, variability within note types can be seen.

'female scree') and the provisioning male using two different note types (the 'male scree' and the 'male yoohoo'). Subsequent repeated observations of these and other pairs in which individuals can be identified by unique feather markings confirm that this pattern of sex-specific note type use is consistent within and across pairs. Notes within each duet were assigned to type by reference to spectrograms and the video tape recordings. We found good inter-

Table 1. Summary of the number of duets and duet notes analyzed.

Pair	Site	Duet sessions	Duets	Total notes	Female screes	Male screes	Male yoohoos
Palm	Pelon Altura	2	31	259	127	64	68
Mango	Pelon Altura	2	43	284	123	83	78
Paddock	Pelon Altura	2	41	335	172	77	86
Panama	Horizontes	1	10	102	51	10	41
Twelve	Horizontes	1	17	124	61	21	42
Eight	Horizontes	1	8	75	37	15	23
One	Horizontes	1	21	200	109	43	48
Total		10	171	1379	680	313	386

observer agreement between the two authors for these assignments (Cohen's Kappa = 0.81 for 261 notes from 24 duets). Table 1 lists the number of duets and sex-specific notes of each type recorded for each pair.

To quantify the acoustic structure of duet notes, we measured a number of parameters from female screes and male screes and yoohoos (Figure 2) using on-screen cursors and spectrograms created in Canary software (Charif et al., 1993). Spectrograms had an analysis bandwidth of 380 Hz, frame size of 256 points, grid time resolution of 64 points, 75% overlap of samples, frequency resolution of 46.88 Hz and -30 dB clipping. They were created by playing duet tapes on a Sony EV-C100 Hi-8 VCR, band-pass filtering between 500 and 8000 Hz. on a Krohn-Hite 3550 filter, and digitizing at 16 bits and 24 kHz sampling with a Canary Beluga card and Canary version 1.2.2 running on a Macintosh 7100 computer.

Female and male screes share a similar basic acoustic structure consisting of a variable number of frequency-modulated upsweep elements followed by a noisy broadband section. For these notes we measured the total note duration, the duration of the broadband element, the number of upsweep elements, and the peak frequency of each upsweep element measured on the fundamental. From these measurements we calculated the ratio of the duration of the broadband segment to total note duration, the mean peak frequency of the sweeps, and the change in peak frequency between the first and last upsweep element. Acoustic parameters were compared between female and male screes using hierarchical ANOVAs with a fixed main effect of sex and a random effect of individual nested within sex (Zar, 1999). Both analyses were implemented in JMP v. 5.1 statistical software (SAS, 2003).
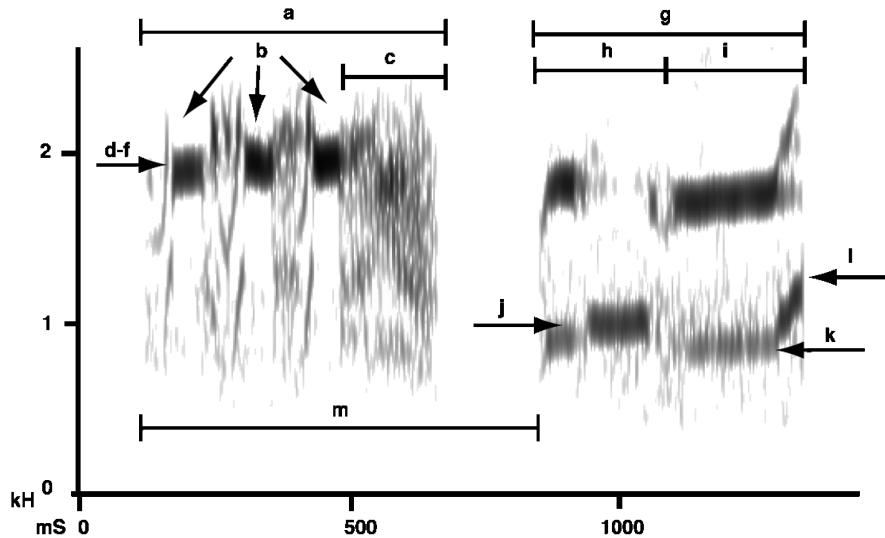
Figure 2. An example of a female scree and a male yoohoo illustrating the structure of the notes and the various parameters measured on each. Parameters measured on female and male screes are: a = total note duration, b = number of frequency sweeps, c = duration of broadband segment, d, e, f = peak frequency of the frequency sweeps. Parameters measured on male yoohoos are g = total note duration, h = duration of yoo segment, i = duration of hoo segment, j = modal frequency of yoo segment, k = modal frequency of hoo segment, l = final frequency of hoo. For all notes, m = the distance from the start of the note to the start of the preceding note.

We corrected for multiple tests using the Bonferroni method (Sokal & Rohlf, 1995).

Male yoohoo notes have a tonal quality not found in the other duet notes due to their relatively high fundamental frequency and the concentration of energy within harmonic bands. The yoohoo is composed of two distinct segments (the 'yoo' and the 'hoo') that each consists of a single constant-frequency band that differs in fundamental frequency between the two segments. In addition, frequency-modulated sweeps may be present at the end of the note (Figure 2). To quantify variation in male yoohoos, we measured the total note duration, the duration of the yoo and hoo segments, the modal frequency of the yoo and hoo segments (e.g., the frequency maintained for the longest duration within the segment, measured on the fundamental) and the final frequency of the hoo segment, which sometimes ended with an up-sweep element. From these measurements we calculated the ratio of yoo modal frequency to hoo modal frequency, the ratio of the yoo duration to

hoo duration, and the change in frequency between the final hoo frequency and the modal frequency.

Analysis of duet syntax

We used lag sequential analysis (Bakeman & Gottman, 1986) to determine whether there was an underlying syntactical organization to the sequence of note types within duets. Lag sequential analysis detects non-random associations of behavioral acts within longer sequences by identifying those transitions between two events that occur at a rate significantly different than expected given the frequency of those events under consideration (Bakeman & Gottman, 1986; Waas, 1991). It does so by calculating the observed number of times a certain event category (a 'criterion') is followed by another (the 'target') at a specified unit (a 'lag') in a string of events. The observed probabilities of a certain event category following another and the expected probabilities given the overall occurrences of these events in the data set are then used to calculate a *z*-statistic. When the number of transitions between these two events is sufficiently large, the distribution of this *z*-statistic approximates the standard normal distribution and can be used as a statistical measure of the likelihood of transitions (Bakeman & Quera, 1995). Thus lag sequential analysis can be used to distinguish between transitions that occur frequently simply because the two events involved are themselves common, and those transitions that are more common (or rarer) than might be expected based on the overall frequency of the constituent events.

We scored the sequence of notes within each duet using five categories of note types: the three sex-specific note types (female screes, male screes and male yoohoos) and the contact calls of each sex. We also included silence as the sixth category of event to code for the end of duets, as defined by greater than two seconds of silence. The caller of each note was identified from head, throat, and beak movements in the videotaped image and note types classified visually from spectrograms. Contact calls can occur in long string that may or may not be followed by sex-specific notes. Because we were primarily interested in the syntax of the sex-specific notes, we limited the analysis for each duet to the sex-specific notes and the four contact calls immediately preceding them. Other types of notes occurred at a low frequency (3.4% of all notes) and were combined with the contact call category of the appropriate sex to minimize the number of categories, an important consideration for lag sequential analysis.

We performed lag sequential analysis on note types using the SDIS-GSEQ program (Bakeman & Quera, 1995). We examined the frequency of notes at lag +1 (the note immediately following the criterion note) and lag +2 (the second note after the criterion). Each note type was used both as a target and a criterion for all other note types, resulting in a 6 × 6 table of *p*-values for the transition probabilities at each lag. We applied a table-wide Bonferroni correction to the significance levels of transition rates at each lag to avoid type I errors (Bakeman & Gottman, 1986). We performed analyses on the duets of all seven pairs combined and for the two sites independently; similar results were found when pairs were examined individually, but the smaller sample sizes generally worsened the approximation of the *z*-statistic to a normal distribution (data not shown).

Analysis of variation within note types

Considerable variation in the acoustic structure of duet note types through the course of a duet is clearly audible to the human ear. To test whether this variation depends on the order of a note within a duet, we performed analyses of covariance in JMP version 5.1 for each acoustic parameter with note order as a continuous predictor, pair as a random effect, and an interaction term of pair by note order. We corrected for multiple tests within each note type with the Bonferroni method (Sokal & Rohlf, 1995).

Results

Duet phonology

Duets consist of contact calls, which are given by both sexes, and three distinct sex-specific note types: female screes, male screes, and male yoohoos. Although male and female screes share a similar acoustic structure, there are significant differences between females and males in several measured parameters of screes, including total note duration, number of upsweep elements, and ratio of broadband to total note duration, but not mean peak frequency of upsweeps or the difference between first and last peak upsweep frequency (Table 2). There were also differences among individuals nested within sex for all acoustic parameters (Table 2). Female and male screes also differ in the manner in which their note parameters change with note order within a duet (see below).

Table 2. Results of comparisons between the acoustic parameters of female and male scree notes using hierarchical analyses of variance.

Acoustic parameter	Means $\pm$ SE		F values	
	Female screes	Male screes	Sex[1]	Individual[1]
Total note duration (ms)	610 ± 6.2	466 ± 5.5	12.9^*	28.8^*
Number of upsweep elements	2.8 ± 0.04	1.4 ± 0.04	46.8^*	7.2^*
Ratio broadband section to total note duration	0.419 ± 0.007	0.690 ± 0.01	87.3^*	3.9^*
Mean peak upsweep frequency (Hz)	1713 ± 11	2168 ± 23	1.8	64.6^*
Difference between first and last peak upsweep frequency (Hz)	-25 ± 5.6	-45.3 ± 5.1	0.3	6.6^*

[1] $N = 993$ notes, d.f. $= 1$ for fixed effect of sex, d.f. $= 13$ for random effect of individual nested within sex.

* Bonferroni corrected $p < 0.01$.

Consistent acoustic patterns were also found in the male yoohoo notes. The modal frequency of the initial yoo segment (mean $\pm$ SE $= 937 \pm 4.2$ Hz) was higher than that of the terminal hoo segment (mean $\pm$ SE $= 772 \pm 4.4$ Hz) in all but one of the notes ($N = 381$). Likewise, the duration of the yoo segment (mean $\pm$ SE $= 247 \pm 7.3$ ms) is generally shorter than that of the hoo segment (mean $\pm$ SE $= 266 \pm 3.9$ ms) although this relationship was less absolute and only occurred in 67% of notes ($N = 383$). The ratio of the modal frequency of yoo to hoo segments was similar to that for the ratio of the durations of the two segments (mean ratio $= 1.2$ for both) but variation around the mean was much less for the ratio of modal frequencies (CV $= 8.7\%$) than for the ratio of the durations (CV $= 125.7\%$).

Duet syntax

Analysis of duet note sequences revealed four distinct patterns within each duet: 1) contact calls precede sex-specific duet notes, 2) males and females alternate their sex-specific notes, 3) both sexes will repeat note types multiple times, and 4) males make a one-way transition from scree notes to yoohoo notes. Lag sequential analysis clearly demonstrates all four patterns (Figure 3). At Lag $+1$ (the note immediately following the criterion note), a contact call was most likely to be followed by another contact call without clear alternation by the sexes. For sex-specific notes, in contrast, the only
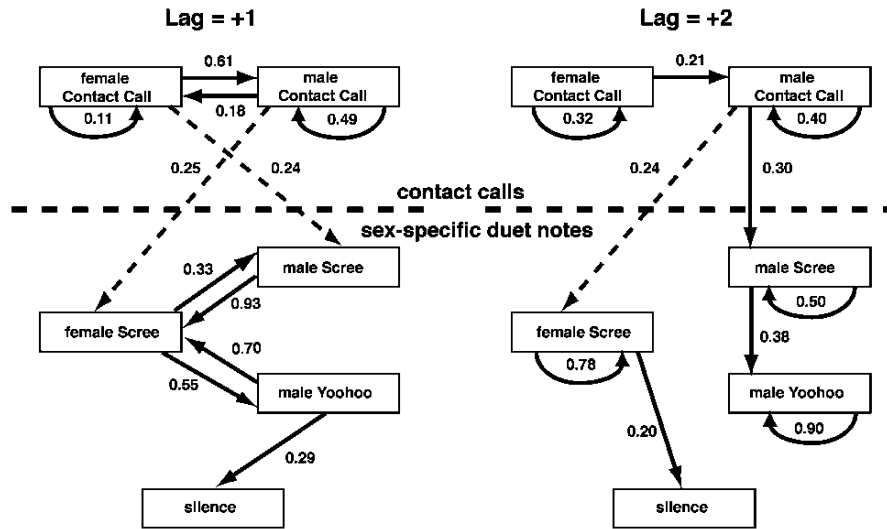
Figure 3. Flow diagrams showing the conditional probabilities at which note types follow others at the specified lags. In the lag = +1 diagram, arrows indicate those note types that occur immediately after a given note type. In lag = +2, arrows indicate those note types that occur after one intervening note. Solid arrows denote conditional probabilities greater than 0.1 and transitions occurring significantly more often than expected. Dashed arrows denote conditional probabilities that are greater than 0.1 but are not significantly greater than expected given the observed frequencies of the two note types in question.

significant transitions were to the sex-specific notes of the opposite sex or to silence, indicating consistent alternation between the sexes. At Lag +2 (two notes after the criterion note), contact calls of either sex were followed by either another contact call or by a sex-specific note. There were no significant transitions in the reverse direction from sex-specific notes to contact calls. Female screes were followed by other females screes at Lag +2 with a probability of 0.78, demonstrating both the strict alternation of notes between the sexes (antiphony) and the repetition of note types within a sex. Female screes were followed by silence with probability of 0.20. Male notes also illustrated the patterns of antiphony and note type repetition, with male notes following other male notes at Lag +2 with a probability of 0.88 to 0.90. In addition, males made a one-way transition in their sex specific notes, with male yoohoos following male screes with a probability of 0.38 while the reverse transition had a probability of less than 0.01. When duets from Pelon Altura and Horizontes were analyzed separately, there were strong corre-

lations between the transition probabilities for the two sites at both Lag +1 (correlation coefficient = 0.98) and Lag +2 (correlation coefficient = 0.99).

A fifth pattern of duet organization not apparent from the lag sequential analysis is the distinct temporal pairing of antiphonal sex-specific notes (visible in Figure 1). Females give the first note of each pair and the male note follows, and often overlaps, the female note. This temporal pairing of notes is reflected in the duration of the interval between the start of a note and the start of the previous note (usually of the opposite sex), which was significantly shorter for male notes (males, mean $\pm$ SE = 555 $\pm$ 8.7 ms, N = 599) than for female notes (females, mean $\pm$ SE = 757 $\pm$ 11.8 ms, N = 562; repeated measures ANOVA with pairs as a random effect nested within the fixed effect of sex: sex effect F = 6.2, d.f. = 1, p < 0.05, pair effect F = 24.2, d.f. = 12, p < 0.05). Despite this pattern of females giving the first note within each pair of sex-specific notes, either sex may initiate the transition from the contact call phase to the sex-specific note phase. Overall, females called the first sex-specific note in 51% of duets. Males were more likely to call last in duets, giving the last note in 75% of duets. Incomplete duets in which only one sex called sex-specific notes were rare (4% of the 171 duets examined).

Variation in duets

Within the constraints of the phonological and syntactical patterns described above, duets exhibited considerable variation in the number and acoustic characteristics of notes given. Duets ranged in length from one to 18 sex-specific notes (mean $\pm$ SE = 8.2 $\pm$ 0.3). Models incorporating note order, pair identity, and an interaction term were significant predictors for all but one of the acoustic parameters of duet note types (Table 3).

The order of a note within a duet was a significant predictor of all acoustic parameters measured for female screes (Table 3). Total note duration, number of upsweep elements and the change in peak frequency of these upsweep elements all increased with note order, while the ratio of the broadband section duration to total note duration and the mean peak frequency of the upsweep elements decreased through the course of a duet. Pair identity was also a significant effect for five parameters for female screes (Table 3), and the interaction term was significant for the ratio of the broadband section duration to total note duration and the mean peak frequency of the upsweep

Table 3. The effect of note order and pair identity on acoustic parameters of duet notes using analyses of covariance.

Note type	Acoustic parameter	r^2 for model	F value		
			Note order[*]	Pair[*]	Interaction[*]
Female scree	Total note duration (ms)	$0.38^{\dagger}$	$79.4^{\dagger}$	$37.0^{\dagger}$	2.7
	Number of upsweep elements	$0.31^{\dagger}$	$142.6^{\dagger}$	$11.4^{\dagger}$	2.0
	Ratio broadband section to total note duration	$0.26^{\dagger}$	$139.6^{\dagger}$	$4.1^{\dagger}$	$3.1^{\dagger}$
	Mean peak upsweep frequency (Hz)	$0.42^{\dagger}$	$42.9^{\dagger}$	$36.5^{\dagger}$	$5.8^{\dagger}$
	Difference between first and last peak upsweep frequency (Hz)	$0.14^{\dagger}$	$17.2^{\dagger}$	$9.3^{\dagger}$	2.5
Male scree	Total note duration (ms)	$0.23^{\dagger}$	$11.6^{\dagger}$	$5.2^{\dagger}$	$3.9^{\dagger}$
	Number of upsweep elements	$0.19^{\dagger}$	5.0	$3.5^{\dagger}$	1.8
	Ratio of broadband to total note duration	$0.26^{\dagger}$	0.2	3.5	$6.2^{\dagger}$
	Mean peak upsweep frequency (Hz)	$0.79^{\dagger}$	$8.5^{\dagger}$	$77.4^{\dagger}$	$3.1^{\dagger}$
	Difference between first and last peak upsweep frequency (Hz)	0.1	0.1	2.9	0.8
Male yoohoo	Total note duration (ms)	0.42^{**}	60.3^{**}	30.6^{**}	1.0
	Ratio yoo section to hoo section duration	0.39^{**}	34.5^{**}	22.2^{**}	7.7^{**}
	Modal yoo section frequency (Hz)	0.34^{**}	2.5	28.2^{**}	1.6
	Modal hoo section frequency (Hz)	0.33^{**}	1.4	27.8^{**}	1.1
	Ratio yoo to hoo modal frequency	0.12^{**}	0.1	8.7^{**}	0.6
	Difference between final and modal hoo frequency (Hz)	0.32^{**}	8.5^{**}	13.2^{**}	6.8^{**}

[*] $N = 680$ female screes, $N = 313$ male screes, $N = 386$ male yoohoos, d.f. $= 1$ for continuous predictor note order, d.f. $= 6$ for random effect of pair, d.f. $= 6$ for interaction between note order and pair.

[**] Bonferroni corrected $p < 0.008$.

[†] Bonferroni corrected $p < 0.01$.

elements. In contrast, male screes showed a significant effect of note order only for the total note duration and the mean peak upsweep frequency, both of which increased with note order (Table 3). It should be noted, however, that male screes typically occurred only within the first few notes of the duet, providing less scope for variation with note order than female screes. Both of these parameters also showed significant differences among pairs, as did the number of upsweep elements (Table 3). Thus both male and female screes

had multiple parameters that changed with their order within a given duet, and varied among pairs.

Male yoohoos showed similar patterns of variation, with multiple parameters changing with note order and varying among pairs. Both temporal measures (total note duration and the ratio of the yoo section to hoo section durations) increased with note order, while the difference between the final hoo frequency and the modal hoo frequency generally declined through the course of a duet, indicating that fewer notes with final frequency upsweeps were used later in duets (Table 3). All six yoohoo parameters showed a significant effect of pair identity.

The spacing between notes also changed as duets progress. ANCOVAs of the time to the start of the previous note versus note order with pair as a random effect found significant responses to both note order and pair for females (overall $r^2 = 0.32$; for note order $F = 108.2$, d.f. $= 1$, $p < 0.0001$; for pair $F = 17.5$, d.f. $= 6$, $p < 0.0001$; for note order by pair interaction $F = 2.3$, d.f. $= 6$, $p < 0.05$) and for males (overall $r^2 = 0.26$; for note order $F = 14.3$, d.f. $= 1$, $p < 0.001$; for pair $F = 22.7$, d.f. $= 6$, $p < 0.0001$; for note order by pair interaction $F = 2.4$, d.f. $= 6$, $p < 0.05$), reflecting the increased spacing between note pairs through the course of a duet. Thus for all note types there is tendency for at least some note parameters to vary through the course of a duet, particularly temporal parameters describing the relative durations of different note segments and the spacing between notes.

Discussion

Pair duets of the yellow-naped amazon are complex signals composed of a limited number of note types repeated many times during a single rendition. There is considerable variation in the number of notes and the acoustic parameters of these notes across different duet renditions. There are, however, several syntactical rules that underlie and organize this variation: i) some duet note types are used by only one sex; ii) these sex-specific notes are delivered antiphonally and in pairs, with the female producing the first note of each pair and the male following and often overlapping his note on that of the female; and iii) duet notes are used with a combinatorial syntax in which note types appear in a strict sequential order but may be repeated a variable number of times, resulting in many different duet variants. Contributing

to this variation is the pattern that many acoustic parameters of notes vary both among pairs and progressively with their order of appearance within a single duet. Below we contrast the syntactical rules exhibited by these yellow-naped amazon duets to those identified in other animal communication signals and discuss the potential relationship between these rules and the function of duets. While these discussions are post-hoc, they do provide a number of preliminary hypotheses that can be tested in future work on the yellow-naped amazon and other species through observational studies, playbacks of natural and synthetic duets, and other experimental manipulations.

Potential functions of sex-specific phonology

Yellow-naped amazon duets at the Pelon Altura and Horizontes sites in the Northern dialect are composed of contact calls and three sex-specific note types: female screes, male screes and male yoohoos. Sex specific notes are found in the duets of many species (Farabaugh, 1982). Quantitative descriptions or representative spectrograms suggest that all species of parrots for which duets have been described have at least one class of duets with sex-specific notes (Table 4). Moreover, sex-specific notes or songs are described in the duets of many other species from such taxa as the oscine songbirds (Watson, 1969; Vencl & Soucek, 1976; Levin, 1996a; Mennill & Vehrencamp, 2005; Rogers, 2005), suboscine songbirds (Seddon & Tobias, 2006), barbets (Payne & Skinner, 1970; Short & Horne, 1983), mesites (Seddon, 2002), and gibbons (Mitani, 1985; Raemaekers & Raemaekers, 1985). In contrast, sex-specific notes are not present in the kokako, *Callaeas cinerea*, a New Zealand endemic passerine (Molles et al., 2006), the white-browed sparrow weaver, *Plocepasser mahali* (Voigt et al., 2006), or several other species (Farabaugh, 1982).

Sex-specific notes could potentially serve to communicate a caller's sex, broadcast the mated status of a pair, aid the identification of individual contributions to duets or facilitate communication with different intended receivers. These aspects of sex-specificity are consistent with a number of hypotheses for duet function, including those that emphasize coordinated resource defense (Seibt & Wickler, 1977) or different strategies for the two sexes (Levin, 1996b).

Although male and female scree notes differ significantly in most measured parameters, they do share acoustic characteristics (broadband energy,

Table 4. Summary of phonological and syntactical features of duets from parrot species.

Species	Duet name	Duet type[*]	Sex-specific notes	Variability[**]	Source
Brotogeris	Rich-timbred	A	Yes	L, N(?)	Arrowood (1988)
versicolor	Bik ah	A	Yes	L, N(?)	
Brotogeris	High intensity	A	Yes	L, N(?)	Power (1966)
jugularis	Medium intensity	A	Yes	L, N(?)	
Agapornis	Class 1	A	Yes	L	Mebes (1978)
roseicollis	Class 2	A	No	L, N	
	Class 3	A	No	L	
Amazona	Loud duets	A	Yes	L, N	Present study,
auropalliata	Gurgles	A	Undescribed	L, N	Wright (1997)
	Squeals	A	Undescribed	L, N	
Trichoglossus	Several types	A, P	Both	L(?), N(?)	Serpell (1981)
haematodus					
Trichoglossus	Several types	A, P	Undescribed	Undescribed	Serpell (1981)
chlorolepidotus					
Alisterus	Duos	A	Yes	L(?), N	Tembrock (1972)
scapularis					
Amazona	Warble-squawk	A	Yes	N(?)	Snyder et al. (1987)
vittata					

[*] A = antiphonal (alternating male and female notes); P = polyphonic (no strict temporal ordering).

[**] L = variation in duet length (number of notes used); N = variation in note structure or note types within duets, (?) indicates that the presence of a type of variability is suspected but could not be unambiguously determined from published study.

low frequency) that are hypothesized to communicate aggression over short distances (Morton, 1977). The broad similarity in structure between male screes and female screes and their coordinated use by both sexes in duets suggests that these note types convey a shared message, such as joint defense of a resource. One such resource might be nest sites. Yellow-naped amazons often use the same nest cavity for several successive years (T. Wright, unpubl. data) and will regularly engage in counter-duetting with other pairs or playbacks of duets near their nests (Wright & Dorin, 2001). The observed variation among pairs in the acoustic parameters of scree notes could aid in effective territory defense by permitting the recognition of neighboring territory holders versus non-territorial floating pairs (Temeles, 1994). Duets are thought to function in joint defense of territories in several species including

the canary-winged parakeet, *Brotogeris versicolorus* (Arrowood, 1988), the magpie-lark, *Grallina cyanoleuca* (Hall, 2000; Mulder et al., 2003), and the gibbon species, *Hylobates lar* and *H. muelleri* (Mitani, 1985; Raemaekers & Raemaekers, 1985). Defense of other resources such as ephemeral food sources is also possible and may account for the occasional observation of duets by pairs at non-nesting locations (T. Wright & J. Bradbury, unpubl. data).

The distinctly different structure of the male yoohoo suggests that males may communicate a different message during the later stages of each duet. High-frequency tonal calls are effective for long-range signals because they concentrate most of their energy into a single frequency band (Wiley & Richards, 1982). The fact that yoohoo notes are detectable by human observers at a greater distance than are either type of scree note (Wright & Dahlin, unpubl. data) suggests they may be intended for more distant receivers, but the nature of these receivers remains uncertain. Playback experiments examining the behavioral responses of the two sexes to duets with different note compositions could shed light on the function of the yoohoo note and test the hypothesis that different notes communicate different messages.

Potential functions of antiphony and note pairing

One prominent syntactical feature of yellow-naped amazon duets is that duet notes are used antiphonally and in distinct pairs with female notes leading male notes. Antiphony is a common feature of the duets of parrots (Table 4) and other birds (Farabaugh, 1982) and may simply serve to reduce masking of one bird's notes by the other. The temporal pairing of notes (rather than strict alternation) is less commonly documented in duets. One explanation for note pairing in the yellow-naped amazon is that females set the pattern of acoustic changes in duets and males choose note types or acoustic variants based on the structure of the preceding female note; the reverse pattern has been documented in duetting black-bellied wrens, *Thryothorus fasciatoventris*, in which females choose a response based on the prior sequence given by a male (Logue, 2006). If duets serve a territory defense function, the precision of the note pairing may also signal to potential territory usurpers how effectively a pair cooperates and how readily they will defend their territory. Alternatively (or additionally), note pairing, and particularly the observed overlapping of male notes onto female notes, could function as acoustic mate guarding by males (Smith, 1994).

Potential functions of combinatorial syntax

Yellow-naped amazon duets are composed of a limited number of note types that appear in a strict sequential order. Within this sequential order, each note type may be repeated several times within a duet or omitted entirely. Signals exhibiting these syntactical rules have been termed 'combinatorial' because they use a small repertoire of distinct note types combined in a defined order to create a very large set of different signals (Hailman et al., 1987). Combinatorial syntax has been well documented in the solo 'chick-a-dee' calls of the genus *Poecile* (Hailman et al., 1987; Ficken et al., 1994; Freeberg & Lucas, 2002), and the male song of the black-chinned hummingbird, *Archilochus alexandri* (Rusch et al., 1996). Yellow-naped amazon duets are the first duets in which combinatorial syntax has been identified, but duets with different note types and variation in note number have been noted in other parrot species (Table 4), and closer examination may reveal combinatorial syntax in these duets as well.

Explanations for the communicative function of combinatorial signals range from the extreme view that variation is meaningless and all calls are functionally equivalent to the opposite view that each call variant communicates a different message (Ficken et al., 1994). Intermediate to these extremes is the possibility that different note types within a call communicate different messages while the number of repetitions of a note indicates the intensity of this message (Hailman et al., 1987). The latter hypothesis received some support in studies of the Mexican chickadee, *Poecile sclateri*, in which the frequency of use of different note types varied with behavioral context and the activity of the birds (Ficken et al., 1994), and in the Carolina chickadee, *P. carolensis*, in which responses varied with frequency of different note types in playback exemplars (Freeberg & Lucas, 2002).

Each of the three sex-specific note types also exhibited directional trends in multiple acoustic parameters through the course of a duet. Modeling these trends as linear effects of note order within a duet explains a significant degree of variation for many of these parameters. In all cases, however, there remained a substantial amount of unexplained variation. The relatively loose fit between these linear models and the data suggests that acoustic variation may depend on factors that are only roughly approximated by the order of a note within a duet. Variation in the acoustic form of notes through the course of a duet could serve as an additional means of modifying the basic

message conveyed by repetition of different note types. Further playback experiments employing duets with varying note compositions are essential for testing whether changes in either note number or acoustic structure alter the communication function of these complex signals.

Acknowledgements

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