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Does syntax contribute to the function of duets in a parrot, *Amazona auropalliata*?

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Abstract Complex acoustic signals in many animal species are characterized by a syntax that governs how different notes are combined, but the importance of syntax to the communicative function of signals is not well understood. Mated pairs of yellow-naped amazons, *Amazona auropalliata*, produce coordinated vocal duets that are used for territory maintenance and defense. These duets follow rules that specify the ordering of notes within duets, such as a strict alternation of sex-specific notes and a defined progression of note types through each duet. These syntactical rules may function to define sex-specific roles, improve coordination, and allow individuals to combine calls into meaningful sequences. As a first step toward understanding the functional significance of syntax, we conducted two separate audio playback experiments in which we presented nesting pairs with normal duets and duets with broken syntax (i.e., one of the syntactic rules was broken). In Experiment One, we reversed the order of female and male notes within note pairs while retaining the typical progression of note types through a duet. In Experiment Two we reversed the order of note types across a whole duet while retaining the typical female–male ordering within note pairs. We hypothesized that duets with broken syntax would be less-effective signals than duets with normal syntax and predicted that pairs would respond less to broken syntax than to normal duets. Contrary to predictions, we did not observe differences in response between treatments for any variables except latency to approach the speaker. After we combined data across experiments post hoc, we observed longer latencies to approach the speakers after playbacks of broken syntax duets, suggesting that pairs could differentiate between playbacks. These responses suggest that breaking one rule of duet syntax at a time does not result in detectable loss of signal efficacy in the context of territorial intrusions.

Keywords Acoustic signal · Duet · Parrot · Syntax · Yellow-naped amazon

Introduction

In many species, complex vocalizations such as songs and duets are characterized by syntactic rules that organize how notes are combined within a signal (Marler and Pickert 1984; Hailman and Ficken 1987; Ball and Hulse 1998; Podos et al. 1999; Marler 2004; Clarke et al. 2006; Logue 2006; Wright and Dahlin 2007; Catchpole and Slater 2008). Despite the ubiquity of such organizational syntax in animal signals, the relationship between signal structure and communication function is not always well understood (Balaban 1988; Marler 1997). The syntax of signals in many species appears relatively invariant, although a bird may have multiple song types in its repertoire, for example, the underlying structure of those songs do not vary across types (Peters et al. 1980; Marler and Peters 1989; Slabbekoorn and Smith 2002; Collins 2004; Podos et al. 2004; Lachlan et al. 2010). Such syntax may have a species recognition function. Other species use a combinatorial form of syntax, where note composition varies from one

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song to the next but is governed by probabilistic rules. Syntax in those species may function in a manner similar to grammar in human language, in which a potentially infinite number of meanings can be derived from a finite number of symbols (Jackendoff 1999; Nowak et al. 2001, 2002) Although animal communication systems are simpler than human language and appear to lack the capacity for recursion and generativity (Hauser et al. 2005), animal syntax still may allow animals to increase the variety of messages they can send or more finely modulate a limited number of messages (Smith 1988, 1991; Freeberg and Lucas 2002; Freeberg et al. 2003; Arnold and Zuberbuhler 2006). For example, chickadees in the genus *Poecile* change the composition of their 'chick-a-dee' calls in order to use them in different social contexts (Hailman and Ficken 1987; Clucas et al. 2004; Charrier and Sturdy 2005; Templeton et al. 2005). Similarly, putty-nosed monkeys, *Cercopithecus nictitans*, and white-handed gibbons, *Hylobates lar*, also use syntax to combine signals to create new ones with different meanings (Arnold and Zuberbuhler 2006; Clarke et al. 2006).

Two experimental methods have been used to investigate the function of syntax in animals. In the first method, researchers manipulate behavioral context and observe how birds alter the structure of their vocal responses. For example, Templeton et al. (2005) presented black-capped chickadees (*Poecile atricapillus*) with a variety of avian and mammalian predators and found that acoustic features of the chick-a-dee call vary with the size and threat posed by a predator. In the second method, researchers conduct playbacks in which they compare responses to playbacks of signals with normal (un-altered or control) syntax versus playbacks in which the rules of syntax are violated ('broken syntax'). This method has been used effectively in Carolina chickadees, *Poecile carolinensis* (Clucas et al. 2004); winter wrens, *Troglodytes troglodytes* (Holland et al. 2000); swamp sparrows, *Melospiza georgiana* (Nowicki et al. 2001); mustached bats, *Pteronotus parnelli* (Esser et al. 1997); and Diana monkeys, *Cercopithecus diana* (Zuberbuhler 2002). In winter wrens, broken syntax and normal syntax playbacks both elicited territorial responses, but responses to broken syntax songs were slightly less intense than responses to normal songs; birds did not approach the loudspeaker as closely and left its vicinity more quickly (Holland et al. 2000). In chickadees, the call composition of the bird's responses differed in response to playbacks with broken syntax during the fall and winter but not during the spring (Clucas et al. 2004). In swamp sparrows, playbacks of both normal and broken syntax songs to males elicited territorial defense responses, while females produced fewer copulation solicitation displays in response to broken syntax song (Nowicki et al. 2001).

These experiments indicate that syntax contributes to the communication function(s) of signals in some species and that communicative significance may be reduced or lost when syntax is broken. Although most species respond either less or in an altered manner to playbacks with broken syntax, responses are not uniformly lower, as evidenced by male swamp sparrows and Carolina chickadees (Nowicki et al. 2001; Clucas et al. 2004). Further experiments conducted in other species are needed to clarify the role of syntax in animal communication. This need applies particularly to species with combinatorial syntax; such syntax may be more functionally versatile than the typical syntax that is observed in relatively invariant birdsong (Clucas et al. 2004; Templeton et al. 2005; Clarke et al. 2006).

One type of signal that particularly warrants investigation is duets, which are jointly produced by two individuals (Farabaugh 1982; Hall 2009). Duets in many species are produced with syntactical rules that vary in complexity (Vencl and Souček 1976; Levin 1996; Slater 1997; Mann et al. 2003; Hall 2004; Marshall-Ball and Slater 2004; Logue 2006, 2007; Valderrama et al. 2008), but the function of syntax in such species has not been tested using the playback methodology described above. Duet signals are distinct from individual signals because both participants must agree on the rules and apply them in a manner that creates a coordinated and effective signal, and the signal is typically directed at multiple receivers. These signals can also have additional types of syntactic rules that individual signals lack, such as rules that depend on the timing or notes of the other signaler. The coordination required to produce many duets thus creates an additional level of difficulty in production that is not experienced by single individuals, and timing rules appear to improve coordination in species such as black-bellied wrens, *Pheugopedius fasciatoventris* (Logue et al. 2008). Yellow-naped amazons, *Amazona auropalliata,* give duets with several types of syntactic rules, including combinatorial rules for note order and rules regarding coordination. These duets thus present an opportunity to investigate different types of syntax in an acoustically complex signal.

Duets in yellow-naped amazons are given by mated pairs of males and females, and both observational and experimental evidence suggests that duets play an important role in territory maintenance and defense (Wright and Dorin 2001; Wright and Dahlin 2007; Dahlin and Wright 2009, 2012; Dahlin 2010). Pairs typically respond to the duets of neighbors by answering with duets of their own (counter-duets) and sometimes by approaching those neighbors. Pairs typically engage in these counter-duet sessions while on their own territories and do not physically engage one another, but disputes occasionally result in territorial transgressions and aerial fights (Dahlin 2010). Yellow-naped amazons give two types of duets: primary

duets, which we will hereafter refer to as 'duets', and warble duets. Primary duets are produced around nest trees on a daily basis during the nesting season, while warble duets appear to be reserved for highly aggressive interactions, such as when a pair has encroached onto another pair's territory (Wright 1997). Playbacks of local duets within nesting territories result in rapid approaches to the speaker and, less frequently, aggressive duets or growl vocalizations (Wright and Dorin 2001; Dahlin and Wright 2012).

Structurally, duets are composed of a series of different sex-specific note types used exclusively in duets. Duets are typically preceded by a series of contact calls, which may also be given in other contexts. Both duet notes and contact calls form large regional vocal dialects that share the same boundaries (Wright 1996, 1997; Wright et al. 2008). Duets are highly variable in length and note composition from rendition to rendition by a pair, but this variation occurs within the constraints imposed by well-defined syntactic rules (Wright 1997; Wright and Dahlin 2007; Dahlin and Wright 2009; Dahlin 2010). These syntactic rules include the following:

i.   Duet notes are sex-specific, and male and female notes differ in acoustic structure.
ii. Male and female notes alternate and are produced in distinct pairs.
iii. Female notes precede male notes within every note pair.
iv. Sex-specific notes follow each other in a defined order within a given duet.
v.   Sex-specific notes may be repeated a variable number of times.
vi. The phonology (small-scale structure) of sex-specific notes changes in predictable ways as duets progress.
vii. The duration between pairs of notes increases as duets progress.

Syntactic rules are stable across sites within a vocal dialect and appear to be stable across dialects as well (Dahlin and Wright 2009); this invariance suggests that syntax is important to the function of duets. Most rules of syntax fall into two general categories: (1) rules that specify sex-specific roles and may aid in synchronization (rules i–iii, vii)) and (2) combinatorial rules that may allow birds to combine calls into meaningful sequences (iv–vi).

We hypothesized that changing the sequences of calls (i.e., breaking the syntactical rules) would lead to a reduction or loss of signal efficacy. To test our hypothesis, we conducted two playback experiments in which we presented birds with duets with broken syntax and normal syntax (Fig. 1). In Experiment One, we altered syntax by breaking rule iii and reversed the order of male and female notes (Reverse Sex Order) such that male notes preceded

female notes within each note pair. In Experiment Two, we broke rule iv and reversed the order of notes (Reverse Note Order) such that pairs of female and male notes typically given at the end of duets were transferred to the beginning of duets, and vice versa. Both of these syntactic rules are followed quite strictly; for example, we have never observed a duet in which male notes preceded female notes (Wright and Dahlin 2007), so duets with broken syntax constitute highly abnormal stimuli in the parrot's environment. We predicted that pairs would respond less to broken syntax duets than to normal duets, with either fewer vocalizations or slower approaches to the speaker.

Methods

We conducted trials at three sites within the northern dialect of the yellow-naped amazon in Guanacaste Province, Costa Rica: Ahogados, Horizontes, and Santa Rosa (map in Dahlin and Wright 2009). We conducted each experiment using 16 mated pairs of yellow-naped amazons, nine of which were used in both experiments. All pairs had established nesting territories that ranged in size from 1.1 to 8.0 km^2, with a mean size of 3.9 ± 0.6 km^2 (Dahlin and Wright unpublished data). We determined the location of territories primarily by observing duet and counter-duet sessions with neighboring pairs in the early morning and late evening. For many pairs, we were also able to locate nest cavities and observe reproductive behavior, such as allopreening, male feeding, and copulations.

Playback experimental design

We conducted two playback experiments: (1) Reverse Sex Order, from January 19 to March 13, 2007 and (2) Reverse Note Order from January 22 to March 3, 2008. Each experiment consisted of two treatments: 'normal' syntax duets in which the syntax was not changed and 'broken' syntax duets in which we manipulated the syntax to break one of the observed syntactic rules that govern duet production (Fig. 1). In the Reverse Sex Order experiment, we changed the sex-specific ordering of notes by placing male notes before the female notes within note pairs but retained the overall order of note pairs across a duet. For example, if notes within a normal duet were in the order F_1M_1 F_2M_2 F_3M_3, then notes within the broken syntax duet would be in the order M_1F_1 M_2F_2 M_3F_3. In the Reverse Note Order experiment, we switched the order of note pairs through a duet while maintaining female precedence within note pairs. For example, if note pairs within a normal duet were in the order F_1M_1 F_2M_2 F_3M_3, then notes in the broken syntax treatment would be in the order F_3M_3 F_2M_2 F_1M_1.
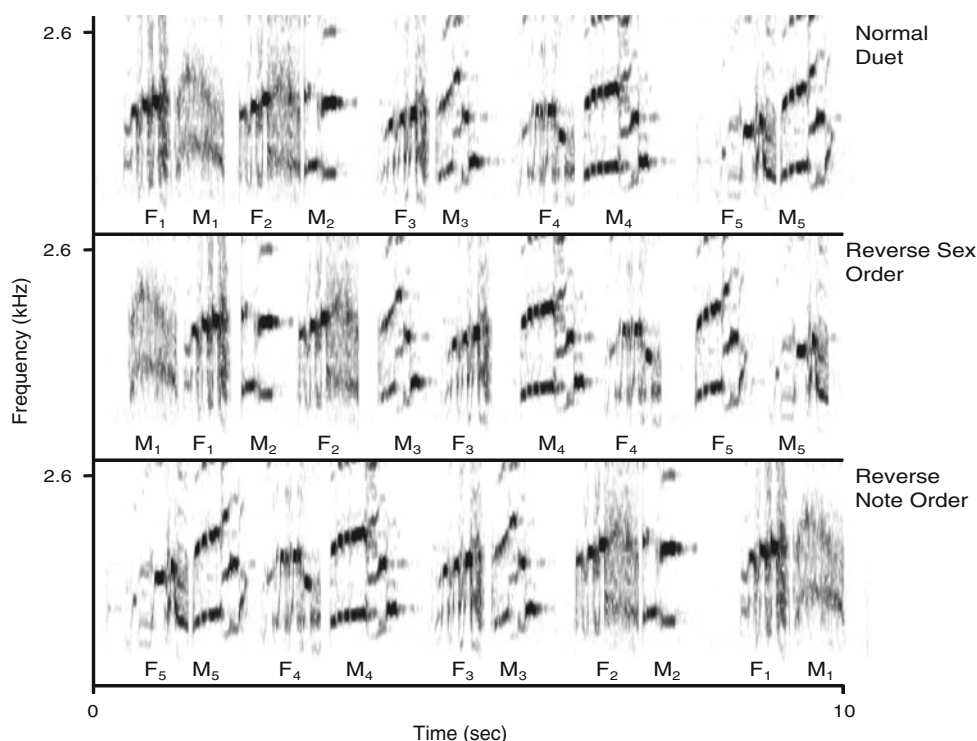
Fig. 1 Spectrograms of the three types of playback exemplars; a normal duet and two types of broken syntax duets: Reverse Sex Order and Reverse Note Order. In the normal duet, female notes precede male notes within the note pairs, and note types change through the course of a duet. In the Reverse Sex Order treatment, the male and female notes are switched within each pair of notes so that male notes precede female notes but the order of note types through a duet remains unchanged. In the Reverse Note Order treatment, pairs of notes are reversed in order across the duet, so that note pairs normally given at the beginning of the duet appear at the end, and vice versa. Individual notes are labeled with an M or F to denote the sex of the individual giving the note and a numerical subscript, which indicates the position of the note in the normal duet

We created duet exemplars using duets from 16 different pairs of yellow-naped amazons recorded in 2002 and 2006 at Ahogados, Horizontes, and Santa Rosa. Detailed analyses of the structure of duets from 1995 and 2002 confirm that duet form is temporally stable over multiple years (Wright and Dahlin 2007; Dahlin and Wright 2009). We digitized calls by playing tapes on a Canon Optura 50 digital video recorder, running the sound through an i-Mic (Griffin Technology) into a Macintosh Power PC G5 computer and digitizing at 44 kHz and 16 bits in Raven 1.2.1 (Cornell Lab of Ornithology). We created spectrograms in Raven with a window size of 512 samples, a filter bandwidth of 61.9 Hz with a Hanning (Hann) window, a hop size of 256 samples, a DFT (discrete Fourier transform) size of 512 samples, grid spacing of 43.1, and 90 % overlap. We scored notes as male and female by observing the video recording on a JVC high-resolution video monitor (model TM-H170VG) and following previously defined syntactic rules, which can be done effectively by trained individuals (Wright and Dorin 2001; Wright and Dahlin 2007). We edited duets to control for peak amplitude and total length in Raven 1.2.1. We then split duets into two channels, one for male notes and one for female notes, using Audacity 1.2.6 (SourceForge.net). Finished exemplars consisted of 3–5 pairs of notes (Fig. 1), which fall within the normal range of duet lengths that ranges from 2 to 9 pairs of notes (Wright and Dahlin 2007).

We selected three high-quality duets (e.g., low levels of background noise and non-overlapping notes) from a single calling bout of each of 16 pairs to be used as a single combined stimulus for playback presentation. These three duets were edited to create a set of normal syntax duet stimuli and further edited by rearranging the notes to create a set of broken syntax stimuli, resulting in 16 normal sets and 16 broken syntax sets. These stimuli sets were used in a matched reciprocal design (Kroodsma 1989; Wright and Dorin 2001) such that one subject pair would receive a normal syntax stimuli set from pair A and a broken syntax duet stimuli set from pair B, while a second focal pair would receive normal syntax duet stimuli from pair B and broken syntax stimuli from pair A. Each stimulus set was only used once in each experiment to avoid pseudoreplication (Kroodsma 1989). We assigned stimuli by choosing duets from pairs that lived at the same site as the subject pair, but were not direct neighbors to the subject pair's territory.

Playback presentation

We conducted playback trials on subject pairs' territories during the parrots' breeding season from January through March 2007 and 2008 between 5:00 am and 8:00 am, when pairs are most active on their territories. We broadcast the duets from MiniVox Pro wireless speakers (Anchor Audio) and either a Macintosh PowerBook G4 or an Alienware Area 51 M5550 laptop. We designated one speaker for the male notes and one for female notes and hung the speakers on different sides of the same tree. The direction that the speakers faced was random. Pair members commonly perch in different areas of the same tree, so our speaker placement simulated normal pair behavior. When the nest tree was known, we placed speakers in an adjacent tree; otherwise, speakers were placed in areas where we had observed intensive pair activity. The average distance from the speaker tree to the focal tree $\pm$ SE was 30.9 ± 3.9 m for the Reverse Sex Order experiment and 43.5 ± 5.7 m for the Reverse Note Order experiment. Each playback trial consisted of a speaker test followed by a 2-min pause, a 5-min pre-period, and a 5-min playback/post-period. Playback presentation began at the start of the playback period. We conducted playbacks in a semi-interactive fashion, which allowed us to counter-call to subjects in a natural manner (Wright and Dorin 2001; Vehrencamp et al. 2003). If pairs responded vocally to a playback stimulus, we immediately broadcast another stimulus until all three stimuli had been broadcast. If pairs did not respond vocally, we waited 30 s before broadcasting another exemplar. Three to five days later, we exposed pairs to the other treatment. We randomized and balanced the order of presentation of treatments across all pairs. We video- and audio-recorded the bird's responses using a tripod-mounted Sennheiser directional microphone (model ME67) and Canon digital video recorder (model Elura 100).

Data and analyses

We collected three types of data from trials: (i) vocalization data, which consisted of the number of single calls (sum of all calls given outside duets), number of growls (an aggressive type of single call), number of duets, and number of warble duets; (ii) temporal data, which consisted of the latency to first movement (measured in sec); and (iii) position data, which consisted of the distance of pair members to the speaker (measured in meters). A single observer (Dahlin) collected vocalization data by digitizing vocalizations using the methods described above, watching trial videos on a JVC high-resolution monitor (model TM-H17-00G) to score latency to first movement during the trial and confirming timing of other movements measured in the field. We measured the initial distance from the pair to the speaker pre-playback and the distance of closest approach to the speaker post-playback in the field after each trial using a 100-m tape measure. We conducted all statistical analyses in JMP 7.0 (SAS Institute Inc., 2007).

Overall playback response

We assessed the overall response of pairs to playbacks by comparing pre- and post-values for each trial, to evaluate whether the bird's behavior changed in response to the playbacks. Each pair of birds had two pre- and two post-trials (one broken syntax trial and one normal syntax trial), so we compared the average pre-values for each pair to the average post-values. We analyzed continuous data by comparing pre- and post-values using Wilcoxon signed-rank tests. These continuous variables were (i) number of single calls, (ii) number of growls, (iii) number of duets, (iv) number of warble duets, and (v) male and female proximity to the speakers. There is considerable debate surrounding the appropriateness of Bonferroni corrections and the relative risk of Type I and Type II errors, especially in behavioral datasets where such corrections can result in severely reduced power and potentially inaccurate acceptance of null hypotheses (Cabin and Mitchell 2000; Nakagawa 2004; Garamszegi 2006). For those reasons, we did not employ Bonferroni corrections and considered all P values that were less than the uncorrected critical value of 0.05 to be significant.

Treatment response

To control for baseline levels of subject behavior, we compared treatments using ratios of the post- to pre-trial values (post/pre) for all variables except latency to first movement, which could only be examined after the playbacks. Prior to calculating the ratios, we added a value of one to all numerators and denominators to avoid divisions by zero. Although the addition of one changed ratios slightly, we felt that it was the most effective way to account for baseline behavior and avoid the problem of zeroes (Zar 1999; Lowe et al. 2008). To validate our results, however, we also subtracted pre-values from post-values and re-analyzed the data. The results from the subtracted data and the ratio data were qualitatively similar (data not shown). For latency to approach the speaker, we also assigned a value of 300 s to pairs that failed to approach, which was the maximum duration of the post-period.

We tested for treatment effects using Wilcoxon signed-rank tests. We did not test for speaker effects, because previous control experiments found that pairs do not respond to playbacks of heterospecific species, indicating that pair response is driven by duet treatments, rather than presence of speakers on their territory (Wright and Dorin 2001).

Results

In the Reverse Sex Order experiment and the Reverse Note Order experiment, pairs approached the speakers more closely after playback presentation than during the pre-trial (Table 1; Fig. 2c). Vocalization rates were typically higher after playback presentation than before, but these differences were not significant in either experiment (Table 1; Fig. 2a, b).

Treatment response

There were no significant differences between normal and broken syntax duets for most variables in either the Reverse Sex Order experiment or the Reverse Note Order experiment (Table 2; Fig. 3). There was a consistent, albeit non-significant, trend across the two experiments toward longer latencies to approach the speaker after playbacks of broken syntax duets than after normal duets (Fig. 3d). To

explore this trend further, we combined data across the two experiments to contrast responses to normal versus broken syntax duets in a post hoc analysis. Since nine of the pairs were represented in both experiments, we analyzed the data with a repeated-measures ANOVA analysis on the square-root transformed data to avoid pseudoreplication (Zar 1999). Prior to combining the datasets, we conducted Wilcoxon tests to assess whether: (i) responses to normal syntax playbacks differed between the two experiments and (ii) responses to broken syntax playbacks differed between the two experiments. Neither test was significant (Normal duets $N = 32$, $Z = 0.12$, $P = 0.718$; Broken syntax duets $N = 32$, $Z = 0.19$, $P = 0.66$). The combined dataset showed a significantly longer response latency to broken syntax duets than normal duets ($F_{1, 44.4} = 4.26$, $P = 0.04$). Similar post hoc combined analyses of other response variables did not detect any differences between normal and broken syntax treatments (data not shown).

Table 1 Overall experimental response to Reverse Sex Order and Reverse Note Order experiments, with pre-playback and post-playback medians and 95 % confidence intervals for the mean presented

Variables	Reverse Sex Order				Reverse Note Order			
	Pre-median (95 % CI)	Post-median (95 % CI)	Z statistic	P value	Pre-median (95 % CI)	Post-median (95 % CI)	Z statistic	P value
Single calls	9.7 (7.1–26.6)	20.7 (16.1–62.9)	37.0	0.05	32.3 (17.8–42.9)	37.0 (21.0–46.8)	16	0.42
Growls	0.0 (−0.1–0.2)	0.0 (−1.1–5.4)	6.0	0.19	0.0 (−0.1–0.7)	0.0 (0.0–0.5)	0.5	0.10
Warble duets	0.0 (0.0–0.0)	0.0 (0.0–0.9)	7.5	0.06	0.0 (0.0–0.9)	0.0 (0.1–0.9)	1.5	0.93
Duets	0.0 (0.1–1.8)	0.75 (0.5–2.8)	23	0.11	0.5 (0.2–1.3)	0.5 (0.4–1.4)	14.0	0.14
Distance to the speaker (m)	86.4 (62.9–91.3)	35.3 (27.5–62.4)	33	0.001*	84.3 (52.8–89.0)	52.8 (32.5–60)	26.5	0.004*

Z values are from Wilcoxon signed-rank tests with $N = 16$. Significant values ($P < 0.05$) are denoted by *asterisk*
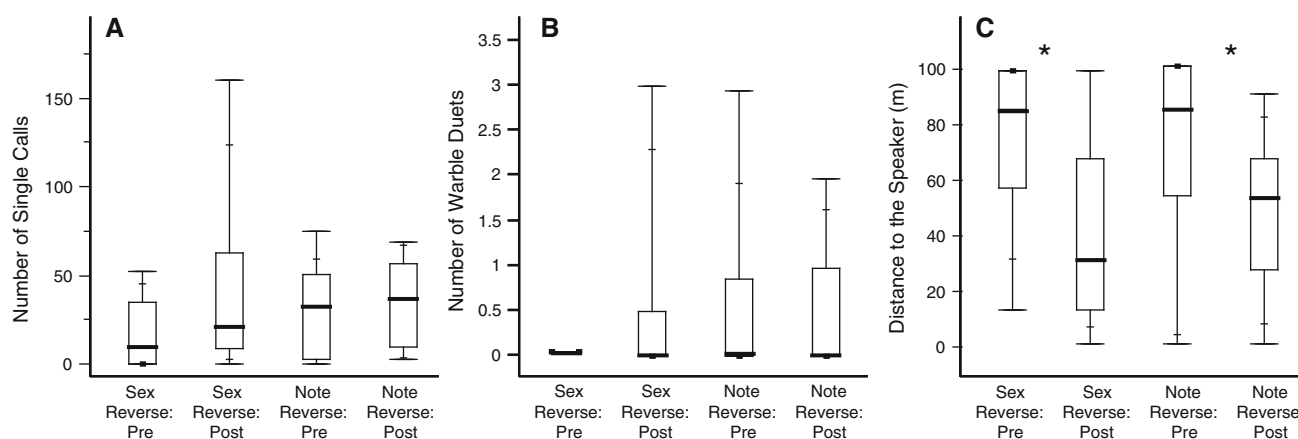
Fig. 2 Behavior of birds during the pre-and post-portions of the trial for the Reverse Sex Order and Reverse Note Order experiments. The graphs show quantile box plots with the median, 25th and 75th quartiles indicated. Median lines are in boldface. The dashes represent either the 10th or 90th quantiles, depending on the direction of the skew. The range of the remaining points are designated by the whiskers. Graph **b** does not have boxes because the majority of values are zero. Significant values between pre-and post-playbacks within an experiment are indicated with an asterisks symbol. **a** Number of single calls. **b** Number of warble duets. **c** Distance to the speaker (m)

Table 2 Differences in responses to the two playback treatments in the Reverse Sex Order and Reverse Note Order experiments

Variables	Reverse Sex Order				Reverse Note Order			
	Normal median (95 % CI)	Broken syntax median (95 % CI)	Z statistic	P value	Normal median (95 % CI)	Broken syntax median (95 % CI)	Z statistic	P value
Single calls	1.4 (1.4–13.1)	1.0 (−3.7–39.4)	2.0	0.93	1.8 (5.1–39.3)	1.0 (0.2–8.3)	34.0	0.08
Growls	1.0 (0.3–3.2)	1.0 (−1.9–10.9)	1.5	0.81	1.0 (0.7–1.6)	1.0 (0.9–1.2)	0.5	1.0
Warble duets	1.0 (0.9–1.6)	1.0 (0.7–1.4)	1.0	0.94	1.0 (0.8–2.2)	1.0 (0.7–1.3)	5.5	0.31
Duets	1.2 (1.0–2.0)	1.0 (0.8–2.8)	4.5	0.77	1.0 (0.9–2.3)	1.0 (0.9–1.7)	10.0	0.55
Distance to the speaker (m)	0.7 (0.5–0.9)	0.9 (0.4–0.9)	1.0	0.97	1.0 (0.5–0.9)	1.0 (0.5–0.9)	2.0	0.84
Latency to approach the speaker (s)	*73.5 (51.5–104.7)*	*300 (114.2–257.8)*	*18.5*	*0.21*	*75.0 (84.1–164.1)*	*300 (147.2–238.2)*	*19.0*	*0.15*

Median values and 95 % confidence intervals for the mean are presented. Z values are from Wilcoxon signed-rank tests and $N = 16$. No values are significant. Median ratios of response = plain text. Medians calculated with raw values = italic

Discussion

We predicted that pairs would respond less to the two types of broken syntax playbacks than to normal playbacks. This prediction was not supported: pairs responded strongly to all duet playback treatments, primarily with rapid approaches to the speaker, and there were no significant differences between normal duets and broken syntax duets in either experiment. A post hoc analysis in which we combined data from the two experiments did detect a pattern of longer latencies to response after broken syntax duets than normal duets. These results suggest that yellow-naped amazons can perceive a difference between duets with broken and normal syntax, but that they generally respond to duets regardless of whether their syntax is normal or broken. Thus, in at least one context, a simulated territorial incursion by another pair, parrots respond to duets with broken syntax as if they pose an equivalent threat as normal duets. These uniformly strong responses contrast with the graded responses seen in a previous experiment in which territorial pairs responded strongly to playbacks of duets from the same site with rapid approaches and aggressive growls and less strongly to duets from different sites within the same dialect and not at all to duets from a different vocal dialect (Wright and Dorin 2001).

The uniformity of response to playbacks in these experiments raises a question: if pairs perceive a difference between playback treatments, as suggested by the difference in latency, then why are responses still strong to the broken syntax treatments? Possible explanations include (i) syntax is unimportant for duet function, (ii) syntax plays a different role in duet function than we hypothesized, or (iii) syntax is more important in contexts different from the territorial incursions we simulated with playback experiments (e.g., pairs assess features other than syntax when determining how to respond to potential intruders). The

first interpretation is a possibility and cannot be excluded based on our data, but we believe it is unlikely for the following reason; if syntax was unimportant, we would expect much higher levels of variation in the structure of syntactic rules than observed. Instead, syntax has been demonstrated to be stable within a dialect (Dahlin and Wright 2009) and appears to be stable across different dialects (Dahlin and Wright unpublished data). Syntactical stability may occur through at least two mechanisms. One is that yellow-naped amazons have innate templates for syntax, as has been demonstrated in species such as song sparrows and swamp sparrows (Marler and Peters 1977; Marler and Sherman 1983, 1985; Marler and Pickert 1984). Alternatively, syntax may be learned, but constancy of rules is maintained through stabilizing selection that reduces the degree of variation produced by copying errors (Nottebohm 1972; Slater 1986; Nowicki et al. 2001).

Regardless of the mechanism, the fact that syntax appears to be stable across dialects lends support to the idea that syntax is functionally important. This brings us to the second possibility, which is that syntax in yellow-naped amazons may not function in the manner we hypothesized. We hypothesized that syntax allows yellow-naped amazons to combine discrete calls into meaningful sequences. Another possibility is that the degree of coordination (e.g., timing of notes) may be more important to receivers than the manner in which notes are combined. Thus, some rules may simply provide a means for pair members to coordinate their calls. If this second possibility holds, then simply switching the note order would not cause receivers to respond differently. Another possibility is that syntax as a composite whole may have a species recognition function, and our experimental procedure of disrupting only one rule at a time may not have been sufficient to impede that function.

The third possibility is that syntax is critical to certain contexts in which duets are used, but that those contexts
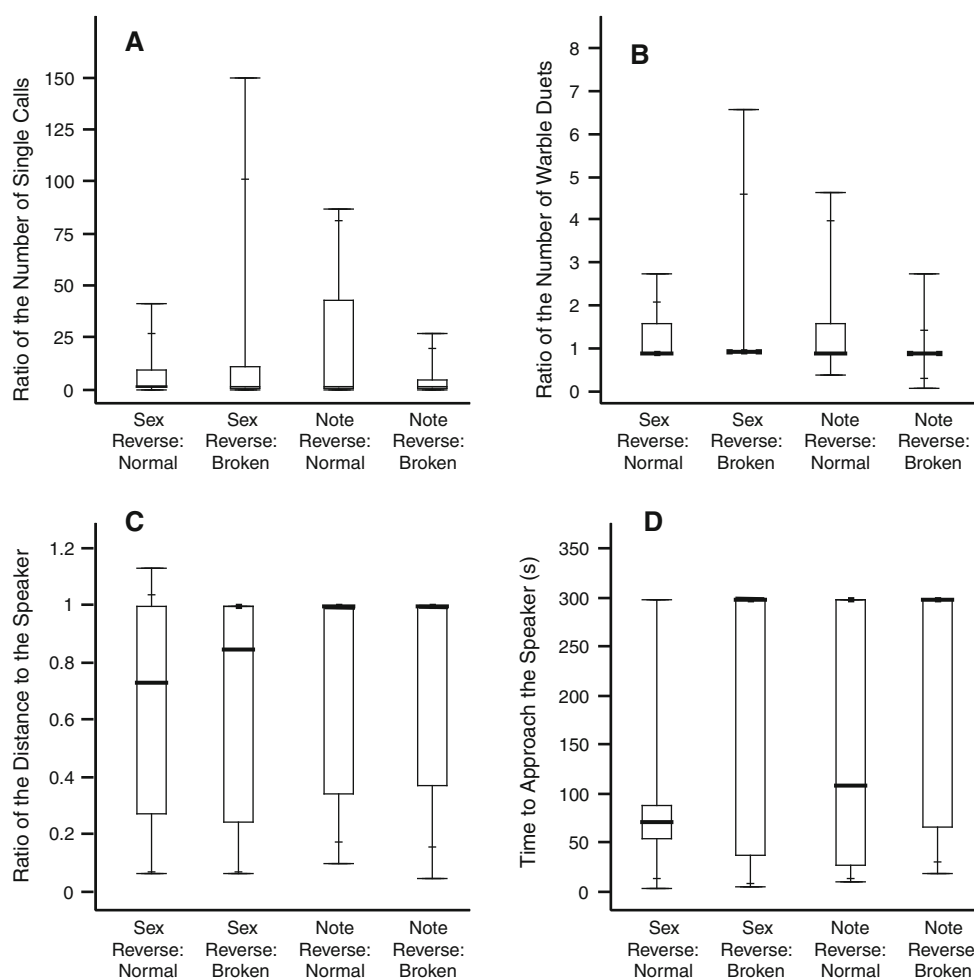
Fig. 3 Responses to playbacks for the Reverse Sex Order and Reverse Note Order experiments for the two treatments, normal syntax and broken syntax. The graphs show quantile box plots with the median, 25th and 75th quartiles indicated. Median lines are in boldface. The dashes represent either the 10th or 90th quantiles, depending on the direction of the skew. The range of the remaining points are designated by the whiskers. Some graphs lack boxes because the majority of points are at a single value. **a** Graph of the ratios of response (Post + 1/Pre + 1) for the number of single calls. **b** Graph of the ratio of results for the number of warble duets. **c** Graph of the ratio of response for the distance to the speaker (initially measured in meters). **d** Graph of the latency to approach the speaker using raw data. When latency to approach the speaker was compared between treatments in each of the individual experiments, there was no significant difference. An analysis of data combined across the two experiments indicated that pairs took significantly longer to approach the speaker after broken syntax playbacks than after normal duets. Otherwise, there were no significant differences between normal and broken syntax duets for the variables shown

were not simulated by our playback experiment. Our experiments simulated the incursion of a strange pair onto the subject pair's territory, which tested how the pairs initially detect and then respond to the signals of intruders. If the costs of ignoring an intrusion are very high for pairs, then they may rely on more simple cues than syntax when determining whether to initiate a response. We hypothesize that the mere presence of duet notes may have been sufficient to warrant an aggressive response by pairs. In previous experiments, playbacks of same-sex solos (notes from one sex only) elicited aggressive responses that were similar in strength to duet playbacks (Dahlin and Wright 2012), while playbacks of duets from different dialects did

not elicit aggressive responses (Wright and Dorin 2001). These experiments suggest that birds giving any form of local duet notes, regardless of their organization, may indicate a potential territorial threat, while non-local birds can be safely ignored. Syntax may be more critical to duet function during other contexts such as formation of pair bonds, maintenance of territories, or in contests with persistent usurpers.

Aggressive responses to playbacks of signals with broken syntax have also been observed in another species, the swamp sparrow. In this species, territorial males responded aggressively to playbacks of songs with both normal and broken syntax (Nowicki et al. 2001). In contrast,

non-territorial females distinguished between the two treatments and gave less copulation solicitation displays in response to songs with broken syntax than to normal songs (Nowicki et al. 2001). Thus, in both yellow-naped amazons and swamp sparrows, birds responded to signals with broken syntax when they were used in a territory maintenance and defense context, while in swamp sparrows, birds were more discriminating in a mating context. These differences in response to playbacks can be understood via signal detection theory and optimal decision making, in which animals change their decision rule based on the context (Bradbury and Vehrencamp 1998). Animals selecting a mate should be choosy because it can be costly to select either a poor quality mate or a member of another species, thus during mate selection, animals would be predicted to only respond to signals with accurate syntax. Alternatively, animals defending their territory have more to lose by underestimating an opponent than by over-responding, as an inappropriately weak response could result in a loss of territory; in this context, animals would be predicted to consistently overestimate signaler quality. We expect that initial responses to potential intruders would be especially aggressive, and adjustment may occur as animals have more time to evaluate intruders.

In summary, the generally strong responses of yellow-naped amazons to playbacks of both normal and broken syntax duets appear to fit the predictions for optimal decision making in a territory defense context. However, longer latencies to approach the speakers after playbacks with broken syntax do suggest that pairs attend to changes in duet syntax. Further experiments using alternative playback designs could clarify the role of syntax in the function of these complex signals.

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