



RESEARCH PAPER

Duet Function in the Yellow-Naped Amazon, *Amazona auropalliata*: Evidence From Playbacks of Duets and Solos

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Abstract

The question of why animals participate in duets is an intriguing one, as many such displays appear to be more costly to produce than individual signals. Mated pairs of yellow-naped amazons, *Amazona auropalliata*, give duets on their nesting territories. We investigated the function of those duets with a playback experiment. We tested two hypotheses for the function of those duets: the joint territory defense hypothesis and the mate-guarding hypothesis, by presenting territorial pairs with three types of playback treatments: duets, male solos, and female solos. The joint territory defense hypothesis suggests that individuals engage in duets because they appear more threatening than solos and are thus more effective for the establishment, maintenance and/or defense of territories. It predicts that pairs will be coordinated in their response (pair members approach speakers and vocalize together) and will either respond more strongly (more calls and/or more movement) to duet treatments than to solo treatments, or respond equally to all treatments. Alternatively, the mate-guarding hypothesis suggests that individuals participate in duets because they allow them to acoustically guard their mate, and predicts uncoordinated responses by pairs, with weak responses to duet treatments and stronger responses by individuals to solos produced by the same sex. Yellow-naped amazon pairs responded to all treatments in an equivalently aggressive and coordinated manner by rapidly approaching speakers and vocalizing more. These responses generally support the joint territory defense hypothesis and further suggest that all intruders are viewed as a threat by resident pairs.

Introduction

Vocal signals mediate many aspects of animal behavior, so it is important to understand the adaptive value and significance of those signals. Traditionally, research on signal function and evolution has focused on signals produced by an individual (Bradbury & Vehrencamp 1998; Searcy & Nowicki 2005). Some vocal signals, however, are produced by multiple individuals: such signals pose new questions concerning signal production, function and evolution (Hall 2004, 2009; McGregor 2005). For example,

jointly produced signals are presumably more difficult to create because they require spatial and temporal coordination, increased attentiveness and potentially more practice by participants (Hall 2009). An important question, then, is what benefits do animals gain from participating in joint signals that outweigh these costs?

One class of joint signals are vocal duets, which are acoustic displays produced by two individuals who coordinate their vocalizations in a temporal manner (Thorpe 1972; Farabaugh 1982; Hall 2004). Over 400 avian species (Farabaugh 1982; Hall 2004,

2009), many insects (Bailey 2003) and several mammals (primarily gibbons) give duets (Mitani 1985). Choruses, which involve more than two individuals, occur as well but appear to be less common than duets (Seddon & Tobias 2003; Mann et al. 2006; Bradley & Mennill 2009a). Numerous hypotheses have been proposed to explain why animals give duets; duets can be either cooperative, conflict-based or a mix of both, and may be directed internally (to one's partner) or externally to other conspecifics (Hall 2004, 2009). For example, internally directed duets may allow animals to maintain the pair bond and signal commitment (Thorpe 1963; Wickler & Seibt 1980; Smith 1994; Elie et al. 2010), identify and localize their mate (Thorpe 1963; Mays et al. 2006), or ensure reproductive synchrony (Elie et al. 2010). Externally directed duets can allow animals to cooperatively maintain and defend territories (Radford 2003; Logue 2005) or engage in a conflict-based function such as mate guarding (Levin 1996a,b; Tobias & Seddon 2009).

Of the many hypotheses, two that have received more attention in the literature are the joint territory defense hypothesis and the mate-guarding hypothesis (for reviews see Douglas & Mennill 2010; Hall 2009; Logue 2005). The joint territory defense hypothesis suggests that cooperative duets are more effective for the defense of territories than solos because they indicate a well coordinated pair committed to joint territory defense (Seddon & Tobias 2003; Bradley & Mennill 2009a). Duets may also be used to establish and maintain territories; these additional functions can be considered to fall under the umbrella of the joint territory defense hypothesis. Alternatively, the mate-guarding hypothesis suggests that signalers duet to illustrate their mated status, to discourage rivals, and possibly to prevent their mate from communicating with potential alternative extra-pair partners (Levin 1996a,b; Mulder et al. 2003; Grafe & Bitz 2004; Hall 2004, 2009; Tobias & Seddon 2009).

One technique that can effectively test both these hypotheses is the use of playback experiments in which three types of stimuli are broadcast to resident pairs: duets, male solos, and female solos (Levin 1996b; Grafe & Bitz 2004; Fedy & Stutchbury 2005; Marshall-Ball et al. 2006; Bradley & Mennill 2009a; Douglas & Mennill 2010). The joint territory defense hypothesis gives rise to the prediction that pair members would respond to playbacks in an aggressive and coordinated manner, by approaching speakers together, remaining in close physical proximity and/or vocalizing together (Hall & Peters 2008). The

relative strength of the response to different types of stimuli has received different predictions, however. Douglas & Mennill (2010) suggest that pair members would respond more strongly to duets than solos, although Benedict (2010) suggests that pair members might respond strongly toward all intruders when jointly defending a territory. Following Benedict (2010), we argue that either type of response would support the joint territory defense hypothesis and would be easily distinguished from a mate-guarding response. If duetting intruders are perceived as more threatening than solo singers, then, individuals will respond more strongly to duets than to solos. If all intruders are considered threatening, then individuals should respond equally strongly to duets and solos. In contrast, the predictions derived from the mate-guarding hypothesis are that pair members will respond in an uncoordinated manner to playbacks. In particular, this hypothesis predicts that individuals will respond more aggressively (e.g. with more vocalizations and approaches) in response to same-sex signals than to duets to deter those solo intruders from gaining access to their mate. Lastly, the rates at which males and females initiate duets can also differentiate between the hypotheses. Herein we follow Hall (2009) in using the term 'initiate' to indicate the first pair member to vocalize and 'answer' to indicate the pair member who responds and thereby turns a solo into a duet. By these terms, the joint territory defense hypothesis predicts that males and females will initiate duets at equal rates in response to all treatments, whereas the mate-guarding hypothesis predicts differences in initiation rates, with more female initiation in response to female solos and more male initiation in response to male solos.

Support for the joint territory defense hypothesis in the form of a strong and coordinated pair response to duet playbacks has been found in many species including black-bellied wrens, *Thryothorus fasciatoventris* (Logue & Gammon 2004), California towhees, *Pipilo crissalis* (Benedict 2010), white-bellied antbirds, *Myrmeciza longpipes* (Fedy & Stutchbury 2005), purple-crowned fairy-wrens, *Malurus coronatus* (Hall & Peters 2008), North Island kokako, *Callaeus cinereus* (Molles & Waas 2006), and magpie-larks, *Grallina cyanoleuca*, (Mulder et al. 2003). Support for the mate-guarding hypothesis is more limited, but in several species either both residents responded more strongly to same-sex solos than duets (e.g. sub-desert mesites, *Monias benschi*; Seddon et al. 2002), or the individual guarding their mate responded more strongly to same-sex solos (e.g. bay wrens,

Thryothorus nigricapillus; Levin 1996b). Duets in some species also appear to have multiple functions, as in tropical boubous, *Laniarius aethiopicus*, in which duets appear to function in both territory defense and mate guarding (Grafe & Bitz 2004). In summary, current evidence, the majority of it from passerines, indicates that duets have different functions in different species. Further insight into the generality of the joint territory defense and mate-guarding hypotheses can be gained by conducting more experiments using the duet/solo playback methodology in other taxonomic groups.

The yellow-naped amazon, *Amazona auropalliata*, is an ideal species for the purpose of investigating the joint territory defense and mate-guarding hypotheses as they give complex vocal duets at nesting territories that are maintained throughout the year (Wright & Dorin 2001; Wright & Dahlin 2007; Dahlin & Wright 2009). Parrots also represent a novel group for the study of duets. Yellow-naped amazons give two types of duets; primary duets, which we will hereafter refer to as 'duets', and warble duets. Both duet types consist of sex-specific calls that are repeated in an antiphonal fashion by males and females. Duets are given frequently, whereas warble duets appear to be reserved for highly aggressive interactions (Wright 1997). Both males and females can initiate duets and do so at equal rates (Wright & Dahlin 2007). Male and female solos that consist of the appropriate sex-specific duet notes are given occasionally but are less common than complete duets. Calls given outside duets do not appear to be sex specific (C. R. Dahlin and T. F. Wright, unpubl. data). Duets have a number of syntactic rules that organize the timing and structure of calls, but within those constraints, duets vary in length and note composition both within and between pairs (Wright & Dahlin 2007; Dahlin & Wright 2009). Pairs give duets year-round, although rates are highest in Jan and Feb, at the beginning of the nesting season (C. R. Dahlin and T. F. Wright, unpubl. data). Yellow-naped amazons also exhibit geographically distinct dialects (Wright 1996) that are temporally stable (Wright et al. 2008) and extend to pair duets (Wright 1997). A previous experiment revealed that pairs respond more strongly to same-dialect duets than to different dialect duets, indicating that duets from another dialect are perceived as less threatening (Wright & Dorin 2001).

Previous observations in yellow-naped amazons led us to expect that duets play a role in territory establishment and maintenance, rather than active territory defense (i.e. when duets are given as an

immediate response to intruders). In a manner similar to male songbirds, pairs of yellow-naped amazons often engage in extensive counter-duet bouts with neighbors and intruding pairs, and appear to handle most territory disputes by counter-duetting, with only rare occasions of physical aggression (Wright 1997). When a foreign pair intrudes onto a resident's territory, the residents typically approach the intruders and give growls (an aggressive vocalization) but do not typically increase their duetting rate (C. R. Dahlin and T. F. Wright, unpubl. data). In a previous playback experiment in which duets from different dialects were presented to pairs, residents also responded aggressively by approaching speakers but did not give more duets (Wright & Dorin 2001).

Although these observations suggest a role for duets in territory establishment and maintenance, experimental tests of this hypothesis and alternative functional hypotheses are lacking. Herein we present the results of a playback experiment in which we tested the joint territory defense and mate-guarding hypotheses using presentations of three types of playback stimuli to territorial pairs: duets, male solos, and female solos. Duet playback stimuli consisted of both male and female calls and simulated an intrusion of a pair onto the territory. Solo playback stimuli consisted of duet calls from one sex, and simulated the intrusion of a single individual onto the territory. A coordinated response, equal duet initiation rates, and either a more aggressive response to duet playbacks or an equally strong response to all playbacks would support the joint territory defense hypothesis. An uncoordinated response (i.e. only one bird approached the speaker or pair members approached at different times), differences between male and female duet initiation, and a weaker response to duets than to same-sex solos would support the mate-guarding hypothesis.

Methods

Site and subjects

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. Our subjects consisted of 17 mated pairs of yellow-naped amazons. All 17 pairs had established territories at one of those sites, which ranged in size from 1.1 to 8.0 ha, with a $\bar{x} \pm \text{SE}$ of $3.9 \text{ ha} \pm 0.6$ (C. R. Dahlin and T. F. Wright, unpubl. 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, allofeeding by males and copulations. Although yellow-naped amazons are sexually monomorphic in size and plumage, individual differences in plumage patterns coupled with observations of reproductive behavior allowed us to identify the sex of vocalizing birds (C. R. Dahlin and T. F. Wright, unpubl. data). We conducted all playbacks between Feb. 2 2006 and Mar. 13 2006. This period corresponds to the pre-laying, incubation and chick rearing stages, although there is considerable asynchrony in breeding between pairs.

Playback experimental design

Playbacks consisted of three treatments; (1) Duets (primary duet with male and female calls), (2) Male solos (male calls only) and (3) Female solos (female calls only) (Fig. 1). We created duet exemplars using duets from 16 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 to 2002 confirm that duet form is temporally stable over multiple years (Wright & Dahlin 2007; Dahlin & Wright 2009) as

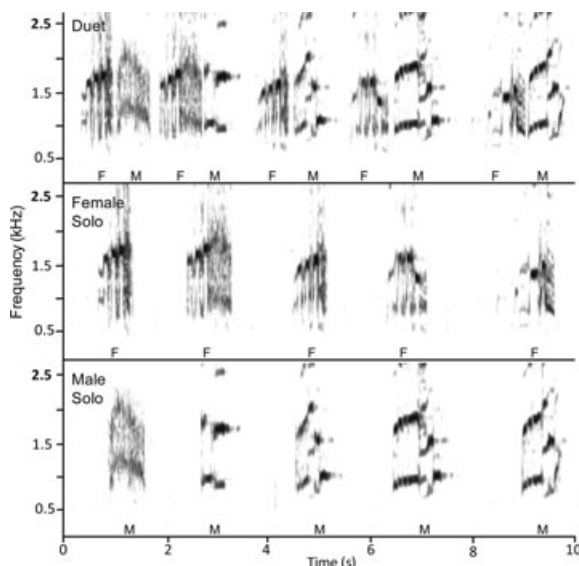


Fig. 1: Spectrograms of duet, female solo and male solo playback stimuli. The duet stimulus is a complete duet with both male and female calls, whereas the solo stimuli consist of the calls of a single sex extracted from the same duet. When creating the solo stimuli, we maintained the time intervals between the calls.

is territory maintenance by specific pairs (C. R. Dahlin and T. F. Wright, unpubl. data). We digitized calls by playing video tapes on a SONY Hi-8 player (model GVD-200) (SONY Corporation, Foster City, CA, USA), running the sound through an i-Mic (Griffin Technology, Nashville, TN, USA) into a Macintosh Power PC G5 computer and digitizing at 44 kHz and 16 bits in Raven 1.2.1 (Cornell Lab of Ornithology, Ithaca, NY, USA). We created spectrograms in Raven following Dahlin & Wright (2009). We scored calls as male and female by following previously defined syntactical rules (Wright & Dorin 2001; Wright & Dahlin 2007; Dahlin & Wright 2009). We amplified calls when necessary to standardize the peak amplitude of duets and solos. Duets were also edited for total length, such that duet exemplars consisted of 3–5 calls of each sex (6–10 calls total), and solo exemplars consisted of 3–5 single male or female calls (Fig. 1). Solos thus contained half as many calls as duets.

We selected three high quality duets (e.g. low levels of background noise and non-overlapping calls) from the same pairs and the same calling bouts to be used as a set of stimuli for playback presentation. These three duets were edited to create a set of three duet stimuli and further edited by removing the notes of one sex or the other to create a set of three male solo stimuli and a set of three female solo stimuli. These stimuli sets were used in a matched reciprocal design (Wright & Dorin 2001) such that one subject pair would receive a duet stimuli set from pair A and a male and female solo stimuli set from pair B, whereas a second focal pair would receive duet stimuli from pair B and solo stimuli from pair A. Four of the pairs from which we recorded duet stimuli were also used as subjects in the study. The number of subjects exceeded our stimulus pairs by one, so to compensate we created two sets of stimuli from a single pair, each of which used three different duets. 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. The subject pairs were never played their own duets.

Playback presentation

We conducted playback trials on subjects' territories between 5:00 AM and 8:00 AM, when birds are most active on their territories. We broadcast stimuli from speakers hung in trees adjacent to the nest tree; if we did not know the exact location of a nest, we placed speakers near focal trees where we had observed

intensive pair activity such as frequent duetting. The distance from the speaker tree to the nest or focal tree ranged from 10 to 54 m, with a mean of 30.6 m; this distance varied because the parrots nest in pasture-land with scattered trees. We began a playback trial once we had visually confirmed that the pair was present within their territory.

Each trial consisted of one duet treatment and one solo treatment, which we broadcast from two different MegaVox Pro wireless speakers (Anchor Audio, Carlsbad, CA, USA) and a Macintosh PowerBook G4 laptop (Apple, Cupertino, CA, USA). After 3–5 d we exposed pairs to a second duet treatment and the remaining solo treatment. We randomized the order of presentation for trial 1, and reversed that order for trial 2. The duet and solo treatments were broadcast from two speakers placed in different trees, with the solo stimuli broadcast from one speaker and the duet broadcast from the other. This design represents a compromise between the number of treatments and the number of subjects that could be included during a single breeding season.

Each playback treatment consisted of a 5 min baseline pre-period and a 5 min post-playback period that included stimuli playback. We conducted playbacks in a semi-interactive fashion to simulate natural calling patterns (Wright & Dorin 2001; Vehrencamp et al. 2003). If pairs responded vocally to a playback stimulus we immediately broadcast another stimulus, whereas if pairs did not respond we waited 60 s before broadcasting another exemplar until all three stimuli in a set were broadcast. Thus, the maximum length of the playback period was 3 min. We began the baseline pre-period for the second treatment at the end of the post-period of the first treatment. We video and audio-recorded the bird's responses using a tripod-mounted Canon Optura 50 digital video recorder and a Sennheiser directional microphone (model ME67; Sennheiser, Wedemark, Germany).

Data and analyses

We collected three types of data from trials: (1) vocalization data, which consisted of the number of single calls, number of growls (an aggressive type of single call), number of duets, number of warble duets, the number of duets initiated by males, and the number initiated by females, and the average length of duets (as calculated by averaging the total number of calls given in the first five duets), (2) temporal data, including the latency to first movement and the latency to near approach to the

speaker, both measured in seconds (we considered a near approach to be within the same tree as the speakers or within 10 m of the speaker) and (3) position and coordination data, including the nearest approach of pair-members to the speaker (measured in meters), and the proximity of pair members to one another (scored as yes/no: were pair members in the same tree or <10 m apart?). We collected vocalization data by watching trial videos on a JVC high-resolution monitor (model TM-H17-00G), and digitizing data using the methods described above, with the exception that tapes were played on a Canon Optura 50 digital video recorder rather than on a SONY Hi-8 player. We scored temporal data during the trial and confirmed times while watching the videos. We measured location data in the field using a 100 m tape measure immediately after trials. We conducted all statistical analyses in JMP 7.0 (SAS Institute Inc, 2007).

Control trials

Heterospecific stimuli control

We conducted heterospecific stimuli trials between Feb. 11 and Mar. 17 of 2007, while conducting another playback experiment, to control for the presentation of natural sounds over loudspeakers near nests. We broadcast calls of two heterospecific species, white-fronted amazons, *Amazona albifrons* and white-throated magpie jays, *Calocitta formosa*. We followed an identical playback protocol as described above, except that each pair of subjects was only exposed to one treatment (either *A. albifrons* or *C. formosa*). We conducted 11 heterospecific control trials, each with a different subject pair.

Length control

Duet exemplars typically contained more individual calls than solo exemplars, so we conducted control trials with six pairs of birds between Feb. 19 and Mar. 14 2006 to test whether the length of the exemplar, rather than the type of treatment, affected the subject's responses. We randomly selected female rather than male calls for the solo treatments. Our length controls thus consisted of three treatments; short female solos with four calls, long female solos with eight calls, and short duets with four calls. These lengths fall within the observed range of calls in duets. Each trial consisted of either a short duet or short solo treatment paired with a long solo treatment. We conducted length trials in the same manner as described for the experimental trials, with the

exception that playback stimuli consisted of two rather than three exemplars. Five of the six pairs included in these control trials were also subjects in the main experiment.

Statistical analyses and considerations

We examined the distributions of all variables and used log transformations where necessary. We elected to use parametric analyses on transformed data rather than nonparametric analyses because of (1) the greater power of the parametric analyses, (2) their general robustness to minor deviations from normality, and (3) because they allowed us to use a repeated-measures ANOVA with a random effect of subject pair that took advantage of our experimental design in which we broadcast all three treatments to each subject pair (Zar 1999). We repeated all analyses using nonparametric Wilcoxon (to compare pre- and post-periods) and Kruskal–Wallis tests (to compare treatments) and obtained qualitatively similar results. We did not employ Bonferroni corrections due to concerns that such corrections can result in severely reduced power in small data-sets (Cabin & Mitchell 2000; Nakagawa 2004; Garamszegi 2006).

Overall playback response

We first assessed the overall response of pairs to playback stimuli by comparing pre- and post-period values. We analyzed continuous data using repeated-measures ANOVAs, in which Period (pre vs. post) was a fixed effect and Pair was a random effect nested within Period. The continuous variables were: (1) number of single calls, (2) number of growls, (3) number of duets, (4) number of warble duets, (5) duet length, (6) number of male and female initiated duets, and (7) male and female proximity to the speakers. We analyzed pair member proximity, a nominal variable, using a likelihood chi-squared test.

Comparisons among treatments

To control for base-line levels of subject behavior while analyzing behavioral data, we calculated ratios of the data in which we divided the post-period by the pre-period data. Prior to calculating the ratios we added a value of one to all numerators and denominators, to avoid division with zeroes. Although the addition of 'one' changed ratios slightly, we felt that it was the most effective way to account for base-

line 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 ratio variables and the difference variables were qualitatively similar.

We initially tested for a within-day order effect, and then compared continuous variables with repeated-measures ANOVAs, in which Playback Treatment was a fixed effect and Pair was a random effect nested within Playback Treatment. We again analyzed pair proximity using a likelihood chi-squared test. In addition to the variables above we analyzed male and female latency to first movement and male and female latency to close approach (<10 m), calculated in seconds. Birds that did not move were assigned 300 s, which was the maximum duration of the post-period. We compared treatments using post-/pre-ratios for all variables except duet length (because many pairs did not duet during part of the trial) and latency (which was only examined after playbacks).

Sex specific responses

In addition to independently examining how males and females responded to the playback treatment, we also analyzed whether there were general differences in the strength of the response between males and females using repeated-measures ANOVAs. We examined the following variables; (1) number of initiated duets (ratio post-/pre-), (2) latency to first movement, (3) latency to near approach and (4) proximity to the speaker (ratio post-/pre-).

Analysis of control trials

For the heterospecific control trials we tested whether or not birds responded to the playbacks by comparing their behavior pre-playback and post-playback using matched-pair *T*-tests on the log-transformed data. For the length control trials we tested whether or not bird's responses differed between treatments by: (1) calculating post-/pre-ratios of continuous data, (2) log transforming the variables, and (3) comparing treatments using ANOVAs. We did not use a repeated-measures design because the sample size was too low (three short duets, three short solos and six long solo replicates). We excluded the response variable duet length from analysis because few duets were given and pair proximity because all pairs were in close proximity during all trials.

Results

Controls

Playbacks of heterospecific trials failed to elicit any responses from the birds; there were no differences between pre- and post-portions of the trials in terms of the number of vocalizations birds gave or their proximity to the speakers ($T_{1,10}$ range 0.0–1.5, $1.0 > p > 0.16$). Pairs also did not respond differently to playbacks of varying length; there were no significant differences among length control treatments for any response variable ($F_{2,9}$ range 0.45–1.49, $0.65 > p > 0.25$). The lack of response to control trials contrasts sharply with the responses pairs gave to conspecific playbacks in this experiment and to another playback experiment conducted in 2007, during the same year as the control trials (C. R. Dahlin and T. F. Wright, unpubl. data).

Overall playback response

Birds approached the speakers and gave more growls, marginally more single calls and marginally more warble duets during the post-playback period than during the pre-playback period across all playback treatments (Table 1, Figs 2 and 3). There were also significant effects of the subject pair (Table 1). There was no difference in the proximity of pairs to one another between the pre and post-portions of the trial (pre-proximity yes = 94%, post-proximity yes = 92%, $\chi^2_1 = 0.12$, $p > 0.05$).

Comparisons between treatments and sex specific responses

There were no differences between the duets, female solo, and male solo treatments for any vocalization or movement variables (Table 2, Figs 2 and 3). There were also no significant differences between treatments in the proximity of pairs to one another; pairs were perched in the same tree or <10 m apart more than 88% of the time ($\chi^2_2 = 2.07$, $p = 0.15$). Males and females were not significantly different in terms of their latency to approach, final proximity to the speaker or the number of duets they initiated (Table 3).

We did not observe consistent effects of the order of presentation within a day for either vocalization or temporal data (F value range: 0.98–1.62, $p > 0.05$). The two position measures did have significant order effects (female proximity to the speaker $F_{1,59} = 2.8$, $p = 0.007$, male proximity to the

speaker $F_{1,62} = 2.6$, $p = 0.01$), in that birds did not approach the speakers as closely in response to the second series of playbacks (Mean ratio of proximity to the speakers for both males and females \pm SE; first presentation = 0.6 ± 0.06 , second presentation = 0.8 ± 0.1). The order effect is a concern, because it indicated a possible habituation effect or general diminishment in movement responses to the second series of playbacks. We note, however, that we balanced the order of presentation across treatments within each pair, which should eliminate any bias due to an order effect. To ensure that the order effect did not qualitatively change the results, however, we also re-analyzed proximity to the speaker using data from the first set of playbacks for each pair only. The results were consistent with the larger data set, with no differences between treatments (F value range: 0.15–1.9, $p > 0.05$).

Discussion

Yellow-naped amazons responded to all three playback treatments with no detectable differences between duet and solo treatments. Pair members responded in a coordinated and aggressive manner to all playback treatments by approaching speakers together, perching near one another and giving more growls, and giving marginally more single calls, and warble duets. There were no differences in the strength of response between males and females. These coordinated and aggressive responses support the joint territory defense hypothesis rather than the mate-guarding hypothesis, which predicts uncoordinated, sex specific responses, particularly to solo songs.

Different authors have suggested alternative predictions for the responses of pairs to duets vs. solos under the joint territory defense hypothesis, with some predicting stronger responses to duets than to solos (Douglas & Mennill 2010) and others predicting equivalently strong responses to both types of stimuli (Benedict 2010). Our results are consistent with the second prediction, and are similar to results found in other species including the rufous-naped wren, white-bellied antbird and California towhee (Fedy & Stutchbury 2005; Bradley & Mennill 2009b; Benedict 2010), although contrasting with results from the plain wren and bay wren, which showed sex specific responses to solo song (Levin 1996b; Marshall-Ball et al. 2006). Strong responses to both duet and solo playback stimuli could indicate that both types of signals play a role in territory defense (Bradley & Mennill 2009b), but this seems unlikely

Table 1: Overall experimental response to duets and solos, with pre-playback and post-playback means shown

Variable	Pre- $\bar{x} \pm SE$	Post- $\bar{x} \pm SE$	Pair nested within Pre- vs. Post-		Pre- vs. Post-	
			F statistic	p-value	F statistic	p-value
Single calls	34.89 \pm 6.3	39.20 \pm 5.1	1.62 _{34,96}	0.034*	3.76 _{1,39.7}	0.06
Growls	0.09 \pm 0.1	0.48 \pm 0.2	2.75 _{34,96}	<0.0001*	4.47 _{1,37.4}	0.04*
Warble Duets	0.28 \pm 0.2	0.45 \pm 0.1	0.93 _{33,95}	0.579	4.05 _{1,38.9}	0.05
Duets	0.66 \pm 0.2	0.84 \pm 0.2	1.34 _{33,95}	0.14	0.87 _{1,37.0}	0.36
Duet length	7.79 \pm 0.5	7.61 \pm 0.5	0.83 _{24,16}	0.67	1.13 _{1,34.2}	0.29
Number of female initiated duets	0.55 \pm 0.4	0.67 \pm 0.2	1.25 _{33,95}	0.21	0.46 _{1,37.4}	0.50
Number of male initiated duets	0.17 \pm 0.1	0.14 \pm 0.1	0.83 _{33,95}	0.73	0.07 _{1,39.6}	0.79
Female proximity to speaker (m)	54.28 \pm 4.3	33.18 \pm 3.5	1.44 _{34,100}	0.08	9.73 _{1,39.6}	0.003*
Male proximity to speaker (m)	52.99 \pm 4.3	29.24 \pm 3.0	1.39 _{34,100}	0.11	17.9 _{1,39.9}	<0.0001*

Values are for repeated-measures ANOVAs. Significant values with an $\alpha < 0.05$ are denoted by *.

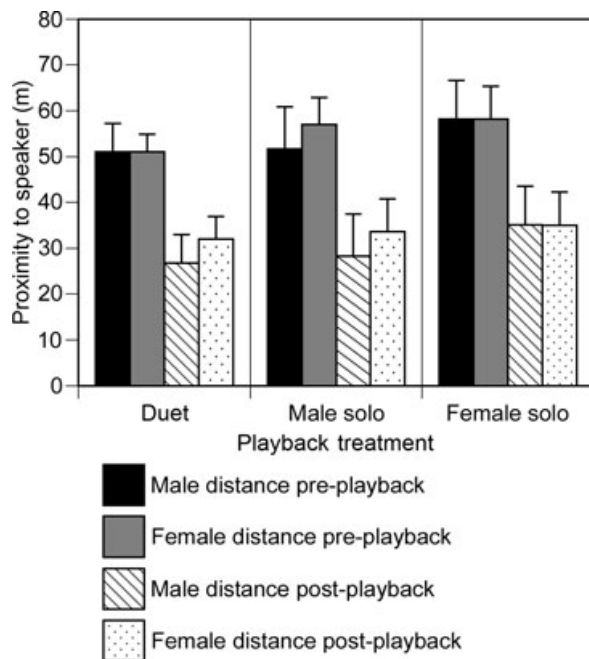


Fig. 2: The distance of males and females to the playback speaker during the pre- and post- portions of the trial in response to playbacks of duets, male solos, and female solos (notes from one sex only).

in yellow-naped amazons, who give solos infrequently. Instead, the parrots may over-respond to all potential threats, including solos, rather than risk losing their territory. This behavior is not unexpected given the likely value of territories, which pairs defend year round and re-use over multiple years (C. R. Dahlin and T. F. Wright, unpubl. data). This style of responding can be understood via the ‘smoke-detector principle’, which states that when the cost of responding to a threat is low compared to

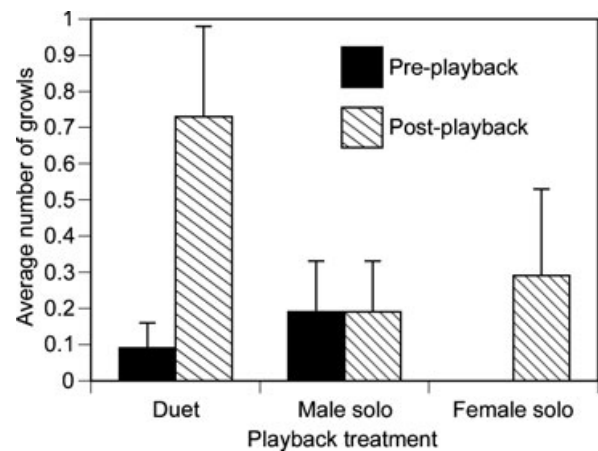


Fig. 3: Average number of growls given during the pre- and post- portions of the trial in response to playbacks of duets, male solos, and female solos (calls from one sex only).

the potential harm it prevents, the optimal system will have many false alarms due to receivers adaptively overestimating threats (Nesse 2001). This strong response may have been exacerbated by our playback design, which simulated intrusions onto a territory; alternative designs that simulated settlement by pairs or solo birds in new territories rather than intrusion onto established territories may have detected more subtle difference in responses to solos vs. duets.

Although the joint territory defense hypothesis typically assumes that duets function in active territory defense against intruders, in some species duets may play a greater role in the initial establishment and maintenance of territories. In these experiments, which simulated a territorial intrusion by pairs or solo birds, resident pairs responded with rapid

Table 2: Responses to the playback treatments; duets, male solos and female solos

Variable	Duet $\bar{x} \pm SE$	Male solo $\bar{x} \pm SE$	Female solo $\bar{x} \pm SE$	Pair nested within playback treatment		Playback treatment	
				F statistic	p-value	F statistic	p-value
Single calls	10.5 ± 4.1	7.7 ± 2.8	11.4 ± 5.6	1.46 _{49,16}	0.21	0.03 _{2,54.3}	0.97
Growls	1.60 ± 0.23	1.1 ± 0.14	1.3 ± 0.23	0.97 _{49,16}	0.56	2.01 _{2,56.6}	0.14
Warble duets	1.30 ± 0.10	1.5 ± 0.29	1.4 ± 0.27	1.07 _{49,16}	0.46	0.69 _{2,56.0}	0.51
Duets	1.40 ± 0.18	1.4 ± 0.37	1.1 ± 0.09	0.71 _{49,16}	0.82	0.31 _{2,58.9}	0.73
<i>Duet length</i>	7.30 ± 0.44	8.6 ± 1.3	7.1 ± 1.5	3.35 _{17,4}	0.13	0.94 _{2,18.4}	0.41
No. of female initiated duets	1.40 ± 0.20	1.4 ± 0.36	1.1 ± 0.13	0.69 _{49,16}	0.84	0.22 _{2,59.1}	0.80
No. of male initiated duets	1.10 ± 0.07	0.96 ± 0.08	1.03 ± 0.07	0.92 _{49,16}	0.61	0.79 _{2,57.0}	0.46
Male proximity to speaker	0.68 ± 0.06	0.72 ± 0.09	0.69 ± 0.09	0.72 _{49,16}	0.81	0.14 _{2,58.7}	0.87
Female proximity to speaker	0.73 ± 0.06	0.72 ± 0.09	0.69 ± 0.09	0.82 _{49,16}	0.71	0.15 _{2,57.8}	0.86
<i>Male latency to 1st movement</i>	240.1 ± 16.5	241.9 ± 27.0	244.9 ± 25.9	2.19 _{48,16}	0.04*	0.12 _{2,51.9}	0.89
<i>Female latency to 1st movement</i>	250.4 ± 15.9	263.7 ± 20.9	244.9 ± 25.9	1.44 _{48,15}	0.22	0.25 _{2,53.6}	0.78
<i>Male latency to near approach</i>	151.4 ± 20.5	164.7 ± 39.0	186.7 ± 31.0	0.98 _{48,16}	0.54	0.54 _{2,56.0}	0.59
<i>Female latency to near approach</i>	164.6 ± 21.0	209.1 ± 36.5	204.0 ± 29.7	0.85 _{48,16}	0.68	0.46 _{2,57.1}	0.63

Mean response values are shown for the duet, male solo and female solo treatments, with mean ratios of response (post/pre) in plain text, and means calculated with raw values in *italics*. Statistical values are for repeated-measures ANOVAs. No values are significant.

Table 3: Responses of males and females to playbacks for number of initiated duets, latency to first movement, latency to near approach and proximity to the speaker

Variable	Male $\bar{x} \pm SE$	Female $\bar{x} \pm SE$	Pair nested within sex		Sex	
			F statistic	p-value	F statistic	p-value
Avg no. of initiated duets	1.03 ± 0.0	1.29 ± 0.0	0.97 _{34,100}	0.51	0.53 _{1,42.4}	0.47
Proximity to the speaker (m)	0.69 ± 0.0	0.72 ± 0.0	1.18 _{34,100}	0.26	1.20 _{1,40.9}	0.28
<i>Latency to 1st movement (s)</i>	454.3	480.8	1.25 _{34,98}	0.20	0.91 _{1,40.6}	0.34
<i>Latency to near approach (s)</i>	277.6	308.3	0.88 _{34,98}	0.65	1.62 _{1,43.4}	0.21

Mean ratios of response (post + 1/pre + 1) = plain text, and means calculated with raw values = *italic*. No values are significant.

approaches, and increased numbers of growls and warble duets, rather than with increased numbers of pair duets. The different types of duets in yellow-naped amazons thus appear to have different functions; duets are likely used to establish and maintain territories, whereas warble duets are used for active territory defense against intruders. Growls may also be favored during active territory defense because they are uncoordinated and easier to produce while birds are moving, and they may also serve as an honest indicator of the pair's willingness to attack (Morton 1975). These responses were consistent with a previous playback study in the yellow-naped amazon, in which pairs also responded to duets by approaching the speakers and giving more aggressive calls, but not significantly more duets (Wright & Dorin 2001). They are also consistent with our observations of unmanipulated pair behavior. Territorial

pairs typically engage in daily duetting sessions in the absence of intruders, and will respond to the duets of neighboring pairs by counter-duetting in a manner analogous to territorial singing in male songbirds (Catchpole & Slater 1995). Documentation of seasonal patterns of duetting and counter-duetting would help clarify the precise function of duets in yellow-naped amazons, including the possibility of additional functions, such as pair bond maintenance, that could not be investigated given the constraints of our playback design.

Conclusions

Yellow-naped amazon behavior in response to playbacks of duets and solos supports the joint territory defense hypothesis rather than the mate-guarding hypothesis. The function of duets in yellow-naped

amazons thus appears to be consistent with many species that have been tested using playback experiments (Mulder et al. 2003; Logue & Gammon 2004; Fedy & Stutchbury 2005; Molles & Waas 2006; Hall & Peters 2008; Benedict 2010). Additional comparisons between species could prove useful in determining the extent to which duets are used in active territory defense against intruders rather than in the establishment and maintenance of territory boundaries.

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