SEX DIFFERENCES AND VOCAL FLEXIBILITY IN WILD PARROT

COMMUNICATION

A Dissertation

Presented to the Faculty of the Graduate School

of Cornell University

in Partial Fulfillment of the Requirements for the Degree of

Doctor of Philosophy

by

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January 2009

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Parrots are renowned in captivity for their vocal flexibility, and although studies of avian vocal learning focus largely on songbirds, there is some evidence that the majority of parrots may be more vocally flexible than many members of the songbird order. In addition, unlike the majority of most temperate songbirds, both male and female parrots produced learned vocalizations and often share a repertoire of calls, although anecdotal evidence from pet owners suggests that males may be the more vocally flexible sex. However, most of what we know about parrot vocal flexibility and sex differences in parrot communication comes from anecdotal evidence and very limited lab studies that have difficulty mimicking natural parrot social conditions. Thus, the purpose of this work was to investigate how wild parrots are using vocal flexibility during interactions with conspecifics, and how sex differences in communication are expressed in vocal interactions in general and vocal flexibility in particular.

I studied two geographically and phylogenetically distant parrot species, the Australian galah (*Eolophus roseicapillus*) and the neotropical orange-fronted conure (*Aratinga canicularis*) to address these issues. I conducted four playback experiments either to wild, free-ranging individuals or to wild-caught captives held temporarily in aviaries. Two of these experiments address how parrots are using and interpreting rapid, short-term vocal flexibility during their interactions and how this differs by sex. The other two experiments address more broadly how male and female parrots respond to male and female affiliative and aggressive calls.

This thesis demonstrates that in at least two species of parrots, males and females differ in how they rapidly modify their vocalizations during interactions with conspecifics. Despite sharing a repertoire of calls, both galahs and orange-fronted conures distinguish the sex of a caller based solely on acoustic cues, and males and females interact differently with conspecific callers, suggesting that the sex of interactants is a highly relevant factor even during interactions that do not seem to be primarily for the purpose of mate attraction. These experiments begin to shed light on the incredible intricacies of flexible parrot vocal communication.

BIOGRAPHICAL SKETCH

Judith C. Scarl was raised in Glen Cove, NY, and spent many happy days as a child collecting frogs, snakes, turtles, fireflies, caterpillars, katydids, and anything else that could fit into a 12"x36" terrarium. When she was not crawling through the mud after a delightfully slimy animal, she could be found on the soccer or softball fields, at the track, practicing the violin, or occasionally at the rifle range.

Judith graduated from Glen Cove High School in 1998. She attended Harvard University from 1998-2002 and graduated magna cum laude in psychology and biology. While at Harvard, Judith was a hooker for the Radcliffe Rugby Football Club, which was as exciting as it sounds, but less illegal. She was an orchestra manager, board member, and eventually the president of the Harvard-Radcliffe Gilbert and Sullivan Players, where she shared her love of animals by introducing Jonathan the Orchestra Monkey as a group mascot and the Presidential Yak as an encouraging presence. Judith also conducted undergraduate honors thesis research on cotton-top tamarins in the Primate Cognitive Neuroscience Laboratory, run by Marc Hauser.

Judith took a year after graduating to conduct field research on frogs in Panama, songbirds in Australia, and parrots in Costa Rica, before starting graduate studies in the Department of Neurobiology and Behavior at Cornell University in 2003. Her hobbies include motorcycle riding, rock climbing, dog fostering, and parrot harassing.

For my parents

Barbara Cohen and Donald Scarl

ACKNOWLEDGEMENTS

I owe many thanks to my advisor, Jack Bradbury, who trusted me to work on another continent with big pink biting birds, and who generously funded much of my parrot research. My committee members Tom Seeley, Elizabeth Adkins-Regan, Mike Goldstein, and Andre Dhondt provided helpful discussions on parrots, academia, and life in general, and for this I am grateful. Sandy Vehrencamp provided much-welcomed constructive criticism that vastly improved my scientific research.

The Department of Neurobiology and Behavior at Cornell is an intellectually rich and scientifically fostering environment, as well as just a generally friendly place to be. I would like in particular to thank faculty members Carl Hopkins, Joe Fetcho, Christiane Linster, and Kern Reeve for their friendship and encouragement. The NB&B graduate students, in particular Bernard Brennan, Lynn Fletcher, Maggie Kirkland Wray, Biz Turnell, and Chris Wilson provided stimulating discussions on all manner of topics, as did the BioNB Lunch Bunch discussion group. This department is held together by its amazing administrative assistants, and I would like to thank them for their support, particularly Terri Natoli. Francoise Vermeylen, the director of the Cornell Statistical Consulting Unit, taught me almost everything I know about statistics and finally succeeded in convincing me that SAS is not a big scary monster.

although I never would have believed this five years ago, I will always bear a fondness for the color pink.

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INTRODUCTION

Vocal flexibility, which is the ability to learn new vocalizations or modify existing ones, is a characteristic of several avian and mammalian species. Songbirds, for example, are well-known for their abilities to learn their songs (Marler 1970), and mammals such as dolphins (Janik 2000) and marmosets (Snowdon and Elowson 1999) also seem to be somewhat vocally flexible, even as adults. Of course, human vocal flexibility is well-documented, both in terms of children's language learning abilities (Oller 2000) but also in our ability to learn new words vary language use based on situational context (Perdue 1999; Hauser et al. 2002). In most vocally flexible systems that have been studied, including songbirds and humans, most attention has been paid to the initial process of learning a repertoire. However, acquiring a repertoire as a juvenile is not the only manifestation of vocal flexibility; several species are able to modify their vocal signals even after they've acquired a repertoire, and less attention has been paid to this vocal flexibility later in life.

Parrots are notorious for their vocal flexibility. Many parrots make extremely popular pets due to their ability to imitate human voices and household sounds, and laboratory studies demonstrate that parrots are vocally flexible both in reproducing human speech (Pepperberg 2000) and modifying their calls based on their social situations (Farabaugh et al. 1994; Hile et al. 2000). In addition, unlike the majority of songbirds, parrots are open-ended learners, which means that they can modify their vocalizations throughout their lives (Bradbury 2003). Vocal flexibility thus seems to be a skill that is highly developed in parrots. However, the fact that parrots are so vocally flexible and are such adept vocal learners also means that they can quite easily adapt their communication systems to their captive situations, and studying parrots in captivity has limited use when asking questions about parrot communication in the

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wild. Compared to another avian order that demonstrates vocal learning, the songbirds, wild parrot vocal communication has received scant scientific attention.

Another important aspect of a communication system is the relative role that males and females play. Often, sex differences in communicative behavior reflect pronounced differences in sex roles within the social system. While both male and female parrots produce vocalizations in most species, and the repertoire seems to largely overlap by sex, anecdotal evidence from captive birds suggests that in many species, males are more adept at modifying their vocalizations in captive settings. Despite this, much less is known about sex differences in wild parrot vocal structures or usages.

The purpose of this thesis was to investigate the communication system of wild parrots, focusing on parrot vocal flexibility and sex differences in parrot calls and parrot vocal behavior. I include four studies in this work:

1. <u>Rapid vocal convergence in an Australian cockatoo, the galah (*Eolophus roseicapillus*).</u> (J.C. Scarl and J.W. Bradbury, in press, *Animal Behaviour*.) Recent studies have demonstrated that one species of parrot, the orange-fronted conure, uses rapid, directional call modification during its interactions with conspecifics. Since many parrot species have similar social systems, similar selection pressures may exist on their communication systems. I conducted a study on a phylogenetically and geographically distant species of parrot, the galah (*Eolophus roseicapillus*) to determine whether other parrot species use this type of call modification, and to see whether there are sex differences in vocal modification behavior. If wild parrots use the ability to rapidly converge or diverge the acoustic structures of their calls as a mechanism of communication, this may explain the extraordinary vocal flexibility seen in captive parrots.

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2. <u>Subtle vocal sex differences influence behavior in an Australian cockatoo, the galah.</u> (J.C. Scarl, submitted, *Emu*.) In some monogamous, monomorphic species in which males and females share a repertoire, subtle acoustic differences between male and female calls exist. While male and female galahs share a complete repertoire of call types, my observations indicate that vocal behavior may differ more subtly by sex in this species. I conducted an experiment to determine how male and female galahs respond to three types of vocalizations produced by male and female conspecifics. In a largely monomorphic species with shared vocalizations, understanding subtle sex differences in communicative behavior may elucidate male and female roles in a parrot social system.

3. <u>Heightened responsiveness to female-initiated aggressive interactions in an Australian cockatoo, the galah (*Eolophus roseicapillus*)</u>. (J.C. Scarl, submitted, *Behaviour*.) Sex differences in defense against threat exist in many species, from responding more aggressively to same-sex conspecific intruders to a sexual division of labor in defense against heterospecific threats. While parrots generally do not defend large territories, galahs and many other parrots will defend a small area around their nest cavity during the breeding season. Both male and female galahs produce a Scree vocalization near potential nesting cavities, and I conducted an experiment to determine whether members of a male-female pair respond differently to male, female, and paired intruders.

4. <u>Sex-specific responses to vocal convergence and divergence of contact calls in orange-fronted conures (*Aratinga canicularis*)</u>. (T.J.S. Balsby and J.C. Scarl, 2008, *Proceedings of the Royal Society of London, Series B,* 275(1647), 2147-2154). With

evidence that convergence is a vocal technique used by at least two parrot species, and that subtle sex differences influence parrot communication, we conducted a study that focused on sex differences in response to rapid vocal modifications. The previous studies on rapid parrot vocal convergence have been sender-based, asking whether birds modify their calls in response to a stimulus. Our study asks the question from the receiver's perspective: how does a bird respond when its interaction partner directionally modifies its calls, and how does this response differ based on the sex of the subject and the sex of the interaction partner? This experiment aims to clarify how parrots are using convergent and divergent series of calls and attempts to address how birds interpret rapid directional call change.

These four papers document sex differences in parrot communication systems as well as explore the prevalence and functional relevance of rapid vocal modification, specifically with respect to sex.

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CHAPTER 1

Rapid vocal convergence in an Australian cockatoo, the galah (*Eolophus roseicapillus*)[1]

Abstract

There are several mechanisms for producing vocalizations that are similar to those of a conspecific, including song type matching during a vocal contest, group convergence on a signature call over time, or one-to-one matching of another individual's signature call. A novel category of conspecific matching has been described in a parrot, the orange-fronted conure (*Aratinga canicularis*), which exhibits rapid and directional modification of vocalizations over the course of a single vocal interaction. This study examined whether a geographically and phylogenetically distant parrot, the galah (*Eolophus roseicapillus*), employs similar rapid call modifications during contact call exchanges, and sought to better define the conditions under which wild parrots directionally modify their contact calls. In each trial, we interactively broadcast a single call exemplar recorded from wild galahs and recorded the vocal responses of nearby galahs. Temporal parameters of response calls converged on the stimulus over the course of an interaction. Frequency measures also showed convergence, although this effect was less pronounced. Male galahs were more vocally responsive overall, and birds tended to converge more closely on male stimuli over the course of an interaction. This experiment confirms that other parrots, in this case galahs, are capable of rapid, directional call modification, and we suggest that this vocal

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[1] Co-authored by Scarl, Judith C. and Bradbury, Jack W.

technique may be an efficient mechanism for mediating the fission-fusion social system that is characteristic of many parrot species.

Introduction

Producing a vocalization with acoustic features similar to another individual's call is a vocal technique used by several avian and mammalian species. Behavioural mechanisms of such conspecific vocal convergence divide into four major categories. In many species of passerine, territorial males match the song types produced by their neighbors during aggressive interactions (Beecher et al. 2000; Vehrencamp 2001). This matching is discrete and variable, since a bird with a similar repertoire can either choose to produce a matching or a non-matching song from its repertoire at any point in the interaction (Vehrencamp 2001). Since most passerines learn their songs during a sensitive period in development (Marler 1970), adults are limited to matching neighbors' songs that are already in their repertoire. Black-capped chickadees *Parus atricapillus* (Nowicki 1989), cardueline finches *Cardeulis sp.* (Mundinger 1970), pygmy marmosets *Callithrix pygmaea* (Snowdon and Elowson 1999), and captive budgerigars *Melopsittacus undulatus* (Hile et al. 2000; Hile and Striedter 2000) demonstrate a second category of vocal convergence in which changes in semi-permanent group affiliations are accompanied by progressive changes in vocalizations over days or weeks which lead to a shared call type between individuals. A third type of conspecific vocal convergence exists in bottlenose dolphins *Tursiops truncatus* (Janik 2000) and captive spectacled parrotlets *Forpus conspicillatus* (Wanker et al. 2005) in which individuals match the features of a conspecific's individually-unique contact calls during a single vocal interaction; this matching may serve to address (Janik 2000; Tyack 2003) or name (Wanker et al. 2005) a specific interaction partner. It is not known whether these interactions serve an aggressive or an affiliative function

(Janik 2000), and it is not clear whether this matching is caused by individuals discriminatingly producing existing signals in specific contexts, or whether they are modifying signal features at the time of the interaction.

There is some evidence that a Central American parrot, the orange-fronted conure *Aratinga canicularis*, may employ a fourth type of vocal modification that is characterized by continuous, directional call changes that rapidly and systematically lead to increased (Vehrencamp et al. 2003) or decreased (Balsby and Bradbury In preparation) similarity to an interaction partner's calls over the course of a single interaction. Unlike the one-to-one matching of calls exhibited by songbirds, dolphins, and captive spectacled parrotlets, orange-fronted conures produce sequences of calls that demonstrate trajectories of increasing or decreasing similarity. Systematic convergence and divergence of acoustic features may have different signal meanings to conures, and it has been suggested that such rapid modification may serve to mediate transient affiliation with an individual or group or to negotiate dominance or group decisions (Balsby and Scarl In press).

Many species of parrots are non-territorial, have large home ranges, and live in fission-fusion flocks whose composition may change daily. Constantly changing social groups may necessitate a mechanism for rapidly mediating affiliations or social hierarchies within a group, and the production of contact calls accompanies flock formation and reunification of individuals in many species of parrots (Bradbury 2003). We thus wanted to determine whether other parrot species employ rapid vocal modifications of contact calls during interactions with conspecifics in a manner similar to the orange-fronted conures. The galah (*Eolophus roseicapillus*), an Australian cockatoo, is geographically far removed from the Central American orange-fronted

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conure, and these two species of parrots are from different families within the parrot order (Brown and Toft 1999; Wright et al. 2008). However, both species are non-territorial, have large home ranges, share a fission-fusion social system, and use contact calls to mediate interactions between individuals and flocks (Rowley 1990; Bradbury 2003). Therefore, social pressures that might necessitate rapidly mediating affiliations with changing groups of individuals exist in both species. Although galahs seem to use contact calls to recognize specific individuals (Rowley 1990) and to discriminate between the sexes (Scarl, unpublished data), we have noted that the double chet (DC) contact calls in interactions between two birds can be quite similar. Thus, the purpose of this study was to determine whether galahs rapidly modify DC call features to become more similar to a conspecific's calls over the course of a single interaction. In addition, since galah vocal behavior varies by sex (Scarl, unpublished data), we tested whether male and female galahs change their calls differently based on whether they are interacting with a male or a female.

Methods

Study Site

This research was conducted in the Mount Ainslie and Mount Majura Nature Parks in the northeastern section of Canberra, Australia (approximate center S 35 15' E 149 10'). The study site consisted of mature eucalypt forest interspersed with small cleared fields and paddocks and several pedestrian and bike trails. Galahs used this park for both breeding and feeding during the time of the study and both male and female galahs could frequently be seen perched in trees, foraging on the ground, or flying overhead.

We conducted playbacks to free-ranging wild birds from 18 October 2005-4 November 2005 and 8 October 2006-30 October 2006. These periods corresponded with the middle of the galah breeding season; most breeding birds were incubating and feeding nestlings during the study, and a few pairs had fledged offspring by the end of the study. As part of a longitudinal study on galah vocal communication, some of the galahs frequenting this site had been wing-tagged for individual identification (Brereton and Pidgeon 1968; Rowley and Saunders 1980).

Stimulus Selection and Processing

As part of a larger study on galah communication, we recorded double chet calls from 16 male and 10 female galahs in 2004, 2005, and 2006 using a Sennheiser MKH 816 or ME67 microphone and a Marantz PMD690 or an HHB portaDAT PDR1000. All except 2 of the males and 2 of the females were individually marked using rigid aluminum wing-tags (Brereton and Pidgeon 1968; Rowley and Saunders 1980) which allowed us to control for the number of calls presented per stimulus bird. Only double chet stimuli with high signal-to-noise ratio were used for playback, as determined by a visual inspection of spectrograms and by listening to each call.

We eliminated the majority of background noise from each stimulus by high-pass filtering at 500 Hz; as the majority of energy in the double chet call is above 2000 Hz (see Figure 1), this did not affect the acoustics of the stimulus. We then amplified the stimulus using Syrinx (www.syrinxpc.com) so that the peak amplitude of the call was at 90% of the maximum amplitude possible without overloading the signal. All stimuli were broadcast using either a Sony VAIO PCG-8H1L notebook computer or a

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Dell Latitude C540 laptop computer connected to a Pioneer GM-3000T power amplifier and a JBL Control speaker.

The study site consisted of two areas, north and south, separated by approximately 1 kilometer of lower, denser vegetation less suitable for galah feeding or breeding. Birds trapped in one location were rarely seen in the other location, although birds from these two areas were very occasionally sighted foraging together outside of the park. We played back calls recorded from northern birds at locations in the south and vice versa. However, since parrots have such large home ranges, it is certainly possible that responding birds were familiar with the stimulus birds. There is some evidence that galah dialects can vary over short distances (Baker 2003) and this protocol represented a compromise between the necessity of broadcasting calls that matched the dialects of responding birds (Wright 1996) and the attempt to present respondents with calls from unfamiliar birds.

Playback Protocol

Individual playback sites were interspersed throughout the study area, separated from each other by at least 75 meters, and were within acoustic range of both foraging sites and nest cavities. The speaker was elevated at least 1.5 meters by hanging it from a tree branch. During the playback, one person (JCS) sat within 20 meters of the speaker and interactively broadcast a playback stimulus. Two additional observers with Sennheiser MKH 816 or ME67 microphones and Marantz PMD690 recorders moved to record and sex galahs as birds came into the playback arena and vocalized. Untagged responding birds were visually sexed by eye colour; adult females have red irises while adult males have dark brown irises (Rowley 1990). If

we could not determine the sex of a responding bird during a playback, we followed that bird after the playback until we could reliably see the bird's eyes.

Parrots may react differently based on whether they perceive themselves as a leader or a follower in a vocal interaction (Balsby and Scarl In press), so to ensure that our playback stimulus initiated all vocal interactions, we commenced playbacks only when no other bird had given a DC in the area for at least 30 seconds prior to playback. This method increased the chances that calling birds were directing their calls at our stimulus, or at least were aware of the stimulus when they started calling. However, if no birds responded to the stimulus, it was impossible to tell whether this was due to a lack of interest or a lack of birds within hearing range of the playback. Thus, trials in which no birds came into the area or vocalized during the playback were disregarded. If any bird responded to the stimulus during the trial, that stimulus was never used in another trial, and once a response was achieved at a playback site, that site was not used for additional trials that year. If no birds responded to a stimulus during that trial, the stimulus and playback location could be used again in a future trial.

In each trial, one experimenter (JCS) repeatedly broadcast a single double chet call at 5 second intervals with minor (<1 second) fluctuations in interval duration. If no bird vocally responded after 50 repetitions, the trial was aborted and coded as a no response. If a bird moved into the area or called in response to the playback, the experimenter increased the playback rate and broadcast a stimulus within one second of the responding bird's call. If the bird did not respond again another stimulus call was played within 5 seconds. Additional playback calls were broadcast at 5-second intervals. Playback continued until the responding bird had been silent for ten

stimulus call playbacks, or if no birds were responding, playback ceased when 50 stimulus calls had been played overall. In a small number of trials, the responding bird eventually landed within 3 meters of the speaker and produced scree calls, which are given in response to threat (Pidgeon 1981; Rowley 1990), and these playbacks were also terminated. Successful trials on the same day were temporally separated by at least 30 minutes and spatially separated by at least 150 meters to minimize the possibility of sampling the same birds. A total of 38 trials were conducted in 2005 and 94 trials were presented in 2006; these included 67 trials with a male stimulus and 65 trials with a female stimulus. Ultimately, birds responded to stimulus calls produced by 7 males and 6 females; six stimulus birds had calls in more than one successful trial (range 1-4), but the same call exemplar was never used in more than one successful trial, and we controlled for the repeated use of certain individuals as stimulus birds as described below.

Response Criteria

Since we were interested in the acoustic changes in a bird's calls over the course of a trial, a responding bird needed to produce at least 5 high-quality double chet calls over the course of a single trial in order to be classified as responding to the trial. When more than one bird responded in a trial, as was the case in 8 trials, all responding birds were recorded and it was noted which birds produced which calls. It was not possible to determine how often the same bird responded to multiple trials, since most of the responding birds were not tagged. However, a total of 10 tagged birds (7 males and 3 females) vocalized in response to an experimental trial, although not all of these birds obtained the response threshold required for analysis. Eight out of 10 tagged birds vocalized in only one trial, one tagged male vocalized in two trials,

and one tagged male vocalized in four trials. Of the two birds that responded in multiple trials, neither produced enough vocalizations to qualify for analysis in more than one trial. Thus, although it is possible that this experiment repeatedly sampled some of the same individuals, the tagged sample suggests that it is unlikely that more than a very small percentage of analyzed responses came from the same bird.

Coding and Measuring

Each response DC that could be assigned to a specific bird was extracted from the recording of the trial using Syrinx (www.syrinxpc.com); the call was assigned a number based on the sequence in which the responding bird produced calls. Prior studies on orange-fronted conure rapid matching relied on spectrographic cross-correlation to demonstrate vocal matching or convergence (Cortopassi and Bradbury 2000). Since this method has been subject to criticism as a suitable method of measuring similarity (Janik 1999), especially as it may be sensitive to the distance and background conditions at which calls are recorded (Khanna et al. 1996), we used direct measurements of acoustic parameters to characterize potential directional change in galahs. One author (JCS) and one assistant measured frequency and temporal parameters of calls individually using an on-screen cursor in Raven sound analysis software (Charif et al. 2004). Prior to call measuring, both of us measured a set of test calls until our measurements were consistent within and between observers. When measuring response calls, we only measured calls in which the frequency-to-noise ratio was high enough to confidently distinguish the relevant features of the calls; this was determined by eye rather than a strict amplitude cutoff. We created spectrograms using a Hann window set at 420 samples with 70 percent overlap and a hop size of 126, and we set the DFT at 512 samples and averaging to 1 spectrum.

Galah double chet calls are harmonically rich, but we set our spectrograms to only depict up to 12000 Hz and we took all of our measurements from the fundamental frequency, which is the highest-amplitude harmonic. We measured five acoustic parameters of each syllable of the two-syllable Double Chet call (Figure 1.1): start frequency, end frequency, peak frequency, syllable duration, and duration to peak frequency.
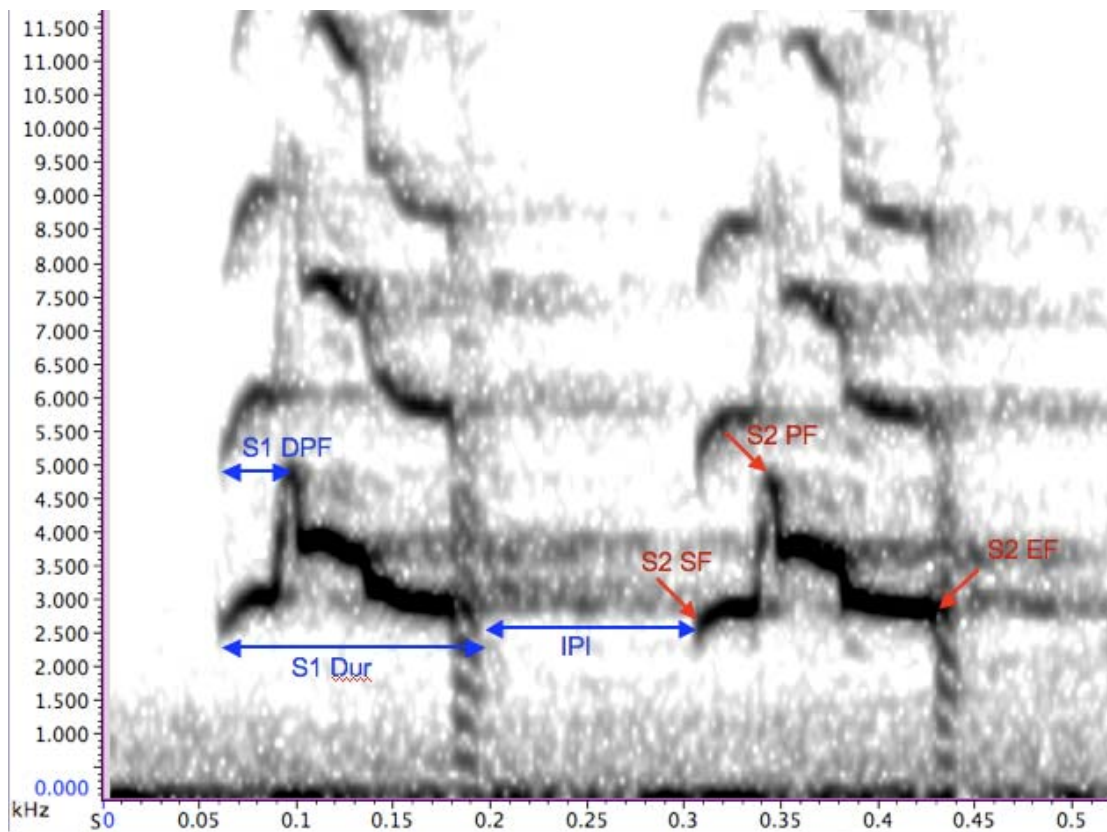
Figure 1.1. Spectrogram of a double chet call. Temporal measurements are depicted on the first syllable and are represented with blue, double-headed arrows (S1 Dur= duration of first syllable; S1 DPF= duration to peak frequency of first syllable; IPI= interpulse interval). Frequency measurements are depicted on the second syllable and are represented with red, single-headed arrows (S2 SF= start frequency of second syllable; S2 EF= end frequency of second syllable; S2 PF= peak frequency of second syllable).

In addition, we measured the interpulse interval between the two syllables, for a total of eleven measurements per call. Initially, we included other measurements such as minimum frequency, duration to minimum frequency, frequency of peak amplitude, and duration to peak amplitude in the analysis, but these measurements either proved to be very closely correlated with other measurements or were unreliable given background noise and they were excluded from statistical analyses.

Statistical Analysis

We subtracted the measurement value for the eliciting stimulus from the measurement value for each response call and took the absolute value of the difference. This gave a measure of how much each response call deviated from the stimulus call for that particular value. We performed visual inspections of the residuals of these responses, grouped by individual, to check for normality prior to statistical analyses; residuals that appeared to differ significantly from a normal distribution were log-transformed (Syllable 2: Duration, Peak Frequency) and subsequently appeared more normally distributed. To test whether each dependent variable (measurement value) differed in its response, we used a random coefficient model in SAS version 9.1 (copyright 2002-2003, SAS institute Inc, Cary, NC, USA). This is a two-level mixed model that nests order of responses within bird to account for the fact that we were taking repeated measures of each responding bird, and thus controls for individual variability within birds. In addition, we included both trial and stimulus bird as random effects, which controls for the fact that multiple calls were used from some stimulus birds, and that some trials had multiple birds responding, and thus deals with the lack of independence of data. Initially, we included all first-order terms (order, sex of stimulus, and sex of respondent) and two second-order

interactions in the model (order*order, order*sex of stimulus) and then sequentially removed the second-order terms that were highly non-significant and thus accounted for very little variability in the response. Additional interaction terms, such as sex of stimulus*sex of responding bird, could not be included due to the small number of individuals responding in each category level. Due to the limited number of responding birds, especially responding females, the power of these tests was low and we did not perform corrections for multiple testing. The number of statistical significances found, compared to the number of tests performed, is greater than expected by chance.

A bird's calls can converge with a stimulus in two ways: if the bird starts out producing calls that have greater measurement values than a stimulus (for example, with higher frequency or longer duration), that bird can reduce the values of its acoustic parameters to more closely converge with the stimulus. Alternatively, a bird might begin by producing calls with smaller measurement values than the stimulus (lower frequency, shorter duration), and then increase its own values to more closely converge with the stimulus. It is possible that over the course of an interaction, birds might monotonically reduce or increase the values of the acoustic features of their calls as a byproduct of fatigue or because birds demonstrate a convention of always increasing or decreasing certain acoustic parameters, regardless of the call parameters of other interactants. To ensure that any directional call change in this study was a result of systematic convergence rather than a byproduct of an alternate mechanism, we calculated the difference between the measurements of each response call and the measurements of the corresponding acoustic parameter for the stimulus call used during that trial. For each set of differences from each responding bird, we calculated the slope when the dependent variable was compared with the response order. If the

slope was negative, the bird decreased the measurement value of its call. If the slope

was positive, the bird increased the parameter of its own call. We compared the

average number of decreases to the average number of increases to determine whether

birds were more likely to change their calls in one direction or the other. These

analyses were conducted using JMP software (2007, SAS Institute, Inc.) and were

only employed to demonstrate that birds were capable of both increasing and

decreasing the acoustic parameters of their calls.

Ethical Note

This research was approved under IACUC #1998-0102 (Cornell University,

Ithaca, NY, USA) and complied with Ethics permit F.BTZ.71.04 issued by the Animal

Experimentation Ethics Committee at the Australian National University (Canberra,

Australia). All trapping and tagging of birds was approved by the EnvironmentACT

(License LT2004122 and LT2005156) and the Australian Bird and Bat Banding

Scheme (bander license 2649).

Results

Overall Response

A total of 39 males and 8 females gave double chet vocalizations in response to 28

male and 23 female trials. Of these, 25 males and 6 females met the strict criteria for

analysis inclusion. When birds vocally responded to a playback, the average number

of DCs given to the stimulus was 14.93 (SD 18.71; range 5-116 calls). This number is

likely a slight underestimate, as it was difficult to assign calls to a specific bird when

birds were flying, or when more than one bird was vocalizing at once as an observer approached. The average trial length in response trials, as determined by the bird, was 642 seconds (SD 416 seconds; range 141-1646 seconds) and the average number of playback calls broadcast during a response trial was 115 (SD 63 calls; range 27-261) as counted from the beginning of the trial to the stimulus call broadcast immediately prior to final call of the responding bird.

Directional Change

Overall, there was significant convergence in four out of the five duration measurements (Syllable One (S1) Duration: mixed model: $F_{1,494}=4.69$, p=0.03; Interpulse Interval, $F_{1,506}=6.07$, p=0.01; Syllable Two (S2) log Duration: $F_{1,517}=10.04$, p=0.0016; S2 Duration to Peak Frequency: $F_{1,493}=3.89$, p=0.049; Table 1.1, columns C, D, and E; Figure 1.2) and the fifth duration measurement demonstrated a similar trend (S1 Duration to Peak Frequency: mixed model: $F_{1,499}=3.77$, p=0.05;). For three of these variables (S1 and log S2 Duration, S1 Duration to Peak Frequency) these significance values represent the order*order interaction, indicating that the relationship between order of calls and measurement value was best described by a quadratic, rather than a linear, relationship. All three of these quadratic relationships represented an initial rapid convergence followed by a period of leveling off or decreasing similarity (Figure 1.3), indicating that birds changed each subsequent vocalization to converge on the stimulus more at the beginning of the interaction than at the end. Birds were equally likely to increase and decrease the temporal values of their calls (matched pairs, two-tailed t-test=-1.83, p=0.14), indicating that any directional change observed was based on the stimulus and not merely a byproduct of fatigue or directional change by convention.

Table 1.1. Statistical results for eleven measurement values by response order, stimulus sex, response sex, and two interaction terms. NS indicates that a second-order value was highly non-significant and removed from the model. P-values in bold are significant at alpha<0.05. P-values in italics indicate trends at 0.1>alpha>0.05. Significant values for stimsex*order indicate that birds match male stimuli more closely and female stimuli less closely as the interaction progresses. Significant values for respsex indicate that males match the stimulus more closely than do females.

Response Variable	Type	Order Trend	Order	Order*Order	Stimulus Sex	Stimulus sex* Order	Response sex
S1 Duration	Temporal	Converge then level/diverge	$F_{1,498}=0.19$, p=0.67	$F_{1,494}=4.69$, **p=0.03**	$F_{1,18}=0.05$ p=0.83	$F_{1,498}=3.27$ *p=0.07*	$F_{1,27}=3.02$ *p=0.09*
S1 Duration to Peak Freq	Temporal	Converge then level/diverge	$F_{1,505}=2.13$ p=0.15	$F_{1,499}=3.77$ *p=0.05*	$F_{1,23}=0.00$ p=0.96	NS	$F_{1,25}=2.18$ p=0.15
S2 Duration (log)	Temporal	Converge, then level/diverge	$F_{1,510}=0.38$ p=0.54	$F_{1,517}=10.04$ **p=0.002**	$F_{1,19}=0.37$ p=0.55	$F_{1,510}=7.22$ **p=0.008**	$F_{1,26}=1.07$ p=0.31
S2 Duration to Peak Freq	Temporal	Converge, then level/diverge	$F_{1,493}=3.89$ **p=0.049**	$F_{1,489}=3.13$ *p=0.08*	$F_{1,10}=0.49$ p=0.50	NS	$F_{1,18}=2.70$ p=0.12
Interpulse Interval	Temporal	Converge	$F_{1,506}=6.07$ **p=0.01**	NS	$F_{1,23}=0.12$ p=0.73	NS	$F_{1,25}=0.00$ p=0.99
S1 Start Frequency	Frequency	Diverge then level/converge	$F_{1,319}=3.72$ *p=0.05*	F1,479=3.03 *p=0.08*	$F_{1,14}=0.02$ p=0.89	NS	$F_{1,12}=0.61$ p=0.45
S1 End Frequency	Frequency	Converge	$F_{1,506}=4.32$ **p=0.04**	NS	$F_{1,534}=0.00$ p=0.99	NS	$F_{1,534}=0.00$ p=0.99
S1 Peak Frequency	Frequency	Diverge then level/converge	$F_{1,494}=3.04$ *p=0.08*	$F_{1,506}=4.21$ **p=0.04**	$F_{1,18}=1.63$ p=0.22	NS	$F_{1,14}=0.00$ p=0.96
S2 Start Frequency	Frequency	Linear change not demonstrated	$F_{1,490}=0.46$ p=0.50	NS	$F_{1,17}=0.80$ p=0.38	NS	$F_{1,10}=1.68$ p=0.22
S2 End Frequency	Frequency	Converge	$F_{1,522}=7.91$ **p=0.005**	NS	$F_{1,19}=0.83$ p=0.37	NS	$F_{1,534}=2.09$ p=0.1491
S2 Peak Frequency (log)	Frequency	Linear change not demonstrated	$F_{1,448}=2.20$ p=0.14	NS	$F_{1,17}=0.94$ p=0.35	$F_{1,451}=2.68$ p=0.10	$F_{1,19}=0.94$ p=0.59
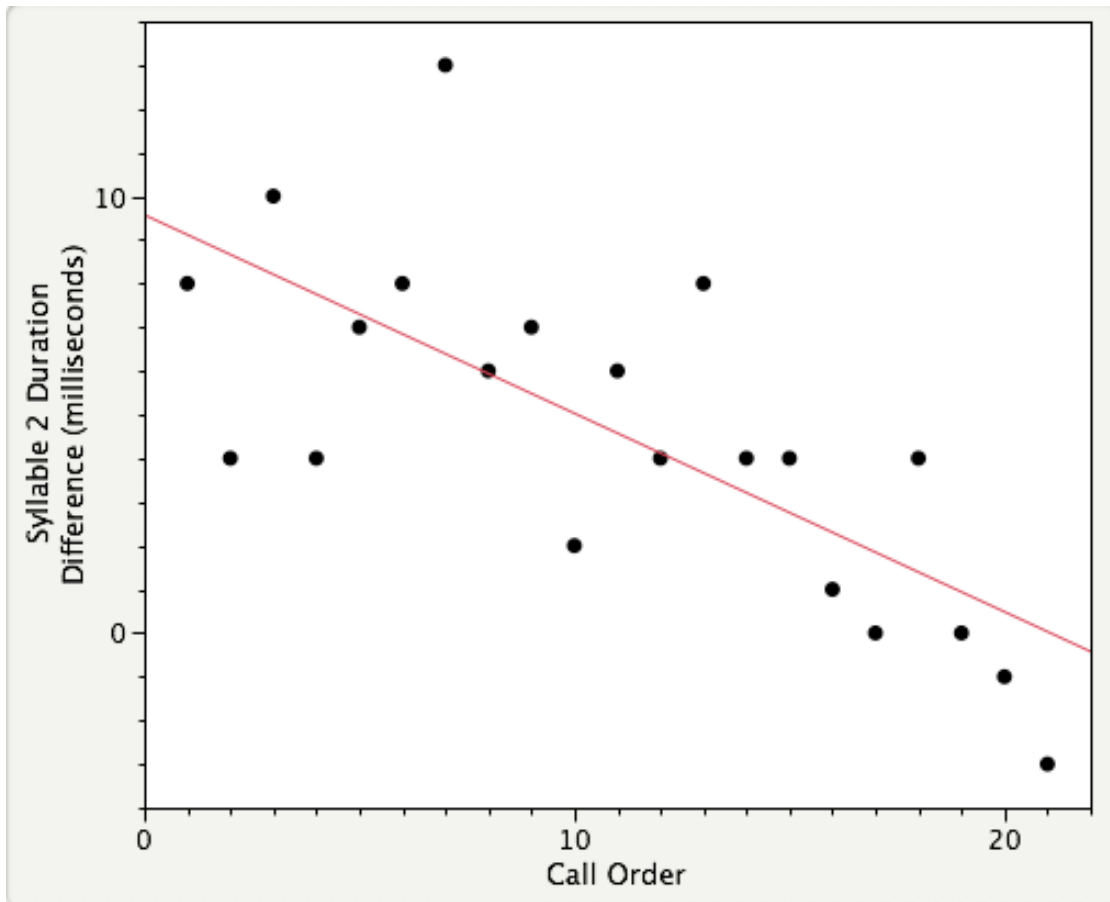
Figure 1.2. This graph represent the difference between the measurement of the respondent's value of the acoustic feature and the acoustic feature value of the stimulus to which this call was a response, versus the order in which the response calls were produced, for one individual in one trial. Higher similarity values are indicated by the difference values becoming closer to zero. This female galah linearly decreased the duration of her second syllable to more closely match the stimulus. Note that after achieving an exact similarity of this measure towards the end of the interaction, the responding bird's calls began to diverge from the stimulus.
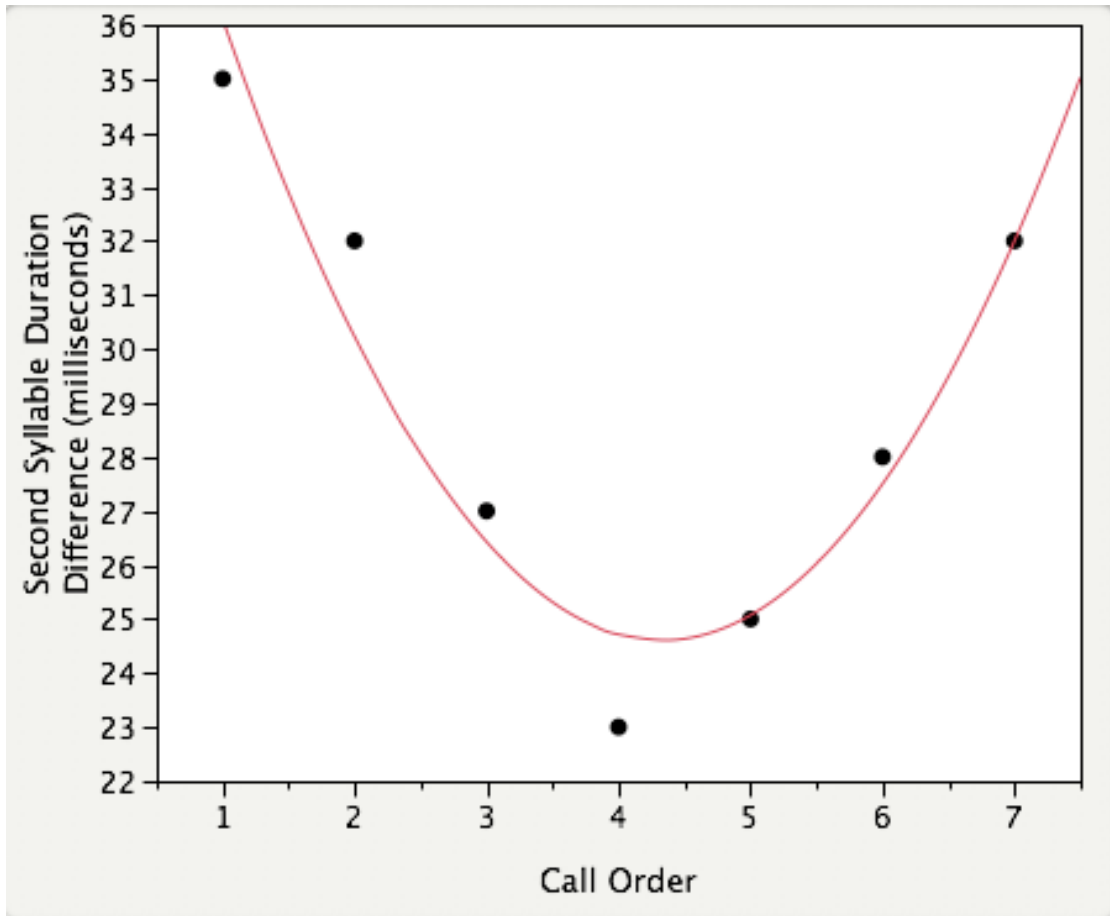
Figure 1.3. This graph represent the difference between the measurement of the respondent's value of the acoustic feature and the acoustic feature value of the stimulus to which this call was a response, versus the order in which the response calls were produced, for one individual in one trial. Higher similarity values are indicated by the difference values becoming closer to zero. This male galah demonstrates significant second-order convergence with the stimulus; it decreases the duration of its second syllable initially to converge with the duration of the stimulus, and then it increases its duration to diverge from the stimulus.

Galahs converged on the end frequency measures for both syllables (S1 End Frequency: mixed model: $F_{1,506}=4.32$, p=0.04; S2 End Frequency: $F_{1,28.9}=4.85$ p=0.04; Figure 2c) but not on the remaining four frequency measures (Table 1, columns C, D, and E); in fact, galahs showed significant second-order divergence (calls became less similar and then leveled off) in the first syllable's peak frequency values (mixed

model: $F_{1,506}=4.21$, p=0.04) and birds demonstrated a similar trend for the start frequency of the first syllable (mixed model: $F_{1,479}=3.03$ p=0.08). As with the duration measurements, birds were equally likely to increase or decrease their duration values over the course of a trial (matched pairs, two-tailed t-test=0.293, p=0.78), indicating that convergence and divergence occurred in relation to the stimulus call properties and not as a byproduct of some physiological or conventional mechanism.
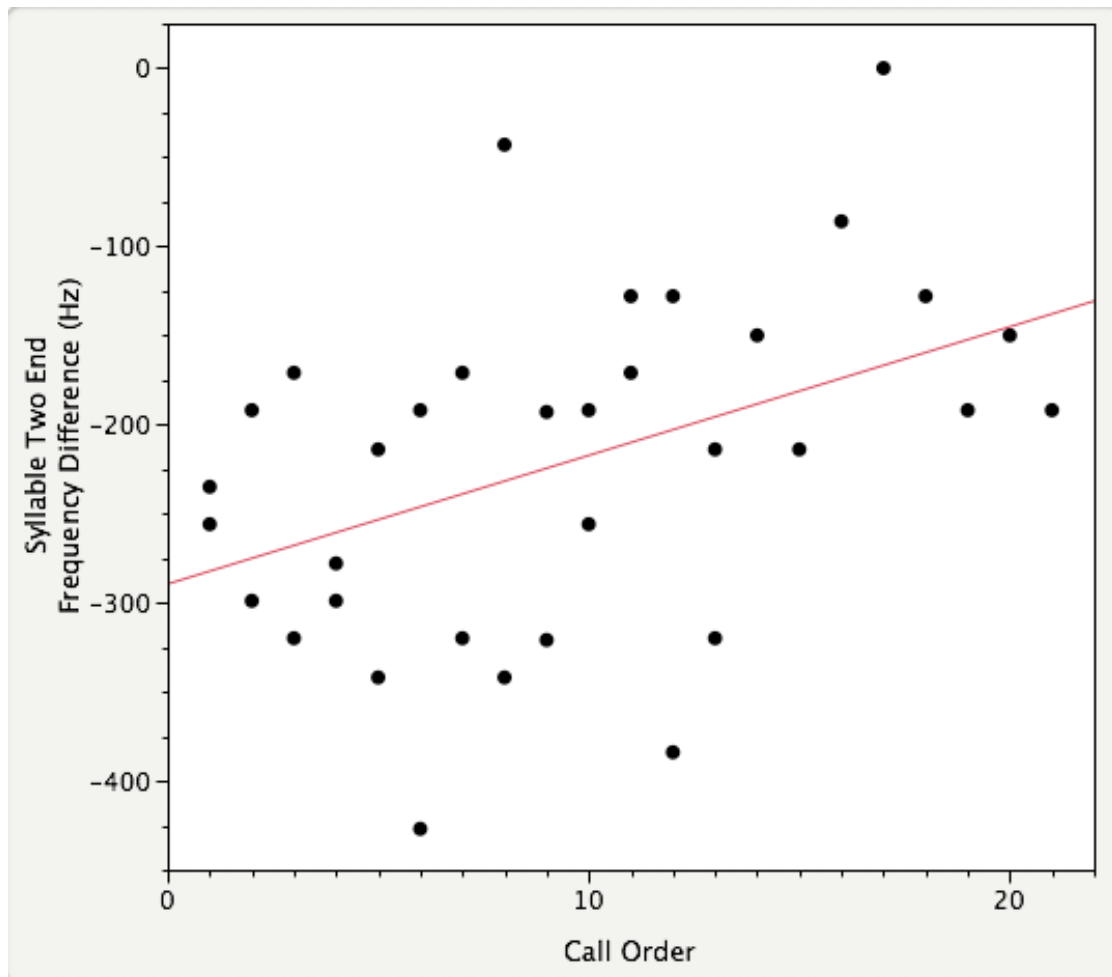
Figure 1.4. This graph represent the difference between the measurement of the respondent's value of the acoustic feature and the acoustic feature value of the stimulus to which this call was a response, versus the order in which the response calls were produced, for one individual in one trial. Higher similarity values are indicated by the difference values becoming closer to zero. This male galah linearly increased the value of the end frequency of his second syllable to more closely match the stimulus.

Sex of Respondent and Sex of Stimulus

The sex of the stimulus call, and less significantly, the sex of the responding bird, influenced the nature of convergence. Birds matched male stimuli more closely but female stimuli less closely as the interaction progressed for the log duration of S2 (mixed model: $F_{1,510}=7.22$, p=0.008; Table 1.1, column G). There was a similar but non-significant trend for the S1 duration (mixed model: $F_{1,498}=3.27$, p=0.07; Table 1.1, column G). When we consider the sex of the respondent, for eight out of eleven measures, female respondents matched stimulus calls less closely than males did. Due to the small number of females responding in this experiment, the standard error for estimates of female matching were very large and these differences only approached significance in the duration of the first syllable (mixed model: $F_{1,26.7}=3.02$, p=0.09; Table 1.1, column H). Due to the small number of responding females, it was not possible to test for an interaction between the sex of the subject and the sex of the stimulus.

Discussion

Galahs significantly modified some acoustic features of their double chet contact calls to converge on the playback stimulus in this experiment (see Figure 1.3), and this convergence was most evident in time domain measures. Not all of these convergences were linear; galahs tended to converge more markedly earlier in an interaction. More males than females responded in this experiment, and birds converged more closely on male stimuli than female stimuli. Overall, galahs were equally likely to increase or decrease the value of an acoustic parameter, indicating

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that call change was in relation to the stimulus call's features, rather than simply a byproduct of fatigue or the result of a convention to increase or decrease call parameters during an interaction, regardless of the features of a partner's calls. This experiment demonstrates that galahs are capable of rapid call changes during interactions that may last fewer than three minutes.

Rapid, directional modification of calls over the course of a single interaction has thus far only been demonstrated in one other parrot, the orange-fronted conure (Vehrencamp et al. 2003; Balsby and Scarl In press) and this experiment provides evidence that a second species of parrot, phylogenetically and geographically very far removed from the conures (Brown and Toft 1999; Wright et al. 2008), shows very similar vocal matching behavior. Finding a similar communication mechanism in two such distant species is consistent with the possibility that this rapid call convergence may be a widespread technique used within the parrot order. Other types of conspecific vocal convergence either involve a time scale of days (Nowicki 1989) or weeks (Mundinger 1970; Farabaugh et al. 1994; Hile et al. 2000; Hile and Striedter 2000) before a shared call is achieved, or involve an immediate match of a call or song without acoustic modification of that vocalization during the interaction (Armstrong 1973; Tyack 2003). While many species of parrots form year-round monogamous pairs, most parrots, including conures and galahs, often travel, roost, and forage in transient fission-fusion groups (Rowley 1990; Bradbury 2003), and thus long-term convergence of contact calls between any group members other than a mated pair, or a prolonged period of learning neighbors' vocalizations, may be inappropriate. The rapid call convergence demonstrated in the present study may allow birds to mediate interactions with individuals that they have not previously encountered and may interact with rarely or never again in the future. Although it has not yet been explicitly

tested, it is possible that other fission-fusion species, such as the bottlenose dolphin, may show similar directional vocal modification behavior. Dolphins are capable of rapid imitation of sounds (Richards et al. 1984), and the ability to rapidly modify vocalizations throughout an individual's life could facilitate interacting with a wide range of conspecifics of different origin, age, sex, and status.

There are at least two potential explanations for how parrots are using these rapid call convergences. First, responding birds in this study may have been attempting to produce a close match of the stimulus initially but required a few minutes' practice and familiarity with the stimulus before they were able to accurately imitate it. Convergence leveled off toward the end of interactions, when galahs had achieved closer matches to the stimuli, which could suggest that galahs modified their calls less once they had achieved a reasonable match. Individuals in many other species require practice or processing before they are capable of accurately matching the calls of other adults. For example, juvenile songbirds undergo a "plastic song" phase during which they practice songs produced by adult tutors; during this stage, imitation is often imperfect (Catchpole and Slater 2008). In addition, in Japanese macaques *Macaca fuscata* (Sugiura 1998), individuals that respond more quickly to a conspecific coo call match the acoustic features less accurately than those that take longer to respond, which suggests that individuals may require time to process a call before they can accurately match it. If galahs are simply practicing prior to achieving a close acoustic match, such vocal matching then appears similar to what is seen in dolphins, where imitation may indicate the intention to interact with a specific individual (Janik 2000), or finches, chickadees, and captive budgerigars, where call convergence denotes affiliation with a certain group (Mundinger 1970; Nowicki 1989; Hile and Striedter 2000).

This explanation has several caveats worth mentioning. First, although we attempted to broadcast stimuli from birds that were unfamiliar to our subjects, we have no way of knowing how much interaction our subjects had with the birds we used as stimuli. If our subjects were familiar with the calls of our stimulus birds prior to the experiment, they could have already learned the call features and thus not required practice to produce a close match. Thus, this experiment does not demonstrate whether galahs are producing new signals at the time of these interactions, or whether they are drawing from their existing repertoires. Also, not all vocal learners require experience or practice in order to vocally match a stimulus; there is evidence that dolphins (Richards et al. 1984) and possibly starlings (West and King 1990) can accurately imitate a stimulus after hearing it only once. Thus, we cannot assume that galahs employ directional change during an interaction because they require practice to match an unfamiliar stimulus.

A second potential explanation for these rapid vocal modifications is that the directional change itself may have signal meaning for parrots. This is suggested by Balsby and Scarl's (In press) study of orange-fronted conures, which demonstrates that males of this species respond differently to convergent and divergent series of calls; isolated wild-caught males respond strongly to convergence but less to divergence, indicating that convergence at least may be an affiliative signal. Convergence in wild conures seems to be a back-and-forth interaction; each individual may converge on the other's calls at different times in an interaction, with one individual converging on the second's calls followed by the second individual converging on the first's calls (T.J.S. Balsby, personal communication), and this may represent a negotiation between individuals. Presenting parrots with a single,

unchanging stimulus may therefore be unrealistic, since in a dyadic interaction both individuals can change the features of their calls. Thus, the initial rapid convergence observed in the present study may represent an initial affiliation or interest, and the subsequent leveling off or divergence may indicate that the responding bird has lost interest in the vocal interaction or is reacting negatively due to a lack of vocal modification by its interaction partner, the playback source. Additional evidence is required to determine whether rapid vocal modification in parrots is used for practice or as a signal in itself.

One benefit of this study over previous studies of rapid vocal modification in parrots is that our measurements allowed us to determine which features galahs modified over the course of a trial. While previous studies of parrot convergence have demonstrated either overall convergence or divergence (Vehrencamp et al. 2003; Balsby and Scarl In press), this study indicates that birds may be converging on some features of a call and diverging from others. In this study, galahs demonstrated convergence on all of the temporal measures, convergence on two of the six frequency measures, and significant divergence in one of the frequency measures, with a similar divergent trend for another frequency measure. Sugiura (1998) suggests that different acoustic components of calls may carry different messages, and convergence on temporal and frequency measures may have different saliences for galahs. An alternate explanation for the results found here is that divergence on frequency measures may represent a constraint on vocal production or rapid modification. Performance constraints (Podos and Nowicki 2004) have been documented in several songbird species (reviewed in Podos et al. 2004) and are often manifested in trade-offs between trill rate and other vocal features such as frequency bandwith (Podos 1997). When galahs systematically modify the temporal and end frequency measures of double chet

calls, they may have less control over certain frequency measures such as peak frequency.

This study has two major limitations. First, only six females responded to the stimuli, which made fine-scale comparisons of female responses to male and female stimuli difficult. More males responded vocally than females in this study, and birds tended to converge more on male stimuli than female stimuli, which suggests that rapid vocal convergence during double chet interactions is a tool used most frequently by males. These results are similar to those found in captive budgerigars, in which males change their calls to converge on the structure of a new female mate's (Hile et al. 2000), males in unisex flocks converge on a shared contact call (Farabaugh et al. 1994), and female call convergence in flocks takes longer than does male convergence (Hile and Striedter 2000). Balsby and Scarl's (In press) study of orange-fronted conures indicates that the interaction between stimulus sex and response sex is a key factor in determining convergent responses in that species; we could not test for this pattern in galahs. While this study demonstrates that sex differences exist in the convergence patterns of male and female interactions, further work is necessary to determine the specific nature of these differences. A second limitation is that despite our efforts to avoid sampling individuals more than once, since most of our responding birds were unmarked, it is possible that some individuals responded in multiple trials. However, since approximately one-third of responding birds were tagged, and none of these birds qualified for analysis (that is, produced at least five double chet calls) in more than one trial, it is unlikely that a large number of the untagged respondents were sampled multiply.

This study provides experimental evidence that Australian galahs, like neotropical orange-fronted conures, will rapidly modify the acoustic features of their contact calls and can systematically employ these changes to imitate a conspecific stimulus. Although further evidence across more species is needed, these results suggest that rapid call convergence may be a widespread affiliative technique utilized within the parrot order to mediate interactions within rapidly changing social networks.

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CHAPTER 2

Subtle vocal sex differences influence behavior in Galahs

Abstract

Subtle vocal sex differences often exist even in species in which males and females share a repertoire of calls, particularly in vocalizations used for long-distance communication. Few studies address how birds respond to and use these sex differences, however. This study investigated whether an Australian parrot, the Galah (*Eolophus roseicapillus*) responds differentially to three types of loud calls (Double Chet, Chechet and Chewp) commonly produced by male and female Galahs. I played back male and female vocalizations of each of the three call types to wild Galahs in Canberra, Australia, and recorded vocal and approach responses of all birds in the focal area. Galahs responded differently to certain male and female call types, with birds approaching male calls more closely but vocalizing more to female calls. In addition, males were more likely than females to vocalize to conspecific calls, regardless of stimulus sex. However, paired males and females tended to approach stimuli together, regardless of stimulus sex, which may indicate that coordination of movement, rather than coordination of vocal behavior, is important in maintaining the pair bond. These experiments demonstrate that in an avian species in which both sexes share a repertoire of calls, the sexes of senders and receivers influence the nature of a vocal interaction.

Introduction

Many species that communicate acoustically have sexually distinct vocalizations that are typically used during competitive interactions between members of the same sex or to attract opposite-sex conspecifics (Andersson 1994). Although sex differences in vocalization types are widespread, in some species, males and females share a repertoire of calls and produce the same call types in similar situations (Sharman et al. 1994; Laiolo et al. 2000). Despite the similarity in structure and situational use, some acoustic analyses have demonstrated subtle but consistent sex differences in the structures of sexually similar calls whose primary purpose does not appear to be mate attraction or same-sex competition; examples can be found in mammals such as Cotton-top Tamarins (*Saguinus oedipus)* (Weiss et al. 2001), Yellow-bellied Marmots (*Marmota flaviventris)* (Blumstein and Munos 2005), and Manatees (*Trichechus inunguis)* (Sousa-Lima et al. 2002), and birds such as *Aptenodytes* penguins (Robisson 1992), Whistling ducks (*Dendrocygna viduata) (Volodin et al. 2005)*, and some birds of prey (Farquhar 1993). Many of the calls for which subtle sex differences have been noted are used for long-distance communication (Norcross et al. 1994), in which visual cues indicating a caller's sex would often be inaccessible. In some species of primate, subtle sex differences in long-distance communicative signals may be used for mate attraction (Norcross et al. 1994; Miller et al. 2004) but, with the exception of a few studies on birds (Nuechterlein 1981; Vicario et al. 2002), less is known about how other taxa use these differences to make behavioral decisions.

Parrots may be an optimal taxon in which to study behavioral responses to subtle sex differences in long-distance signals. Most species of parrots are largely non-territorial, have large home ranges, and travel in fission-fusion flocks, so that each individual interacts with many conspecifics of varying ages, sexes, and familiarities over the course of a day (Rowley 1990; Bradbury 2003). Most species of parrots have

a loud contact call that is used in communication both between individuals and between flocks. While few species of parrot have a specific vocalization used exclusively for mate attraction (Bradbury 2003), calls used for other functions may still play a role in mate attraction or sexual affiliation; for example, captive male Budgerigars (*Melopsittacus undulatus*) converge the structure of their contact call with that of their new mate when initially forming a pair bond (Hile et al. 2000), and female Budgerigars prefer to mate with males whose contact calls are similar to theirs (Moravec et al. 2006). In addition, Orange-fronted Conures (*Aratinga canicularis*) of both sexes produce a "chee" contact call, but birds respond differently to male and female calls (Balsby and Scarl In press) indicating that subtle sex differences are relevant in one type of vocal interaction for this species.

The Galah (*Eolophus roseicapillus*) is a species of cockatoo common in Australia. Galahs often roost and forage in large groups of individuals and thus interact frequently with large numbers of conspecifics (Rowley 1990). Males and females share a repertoire of calls which includes a variety of vocalizations used for long-distance communication, many of which serve to contact other individuals or coordinate flock activity (Pidgeon 1981; Rowley 1990). No previous studies on Galah communication have addressed whether sex differences exist in Galah call structure, production, or response to conspecific calls.

In this study, I examine the responses of wild Galahs to three common call types. One call type, the Double Chet (Figure 2.1a; described by Pidgeon (1981) as the "S" call and Rowley (1990) as Chet-it or Lik-lik calls), is a two-syllable contact call used to locate groups or individuals and coordinate activity. The Chechet (Figure 2.1b; corresponding with Rowley's (1990) Titew call) is another contact call often given during long flights; Galahs sometimes alternate between calling Double Chet and Chechet, although there are consistent acoustic differences between the two call

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types. The third call, the Chewp (Figure 2.1c; described by Pidgeon (1981) as the "C"

call and by Rowley (1990) as a loud Chet call), is a general alarm vocalization and

may serve to coordinate activity in response to danger (Pidgeon, 1981). I examined

whether the sex of a bird producing one of these commonly given call types had any

effect on the responses of conspecifics. In addition, I observed whether males and

females responded differently to these three vocalization categories.
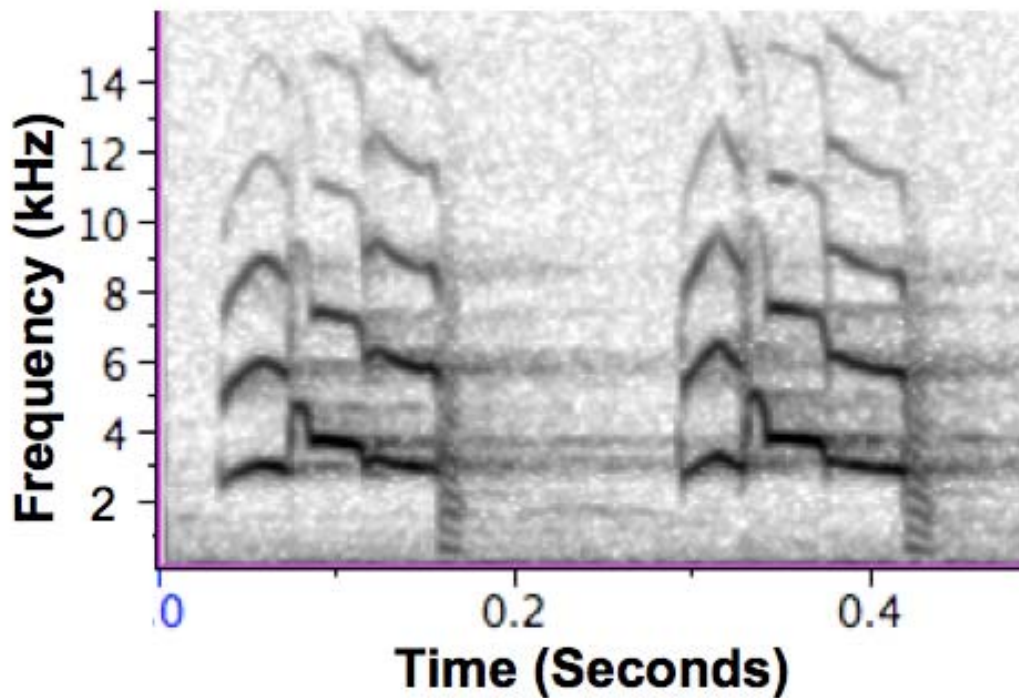
Figure 2.1a. Spectrogram of a Double Chet (DC) call.
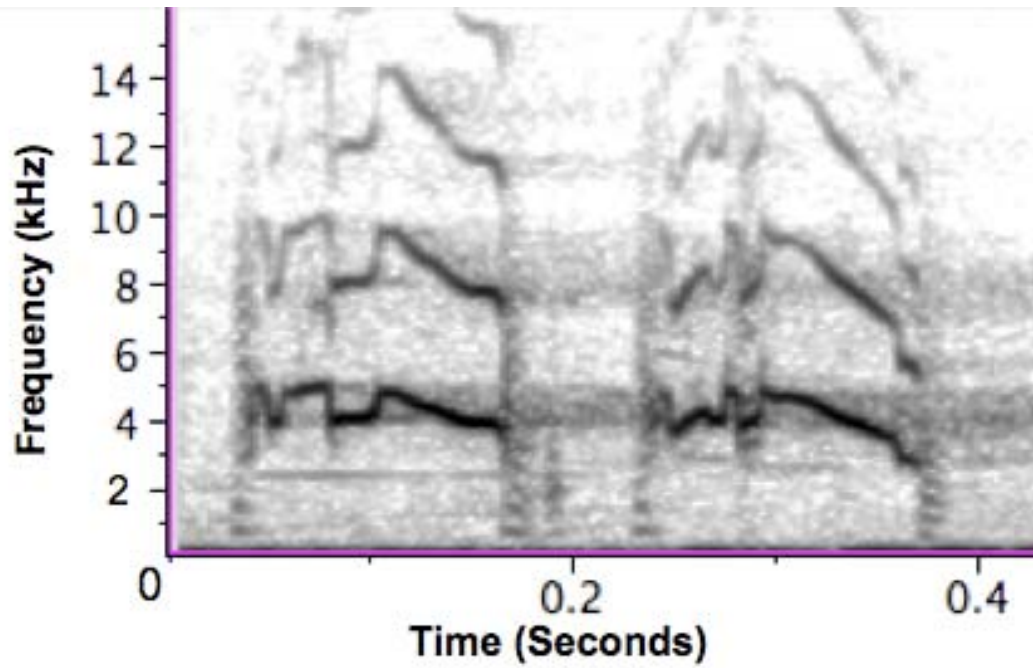
Figure 2.1b. Spectrogram of a Chechet call.
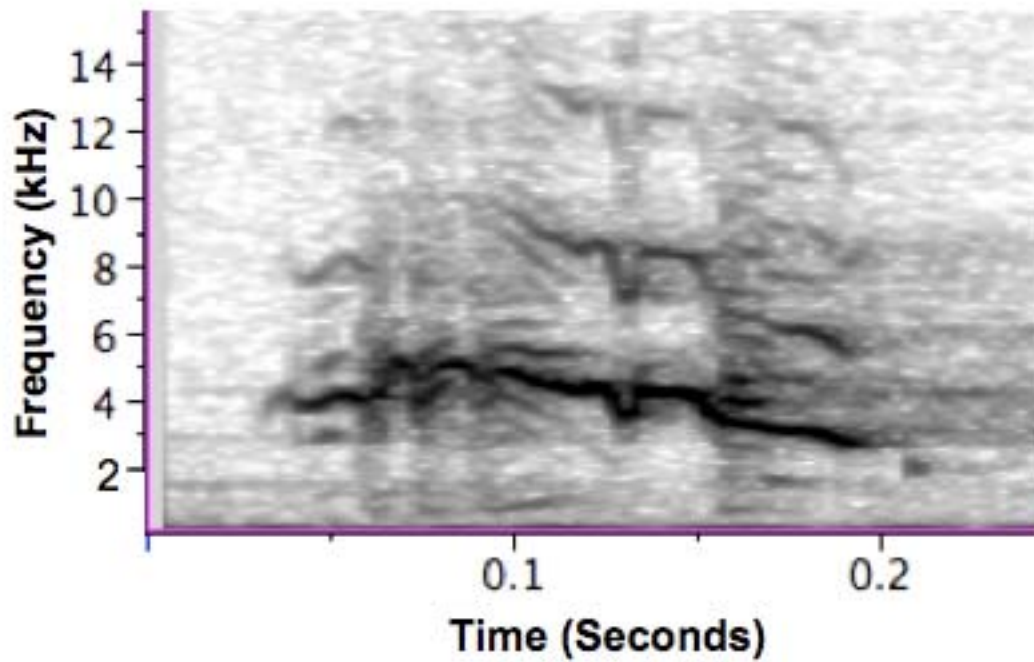
Figure 2.1c. Spectrogram of a Chewp call.

Methods

This research was conducted on a population of wild free-ranging Galahs in the northeastern section of Canberra, Australia (approximate center S 35 15' E 149 10'). The study site consists of two contiguous nature parks (Mount Ainslie Nature Park and Mount Majura Nature Park) containing mature eucalyptus forest interspersed with small cleared fields and horse paddocks, and is bordered by mountains to the east and suburbs to the west. Galahs used this park for both breeding and feeding during the time of the study. Since humans are a regular and relatively non-threatening presence in the park at all times of year, Galahs were not unduly attentive to researchers in their environment.

I conducted playbacks from August through October of 2005 and in September and October of 2006. This is late winter and early spring in the southern hemisphere, when Galahs are prospecting for nesting sites (July-August), incubating eggs (August-September) and caring for young nestlings (September-October). These playbacks were conducted to free-flying Galahs, some of which were individually marked with rigid aluminum wing-tags (Rowley and Saunders 1980). These playbacks were not directed at specific target birds; rather, I broadcast calls from a predetermined location regardless of whether I initially noted Galahs in the area. This somewhat unconventional playback method was due to the results of pilot studies in previous years: since Galahs are largely non-territorial, individuals are only reliably present at their nest-cavity tree, and Galahs rarely vocalize from on the ground, such as when they are at baited feed stations. When I broadcast contact calls to Galahs at their nests, they gave very little response, but Galahs from the surrounding areas would fly in and call. Thus, rather than targeting specific individuals as the focus of each playback, I recorded the responses of any birds that were in the playback area during any part of

the playbacks. Some responding Galahs may have already been in the area prior to playback, whereas others were called in by the playback.

I performed three parallel experiments to test Galahs' responses to male and female playbacks of three different call types (Double Chets, Chechets, and Chewps). I presented Galahs with approximately the same number of male and female trials in each experiment (DC experiment, 27 female-stimulus trials, 29 male-stimulus trials; Chechet experiment, 26 female-stimulus trials, 27 male-stimulus trials; Chewp experiment, 24 female-stimulus trials, 24 male-stimulus trials). In each experiment, a trial consisted of a single Galah call broadcast 20 times with 5 seconds between each call.

I created playback stimuli from recordings taken at my study site in 2004 and 2005 of 8 wing-tagged males, 6 wing-tagged females, and 2 untagged females. No individual call was ever used in more than one trial and no individual bird's calls were used in more than five trials in one experiment; I was unable to limit the stimuli to only one call from each bird due to the limited number of high-quality recordings from marked Galahs.

Six field assistants and I recorded stimulus calls using a Sennheiser MKH 816 or ME67 microphone into either a Marantz PMD690 or an HHB portaDAT PDR1000. I high-pass filtered each stimulus at 500 Hz, which eliminated the majority of low-frequency background noise but was much lower than the fundamental frequency of each call (see Figure 2.1). I amplified each call to 90% of the maximum value possible without overloading the loudest part of the signal. The stimuli were loaded into a Sony VAIO computer or CD player and broadcast through a JBL Control speaker; output volume was adjusted by ear to account for differences in playback equipment.

I divided my study area into two sections, north and south. There was a small (less than 2 kilometer) area of park between these two sections in which Galahs were rarely seen. I played back calls from northern birds in the southern area and calls from southern birds to northern birds. I rarely observed Galahs from the southern part of my study area in the north and vice versa, although I occasionally saw Galahs from these two areas foraging together in the suburbs outside of the park. Thus, it was unlikely that Galahs whose calls were used as playback stimuli had regular interactions with the individuals who responded to a playback in any given area. Since both individual familiarity (McGregor 1993; Stoddard 1996) and regional dialect differences (Wright 1996; Wright and Dorin 2001) may influence animals' perceptions of conspecific calls, my selection of stimuli attempted to compromise between these two influences. Although Baker (2003) observed that Galahs exhibit strong dialects even between regions that are relatively close geographically. However, my two study areas were sufficiently close, and the population of Galahs breeding within these areas interacted sufficiently often outside of the park site, that it was unlikely that strong dialectic differences existed between the two groups.

Within each study area, I had between 10 and 20 unique speaker locations. I played one male stimulus trial and one female stimulus trial at each speaker location on different days to minimize any effect of location on my results. No more than one trial was broadcast at a given location on the same day, and between 1 and 6 trials were conducted per day with at least 20 minutes and at least 50 meters between each trial to minimize the probability of calling in the same birds. Tagging and re-sighting data indicate that resident nesting birds are most likely to be foraging and resting near their cavities very early in the morning, but later in the morning non-resident Galahs move in to feed, (Scarl, own data) and I conducted playbacks throughout the morning (0600 to 0930) if weather permitted to maximize the number of different individuals

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hearing playbacks. Despite my efforts to maximize the number of unique birds exposed to these three experiments, since very few of the responding birds were tagged at the time of this study, and since Galahs are non-territorial and individuals could not be identified based on their location, it was impossible to determine how frequently the same birds responded to the playbacks. Thus, it is possible that there was some pseudoreplication in these studies; likewise, it was not possible to determine the number of unique respondents.

In 2005, I recorded and coded each experiment. In 2006, I was joined by a second observer whose data were used when I did not have a clear view of a responding bird. Prior to commencing the experiment, each observer practiced distance estimates in the field until she achieved a consistent accuracy of within 3 meters for distances up to 30 meters and within 5 meters for distances up to 50 meters. Due to the potential for a few meters' error in distance estimates, during coding I translated exact distance estimates into 10-meter blocks (1-10 meters was coded as 1, 11-20 meters was coded as 2, and so on). Distance estimates for distances greater than 50 meters were less accurate and thus I only included trials in which birds were within 50 meters of the speaker in the distance analyses. A playback trial began when no Galah had given a vocalization in the area for 30 seconds; thus, the playback stimulus initiated all interactions in the area. Birds within 100 meters of the speaker during the experiment were coded as "in play". We described in real-time any movements or vocalizations each bird made. In addition, we noted the sex of each bird if possible, as determined by eye colour (Rowley 1990); if neither observer had a clear view of the bird's eye in a well-lit spot, we recorded the sex as unknown. We also noted whether the responding Galah was in a pair; pair status was determined when two birds of opposite sex flew into the playback arena at the same time from the same direction.

I analyzed each trial recording using Raven 1.2.1 (Bioacoustics Research Program 2003-2004). Using the observer's detailed comments, I divided responses into "approach" and "vocalize". In the approach category, I coded the time from the initiation of playback until a bird's first approach towards the speaker (noted when an observer first noticed a bird moving towards the speaker), the time from the initiation of playback until a bird's closest approach to the speaker, the distance to which a bird initially approached the speaker when it first moved towards the speaker, and the closest approach distance during the playback. I coded whether each bird vocalized during the playback, whether it gave a Double Chet, Chechet, or Chewp, and how many of each of these vocalizations the bird gave.

Responding birds did not necessarily all hear the stimulus at the same point in the playback; for example, birds flying overhead during the playback would not hear the beginning of the trial, whereas birds perched in the area would hear all broadcast calls unless they chose to leave the area during the trial. However, due to randomization of location and order of playback of male and female calls, there is no reason to expect that birds differed in their likelihood of hearing more or less of specific types or classes of calls. Thus, any differences in approach or vocal timing due to differences in arrival in the study area should create random noise in the data rather than systematic bias. Responses were thus coded for all birds that vocalized or moved within the playback area, regardless of when they entered or left the playback area.

This research was approved under IACUC #1998-0102 and complied with Ethics permit F.BTZ.71.04 issued by the Animal Experimentation Ethics Committee at the Australian National University. All trapping and tagging of birds was approved by the EnvironmentACT (License LT2004122 and LT2005156) and the Australian Bird and Bat Banding Scheme (bander license 2649).

STATISTICAL ANALYSES

Initially, I analyzed each of the three playback experiments separately to determine whether Galahs responded differently to male and female calls of each type and whether males and females responded differently to each specific call type. Since I was doing non-targeted playbacks where there were not necessarily birds present at the start of the playbacks, I did a test using JMP version 7.0 software (SAS Institute, 2007) to see whether birds were more likely to respond in any way to male or female calls. This test was non-significant (Double Chet: Pearson Chi-square: $X^2_1=1.1$, p=0.30; Chechet: Pearson Chi-square: $X^2_1=0.2$, p=0.65; Chewp: Pearson Chi-square: $X^2_1=1.3$, p=0.27.) and since I had no way of knowing whether a no-response was due to lack of interest in the stimulus or lack of birds in the area, I only ran statistics on trials in which at least one bird responded in some way.

To compare responses to male versus female stimuli by male versus female respondents, I ran a generalized estimating equation in SAS version 9.0 (SAS Institute, 2002-2003) on all discrete responses (distance of first approach, distance to closest approach, did the bird vocalize, did the bird give a Double Chet, Chechet, or Chewp). Since some trials had repeated measures over several birds, I controlled for trial to account for the lack of independence of responding birds within a trial. For continuous data (time to first approach, time to closest approach, number of vocalizations given), I ran a mixed or multilevel model in SAS with trial as a random factor; both of these models allowed me to account for the fact that often more than one bird responded within a trial and thus controlled for the lack of independence of some of the responding birds. Initially, I ran each model with an interaction term of stimulus sex by response sex. These interaction terms were non-significant for all tests and so I excluded them from further analyses. After running each test for each

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experiment, I conducted post-hoc tests to determine how responses to the three call types compared. Both stimulus sex by response sex and response sex by stimulus type were non-significant interactions for all response categories, so I excluded them from post-hoc analyses.

Since many birds responded in male-female pairs that always flew close together, I did not expect that there would be differences in approach behavior between males and females, and thus for all approach data, I ran each treatment variable independently in the mixed model. For all vocalization data, however, it was possible that there was variation that could be accounted for by the sex of the stimulus, the sex of the responding bird, and the type of stimulus in the overall model, so these three factors were included in all vocalization response models. For certain combinations of stimuli and responses, missing values caused the models mentioned above to be inappropriate; for these situations, I ran a chi-square analysis with only one treatment factor in the model.

RESULTS

DOUBLE CHET EXPERIMENT

I ran a total of 61 DC trials; due to equipment failure or observer error/uncertainty I excluded seven trials from the analysis, yielding 56 DC trials (27 female stimulus, 29 male stimulus). Birds responded to 37 of these trials; 16 (59%) female trials, 21 (72%) male trials. A total of 33 birds responded to female trials and 47 birds responded to male trials. Birds were more likely to respond as part of a pair than as solo individuals (Chi-square: X^2_1=4.3, p=0.03). In 34 out of 37 trials in which there

was a response, a bird approached the stimulus (52% of female trials, 68% of male trials). In 33 out of 37 response trials, a bird vocalized in response to the stimulus.

Response by Stimulus Sex. When birds initially approached broadcast DC, their first approach to male DC brought them closer to the stimulus than their first approach to female DC (Chi-square: X^2_1=4.07, p=0.04; Figure 2.2), and birds showed a similar but non-significant trend in their closest approach to male and female DCs (X^2_1=2.62, p=0.1). Birds did not differ in their time to first approach ($F_{1,17.2}$=0.8, p=0.37) or closest approach ($F_{1,17}$=1.2, p=0.28). However, significantly more birds produced a Double Chet response to a female stimulus than to a male stimulus (Chi-square: X^2_1=5.1, p=0.02; Figure 2.3). Birds did not differ in whether they gave a Chechet (X^2_1=1.9, p=0.15) or Chewp (X^2_1=0.6, p=0.40) call to male or female DC stimuli. Birds were equally likely to respond to male and female stimuli as solo responders or in pairs (X^2_1=0.1, p=0.74).

Response by Responder Sex. Male and female responding birds did not differ in their approach responses to DC stimuli (Time to first approach: $F_{1,27.3}$=0.3, p=0.55; Time to closest approach: $F_{1,24.8}$=0.1, p=0.75; Distance to first approach: X^2_1=0.05, p=0.82; Distance to closest approach: X^2_1=1.69, p=0.19). Males and females differed in their vocal behavior, however. Males produced more DCs than females (Chi-square: X^2_1=4.6, p=0.03; Figure 2.4).   Only males ever responded to a DC with a Chechet in this experiment, and only 23% (6 out of 26) of responding males gave a Chechet. It was rare for a Chewp to be given by a known-sex bird in this experiment- of 42 known-sex birds, only three gave Chewps, and these were all males. With such a small number of responding birds, the statistical models used for the rest of the data were

not valid. Females were more likely to respond as part of a pair than were males $(X^2_1=5.2, p=0.02)$.
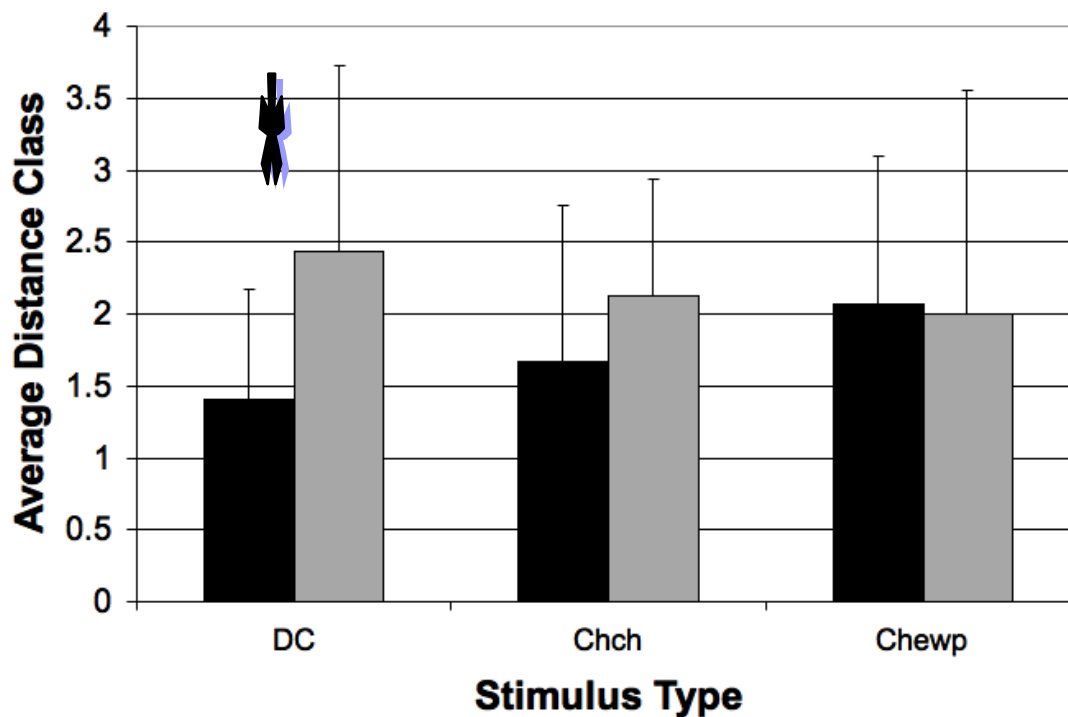
Figure 2.2. Initial approach distances by stimulus type. Black bars represent responses to male stimuli, gray bars represent responses to female stimuli. Distances were estimated every 10 meters and thus each "distance class" represents 10 meters. * indicates p>0.05.
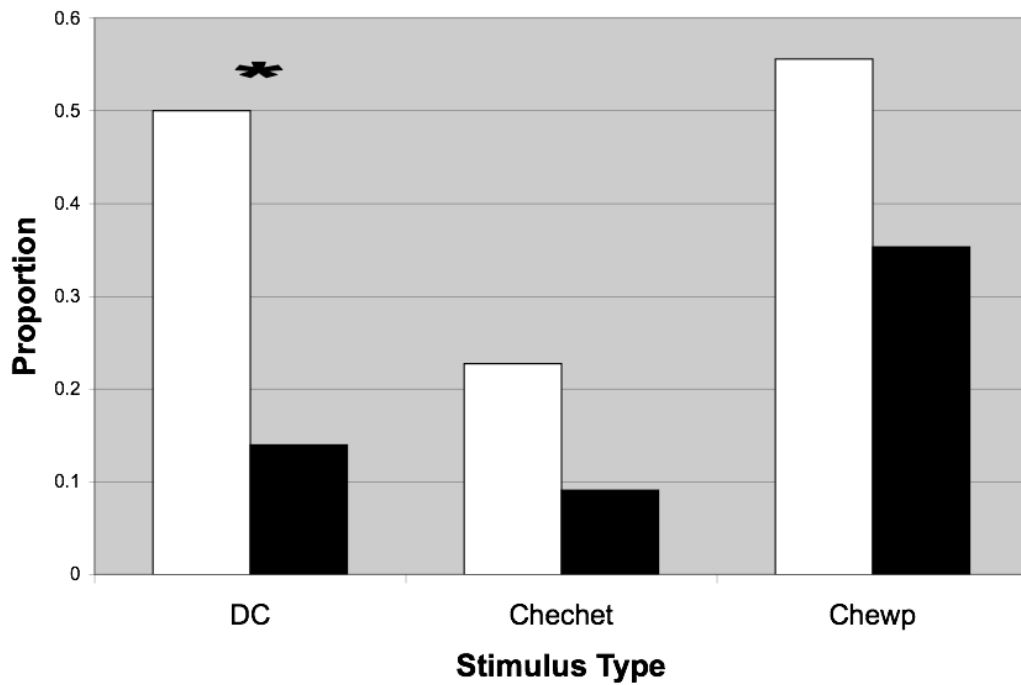
Figure 2.3. Proportion of responding birds producing stimulus call type. Black bars represent responses to male stimuli, white bars represent responses to female stimuli. * indicates p>0.05.
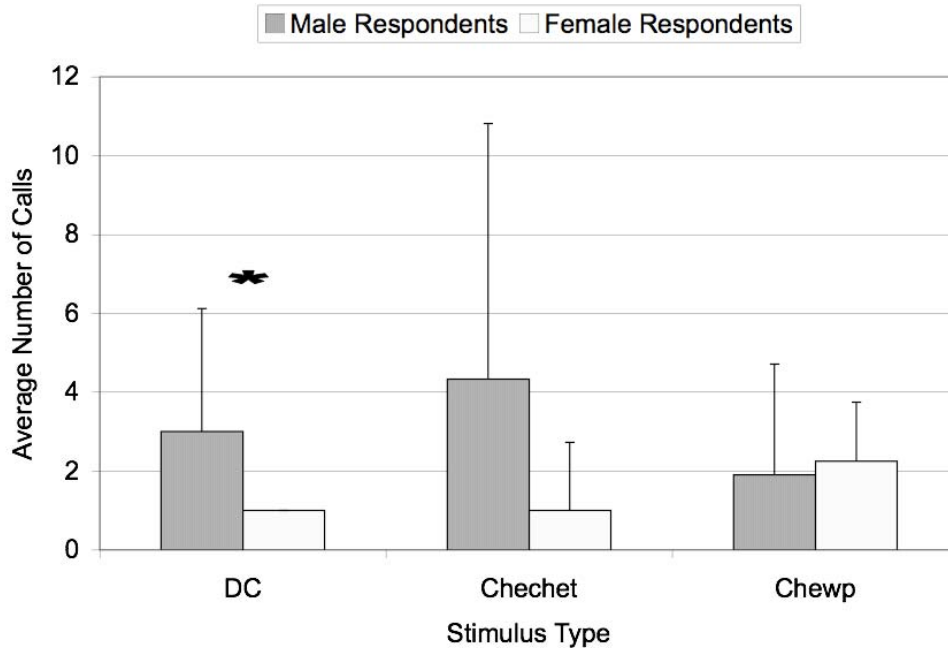
Figure 2.4. Average number of stimulus-type calls given by male and female respondents. The bar for female respondents in the DC experiment lacks an error bar because all vocally responding females gave exactly one DC call.
* indicates p>0.05

CHECHET EXPERIMENT

I conducted a total of 53 Chechet trials; 33 (16 female, 17 male) of which were included in the final analysis after excluding trials with equipment failure or observer uncertainty. One or more birds responded in 21 of these trials (11 female trials, 10 male trials), and a total of 22 birds responded to female trials and 25 to male trials. Birds were more likely to respond to Chetchet stimuli in pairs rather than as solo individuals (X^2_1=9.5, p=0.002). Birds approached the speaker in 8 female stimulus

trials (50%) and 8 male stimulus trials (47%), and birds vocalized in 10 female (63%) and 8 male stimulus trials (47%).

Response by Stimulus Sex. Galahs initially approached male Chechet calls more quickly than female calls, although these differences were not quite significant ($F_{1,12.1}=3.8$, p=0.07). There were no other significant differences in approach behavior based on the sex of the stimulus (Time to closest approach: $F_{1, 11.6}=1.9$, p=0.18; Distance to first approach: $X^2_1=2.6$, p=0.10, Figure 2.2; Distance to closest approach: $X^2_1=1.2$, p=0.26). Unfortunately, the number of birds responding with a vocalization was too small for statistical comparison, although the proportion of birds giving a Chetchet was higher for female stimuli than male stimuli (Figure 2.3). Paired birds and solo birds were equally likely to approach male and female Chetchet stimuli ($X^2_1=0.1$, p=0.75).

    Response by Responder Sex. There were no differences in male and female approach behavior in relation to Chechet stimuli (Time to first approach: $F_{1,14.2}=0.0$, p=0.89; Time to closest approach: $F_{1,13.7}=0.4$, p=0.52; Distance to first approach: $X^2_1=0.9$, p=0.34; Distance to closest approach: $X^2_1=0.6$, p=0.4). A Chechet stimulus elicited a vocal response in 36% of responding females versus 68% of responding males (n=11 females total, 22 males total); these differences were not quite significant (Chi-square: $X^2_1=3.03$, p=0.08.) Only 1 out of 11 females and 5 out of 22 males gave Chechets in response to this stimulus, but once again, the number of responding birds was too small to support the statistical models used here. There was no difference in the percentage of males and females who gave DCs in response to a Chechet stimulus; out of 34 responding birds (12 female, 22 male), only 6 gave a DC (2 female, 4 male).

Once again, responding females were more likely to be part of a pair than were responding males (X^2_1=7.4, p=0.006).

CHEWP EXPERIMENT

I ran 48 Chewp playback trials (24 female, 24 male); all were used in analysis. Birds responded to 17 female playbacks and 13 male playbacks. 31 birds responded to female trials and 26 birds responded to male trials. Unlike in the other two experiments, birds were equally likely to respond to Chewp stimuli in pairs or as solo birds (X^2_1=0.1, p=0.72). Birds approached the speaker in 12 female trials (50%) and 11 male trials (46%), and birds vocalized in 14 female (50%) and 12 male trials (58%).

Response by Stimulus Sex. There were no significant approach differences based on the sex of the Chewp stimulus (Time to first approach: $F_{1,15}$=0.0, p=0.76; Time to closest approach: $F_{1,16.6}$=1.6, p=0.21; Distance to first approach: X^2_1=0.58, p=0.45, Figure 2; Distance to closest approach: X^2_1=0.3, p=0.85). Birds responded with a Chewp in more female stimulus trials than in male stimulus trials, although these differences were not quite significant (Chi-square: X^2_1=3.5, p=0.05; Figure 2.3). Birds did not differ in whether they gave a Double Chet (X^2_1=1.8, p=0.17) or a Chetchet (X^2_1=0.2, p=0.62) in response to male and female stimuli. Birds were equally likely to respond to male and female stimuli as pairs or as solo birds (X^2_1=0.4, p=0.48).

Response by Responder Sex. There were no significant differences in approach behavior based on responder sex (Time to first approach: $F_{1,12}$=2.0, p=0.17; Time to

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closest approach: $F_{1,13.9}=0.4$, p=0.52; Distance to first approach: $X^2_1=0.62$, p=0.43; Distance to closest approach: $X^2_1=0.13$, p=0.72). There were no significant differences in the percentages of males and females who vocally responded to a Chewp playback; 60% of females (n=6 out of 10) responded to a Chewp, while 71% of males (10 out of 14) responded to a Chewp (chi-square=0.34, p=0.55). Only 6 out of 27 responding Galahs gave a DC to a chewp stimulus, and only three Galahs gave a Chechet to a Chewp stimulus, and all three were males (0 out of 9 females, 3 out of 17 males). Females were once again more likely than males to respond to Chewp stimuli as part of a pair ($X^2_1=4.9$, p=0.02).

OVERALL TRENDS

Birds were more likely to produce the stimulus call in response to female rather than male stimuli in all three experiments (Figure 2.2), although these overall differences were not quite significant ($X^2_1=3.0$, p=0.08). Post-hoc pairwise comparisons indicate that females were more likely to give the stimulus call in response to the Chewp playback than in response to the DC or Chechet playbacks (Figure 2.3), although these differences were not quite significant ($X^2_1=3.5$, p=0.06 and $X^2_1=3.0$, p=0.08, respectively). Males showed the same pattern (Figure 2.3), although these differences were not significant (all p>0.20).

Discussion

These experiments indicate that subtle sex differences encoded in at least one of the main Galah vocalizations allow Galahs to distinguish between male and female callers without any visual cues. Birds in this study behaved significantly differently based on whether Double Chet stimuli were produced by male or female birds, and Galahs

showed similar trends for Chechet and Chewp stimuli. In general, birds called more in response to female stimuli but approached male contact call stimuli more closely or more quickly than female contact call stimuli. Thus, subtle sex differences are detected by Galahs and appear to be used to make behavioral decisions.

Sex differences often evolve in situations involving mate attraction or same-sex conspecific competition (Andersson 1994). Although contact calls such as the Double Chet primarily serve an affiliative function to maintain flock cohesion or establish flocks (Bradbury 2003), these calls could also play a role in mate attraction or affiliation preferences based on sex as suggested for captive Budgerigars (Hile et al. 2000; Moravec et al. 2006) and monkeys such as tamarins (*Saguinus sp.*) (Masataka 1988; Miller et al. 2004). This study thus provides a basis for wild, free-ranging Galahs to use a long-distance contact call to mediate sex-related behavior.

Along with differences in response to some male and female stimuli, these experiments also demonstrate differences in vocal behavior based on the sex of the respondents; males vocalize more in response to conspecific Double Chet and possibly Chechet calls, regardless of the sex of their interaction partner. Both males and females are capable of producing all three call types broadcast in this study; however, males were more likely to give Double Chets and Chechets than were females. While female respondents called less than males in this experiment, female double chet stimulus calls were more likely to elicit vocalizations than male stimulus calls. A similar pattern of calling is seen in the Western Grebe (*Aechmophorus occidentalis*), in which both sexes give multifunctional "advertisement" calls. Females of this species call less frequently than males, but a greater proportion of female calls elicit a vocal response (Nuechterlein 1981). In grebes, these differences are caused by males calling more to females. In the present study, the lack of interaction between stimulus sex and response sex indicates that both sexes may exhibit higher calling rates to

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conspecific females, but these results need to be interpreted with caution due to the small number of calling females in this study.

Sex differences in response were evident for vocal behavior but nonexistent for approach behavior. The majority of the birds responding to these playbacks entered the playback area or started off in the playback area as male-female pairs. Like many species of parrots (Bradbury 2003), Galahs form year-round socially monogamous pairs (Rowley, 1990) and Galah pairs are often synchronous in their behavior (Rogers and McCulloch 1981). In long-term monogamous pairs, coordinated vocal behavior may reinforce the pair bond (Rowley 1983) and serve as a signal of commitment to a partner (Wickler 1980). Thus, in this study, Galahs may coordinate approach behavior with their mate, which would lead to similar approach behaviors for males and females within a pair. Unlike in some duetting songbird species for which coordinated vocal behavior is important between partners (Wickler 1980), these results suggest that in Galahs, movement and travel are more synchronized between members of a pair than is vocal behavior. While most songbirds can use calls or song to locate (Hall 2004) or identify (Logue and Gammon 2004) their mate within the confines of a territory, since most species of parrots do not hold year-round territories and regularly travel long distances (Bradbury 2003), synchrony of movement between members of a pair may be essential to ensure that mated birds do not get separated.

Although it is known that subtle sex differences exist in the vocalizations of some avian species in which males and females share a repertoire, very little has been published on how birds use these subtle differences to make behavioral decisions. While the current study does not address what acoustic features Galahs could use to discriminate between the sexes (Scarl, in prep), it demonstrates that subtle sex differences encoded in at least one type of Galah call are relevant to this species. In addition, these experiments demonstrate that while males and females differ in their

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vocal behavior, the sexes are similar in their approach to conspecific calls and this may be a result of pair coordination of behavior.

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CHAPTER 3

Heightened responsiveness to female-initiated aggressive interactions in Galahs

Abstract

In many socially monogamous, territorial species, males and females will coordinate their behavior to defend a territory, and two aggressive individuals are generally more threatening than a solo individual. Even when a pair coordinates defense, though, individuals often respond more strongly to same-sex intruders, or one sex will consistently initiate the pair's aggressive vocal interactions. This study investigates whether male-female pairs in a socially monogamous Australian cockatoo, the galah, coordinate their behavior in response to a vocal threat signal, the Scree call, and whether these birds respond more strongly to Screes from two individuals rather than a solo individual. Solo male Scree calls, solo female Scree calls, paired Screes in which a male called before a female, and paired Screes in which a female called before a male, were presented to pairs of galahs establishing themselves at nest cavities during the pre-breeding season. Birds responded most strongly to female-initiated Scree bouts, regardless of the number of stimulus birds giving vocalizations. While paired birds coordinated their approach responses to the stimuli, males tended to initiate these responses. These results suggest that the sex of the bird initiating a Scree interaction, rather than the number of birds giving Scree calls, is most relevant to galahs when assessing threat near an active cavity.

Introduction

In some territorial, socially monogamous species, both members of the pair engage in defense of the nest or territory (Kraaijeveld and Mulder 2002; Mennill

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2006). Often, both sexes will defend against nest predators by alarm calling, mobbing, or performing a display such as injury feigning to lead a potential predator away from the nest site (Montgomerie and Weatherhead 1988). In many species, males and females also coordinate defenses against conspecific competitors either through joint visual displays such as triumph ceremonies in geese and swans (Kraaijeveld and Mulder 2002) or through coordinated vocal displays such as duetting in songbirds (Hall 2000) and some primates such as gibbons (Leighton 1987). These coordinated displays are often more threatening than similar behaviors performed by a solo individual (Hall 2000; Molles and Waas 2006).

Even when both members of a pair defend a nest, pronounced sex differences in defense behavior can exist. In defense against predators, the relative costs associated with defense may differ for males and females based on relative resources, certainty of paternity, or ability to raise a brood alone or renest, and likewise the relative benefits of brood defense will vary accordingly (Montgomerie and Weatherhead 1988). In addition, when defending against conspecific threats, individuals will often respond more strongly to same-sex intruders (Logue and Gammon 2004; Mennill 2006), and in some duetting species, such as the eastern whipbird (*Psophodes olivaceus*) (Rogers 2005) or the slate-colored boubou (*Laniarius funebris*) (Wickler and Seibt 1982), the male always initiates the duet, while it is the female who initiates the duet in other species (Langmore 1998; Wright and Dahlin 2007).

Unlike many territorial mammals and birds, most parrots only defend a very small area around their nest cavity rather than a larger territory (Rowley 1990; Heinsohn and Legge 2003). However, since most species of parrots are obligate cavity-nesters, they often face high levels of competition over cavities from both conspecifics and heterospecifics (Newton 1994; Heinsohn et al. 2003), as well as

predation risks (Bradbury 2003). In many parrot species, both parents invest heavily in nestling care and nest defense (Rowley 1990; Bradbury 2003), although since many species of parrots are physically monomorphic, previous studies of nest defense behavior often do not indicate the sexes of the participants (Heinsohn et al. 2003).

Galahs (*Eolophus roseicapillus*) are a cavity-nesting species of Australian cockatoo. Males and females form socially monogamous pairs and share in all aspects of parental care including nest-building, incubation, and nestling and fledgling care (Rowley 1990). Cockatoos suffer from both reptilian and mammalian predation (Saunders 1979, 1982) as well as conspecific and heterospecific competition over nest cavities (Rowley 1990), and both parents play a role in nest defense. Males and females produce an aggressive vocalization, the Scree call (Figure 3.1), when defending against a heterospecific threat (Pidgeon 1981), and when establishing or advertising ownership of their nest cavity (Rowley 1990). While differences between male and female Scree calls are not documented, my own observations suggest that these calls may differ acoustically by sex. Near a cavity, often the male and female will call together, and Rowley (1990) suggests that joint Scree calling may also be involved in maintaining the pair bond. However, either pair member can produce this call without the partner responding.
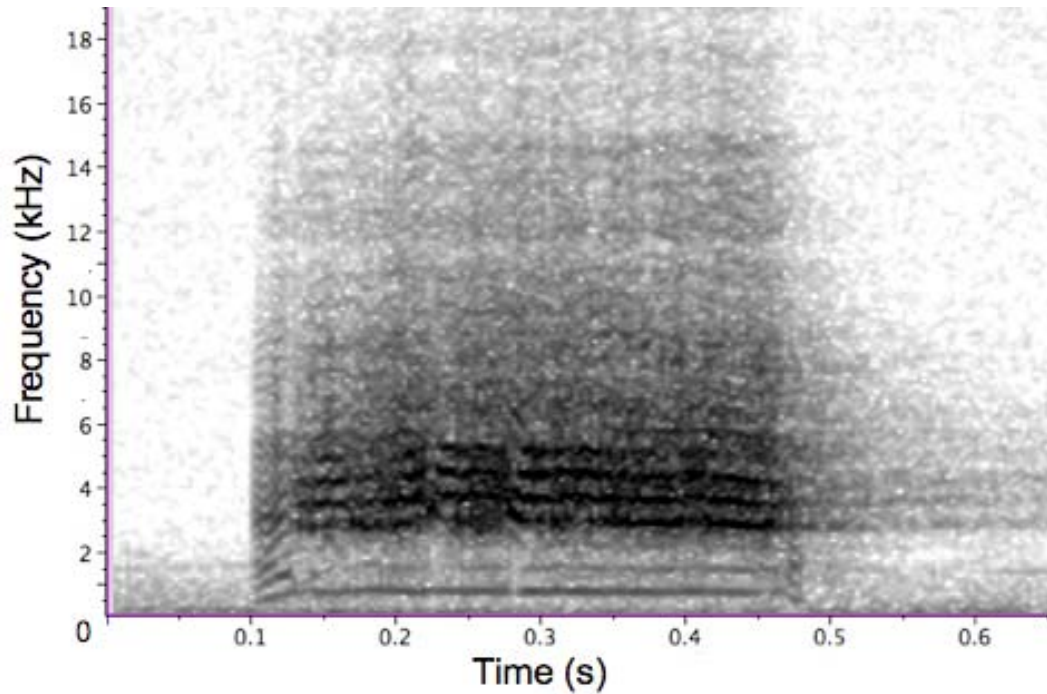
Figure 3.1. Spectrogram of a Scree call.

I conducted a study on wild galahs to examine the defensive behavior of pairs of birds during the pre-breeding season. This study addressed two questions. First, do the sex and number of conspecific individuals producing Scree calls near a desirable nest cavity influence the response of the birds attempting to establish ownership of that cavity? Second, do male and female galahs coordinate their behavior when confronted with conspecific Scree calls near their cavity, and if so, is one bird more likely to initiate this behavior than the other?

Methods

Study Site and Schedule

This research was conducted on a population of galahs in the northeastern section of Canberra, Australia (S 35 15' E 149 10'). The study site was a local nature park consisting of mature eucalypt forest interspersed with small cleared fields, horse

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paddocks, and pedestrian trails. Galahs used this park for both breeding and feeding during the time of the study and were habituated to the presence of humans.

I conducted playback experiments from 11 August to 17 September of 2006. This period is late winter in the southern hemisphere and corresponds with the early galah breeding season. During this period galahs are prospecting at potential cavities, lining nests, and beginning to lay eggs. During prospecting, birds often investigate many potential cavities within their range, and established cavity owners repel intruders (Rowley 1990). In addition, birds are quite responsive to potential predators in breeding areas during this period (Scarl, personal observation). All playbacks with the exception of two trials were conducted during this initial prospecting period, before the target pair began incubating eggs.

Subjects

When a pair of galahs is interested in a potential nesting cavity, they perform a number of stereotyped displays, or prospecting behaviors, which involve bowing into the cavity, waving sprays of eucalyptus both in the vicinity of the cavity and at the cavity entrance, and performing a Heraldic display, in which the galah will spread its wings, bow its head, partially or fully erect its crest, and often give a Scree call (Rowley 1990). In addition, galahs will enter a potential cavity, spend a great deal of time near the cavity, and sit very close to their mate next to the cavity. For this experiment, I selected fifteen pairs of galahs that had been observed performing at least two of the prospecting behaviors listed above on two separate days at the same cavity. All pairs consisted of at least one individually marked bird, so I was able to determine when the same pair was investigating a particular cavity. Adult galahs differ

in eye color by sex (Forshaw 1973), so I was also able to determine the sexes of each pair member.

Stimulus Preparation and Presentation

To obtain and create stimuli for playback, fifteen male and fifteen female Scree vocalizations were recorded from the same population of galahs from birds of known sex and identity. Subject individuals in this experiment were never presented with their own Scree calls. All stimulus calls were recorded using a Sennheiser MKH 816 or ME67 microphone into either a Marantz PMD690 or an HHB portaDAT PDR1000. Prior to playback, each Scree call was high-pass filtered at 200 Hz to remove low-frequency background noise. Each call was then amplified to the maximum level possible without overloading or distorting the signal; this ensured that all stimuli were broadcast at the same output amplitude. All manipulations were conducted using Syrinx sound analysis software (www.syrinxpc.com).

I attempted to present each pair with four sets of stimuli in random order. Each stimulus set consisted of fifteen calls or call sets. In two of the stimulus sets, I presented a single male Scree repeated 15 times or a single female Scree repeated 15 times with 3000 milliseconds between each presentation (solo treatment). In the other two stimulus sets, I presented a male Scree followed by a female Scree, or a female Scree followed by a male Scree, repeated 15 times at 2500 millisecond intervals with 50 to 60 milliseconds between the male and female Scree (pair treatment). The overall length of the solo and pair playbacks were the same on average, with minor variance due to naturally-occurring differences in Scree lengths; male screes presented for playback had an average duration of 490.3 milliseconds (+/- 117 milliseconds; range 316-636 milliseconds) and female scree stimuli had an average duration of 492.1

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milliseconds (+/- 104 milliseconds; range 317-682 milliseconds). The stereo playback stimuli were consolidated in SoundEdit 16 (Macromedia, 1997), and all stimuli were broadcast using Syrinx (www.syrinxpc.com).

I used the same male and female Scree exemplars in each of the four playbacks to a given pair, but no Scree exemplar was used in playbacks to more than one pair. To minimize disruption at potential nest sites and the chance of habituation, I never conducted more than one playback to the same pair in a single day, and I never presented any pair with playbacks on more than two consecutive days. Because of these restrictions, I was unable to present all pairs with all four stimulus sets. Some pairs abandoned their nesting attempt before they received all trials, and other birds began incubating before their trial set was completed; once a pair was incubating, it was impossible to conduct a playback when both birds were outside of the cavity at the same time. Thus, eight pairs received all four stimulus trials, one pair received three stimulus sets, two pairs received two stimulus sets, and four pairs received only one trial, for a total of 43 trials.

Speaker Setup

Speakers were hung from existing tree branches, and thus I used a distance range for speaker placement, rather than fixed distances. The speakers were disguised as much as possible by natural foliage to simulate a natural interaction in which a Screeing galah was in auditory but not visual contact with listeners. Speakers were set up approximately 5 to 15 meters from the target cavity and ranged from approximately 4-10 meters above ground, depending on branch availability. All speakers faced the cavity. These distances reflected realistic between-cavity distances and represented a compromise between presenting stimuli very close to active cavities to simulate

imminent territorial invasion, and camouflaging speakers behind vegetation to realistically simulate a natural interaction in which birds could hear but not see a vocalizing conspecific.

Since some birds respond differently to duet song played from a solo speaker and duet song played from two separate speakers (Molles and Waas 2006), in the stereo treatments, speakers were placed approximately equidistant from the cavity and between 5 and 10 meters apart, depending on branch availability. This spatial separation also allowed the target birds to approach one playback stimulus without approaching both. Speaker locations were maintained throughout the four trials for each pair; the stimulus sex of each speaker was assigned randomly for each trial.

Playback Protocol

I began the playback when both members of the pair arrived at the nest tree, but neither bird was in the cavity. Stimuli were broadcast from a Sony VAIO laptop computer connected to JBL Control speakers. Two observers recorded each trial onto a Marantz PMD690 digital recorder using a Sennheiser Me67 or MKH816 microphone and noted the start time of the playback along with the vocal and movement responses of each bird. In the majority of trials, both observers reported on each aspect of both birds' behavior, but when the target birds were very active one observer verbally identified which bird (male or female) produced each response vocalization throughout the trial, whereas the other observer focused on reporting the specific movements of each bird.

Response Measures

I utilized two overall response measures: approach and vocalization. When a bird left its original perch by flying or jumping, or when it walked more than 0.5 meters from its original position, I coded its behavior as an approach. I measured both the first approach distance- how close the bird came to the speaker the first time it moved during the playback- and closest approach distance over the course of the trial. The first member of the pair to approach was considered to initiate the approach. For all birds that approached during a playback trial, I also measured the change in a bird's distance in relation to the speaker from the start of the playback to when the bird first moved (initial change in distance) and from the start of the playback to the end of the playback (end change in distance). For all trials in which a bird vocalized, I noted the time of the first vocalization for each bird and the number and type of vocalizations given by each bird.

Statistical Analysis

I included all trials in the analysis to determine whether or not birds responded to the stimulus as a pair. When neither member of the pair gave the target response (approach or vocalize), or when both members of the pair gave the target response, the pair was said to act as a unit. When either the male or the female, but not both, gave the target response, each member of the pair was said to behave independently of the other. To determine which bird initiated a response, I only analyzed trials in which at least one bird produced the target response. Thus, a bird was counted as the initiator of a specific behavior if it acted alone or if it was the first member of the pair to perform that behavior. To determine whether initiation or extent of behavior were

affected by sex or the number of callers, I used all trials to determine whether birds were more likely to initiate approach or calling behavior to specific stimulus types. Since most pairs of subjects received more than one stimulus set, I included an analysis of the effect of stimulus presentation order for each response measure.

For the binomial responses of whether a bird approached or vocalized in a given trial, I used a generalized estimating equation (proc genmod in SAS) with a binomial distribution, a logit link, and group as a random effect; this is a form of logistic regression that allowed for the repeated measures of subjects within groups. For continuous data (latency to first approach, latency to first vocalization, number of vocalizations, distance to speaker) I ran a mixed or multilevel model (proc mixed in SAS) with pair and subject within pair as random factors, controlling for the repeated measures of individuals in these trials. Type of stimulus (stimtype), sex of the responding bird (respsex), and the order of trial presentations (order) were all included as fixed effects in these models and thus I was able to determine how responses were influenced by each factor while controlling for the others. For analyses of vocalizations, the independent variable "stimtype" had four levels (solo female, solo male, female-then-male, male-then-female), but since birds could approach one speaker independently of the other within a paired-speaker trial, analyses of approach behaviors by stimulus type had six levels for "stimtype" (Solo Female speaker, Solo Male speaker, Female First speaker, Male Second speaker, Male First speaker, Female Second speaker). Initially, I included the second-order interaction effects of sex*order and sex*stimtype in all models, but when they were non-significant I removed them from a given model. These statistical analyses were done in SAS version 9.1 (SAS Institute Inc., 2002-2003, Cary, NC, USA).

Compliance

This research was approved under IACUC #1998-0102 (Cornell University) and complied with Ethics permit F.BTZ.71.04 issued by the Animal Experimentation Ethics Committee at the Australian National University. All trapping and tagging of birds was approved by the EnvironmentACT (License LT2004122 and LT2005156) and the Australian Bird and Bat Banding Scheme (bander license 2649).

Results

RESPONSE BY STIMULUS SEX/NUMBER

Approach Responses

Birds approached Female-Then-Male and Solo Female stimuli more quickly than Solo Male or Male-Then-Female stimuli (Figure 3.2); post-hoc pairwise comparisons indicate that birds initially approached Female-Then-Male stimuli significantly more quickly than Solo Male (t_{27}=4.26, p=0.0002) and Male-Then-Female stimuli (t_{35}=2.37, p=0.0234). Birds also approached Solo Female stimuli more quickly than Solo Male (t_{35}=2.82, p=0.0078) and Male-Then-Female stimuli (t_{25}=-2.38, p=0.0252). Birds did not differ in how quickly they approached Solo Female and Female-Then-Male stimuli (t_{35}=0.86, p=0.3973) or Solo Male and Male-Then-Female stimuli (t_{35}=0.98, p=0.3359). This effect depended on the order of presentation, as indicated by a significant interaction between stimulus type and presentation order ($F_{5,24}$=6.10, p=0.0009). These differences in approach timing demonstrated consistent trends for each order and differed largely in magnitude; stimulus type by itself was also highly significant both when the interaction was accounted for ($F_{3,25.6}$=0.0084) and when the second-order term was removed ($F_{3,29.6}$=7.33, p=0.0008).
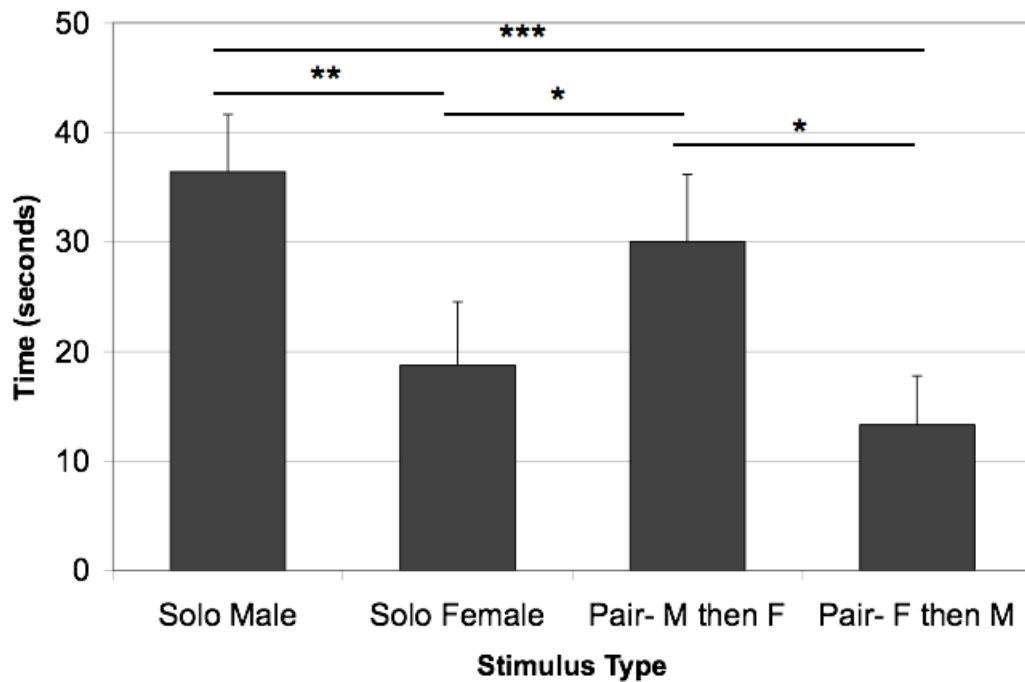
Figure 3.2. : Mean time to first approach for four types of call stimuli. Birds initially approached female-initiated stimuli more quickly than male-initiated stimuli. Error bars represent standard error.
* p<0.05, ** p<0.01, ***p<0.001

To determine whether birds approached certain stimulus types more closely than others, I only considered trials in which birds moved during the experiment. Since birds could start at different distances from the speaker, I controlled for a bird's distance to the speaker at the start of the playback by including this variable as a fixed effect in the mixed model. By the end of the trial, birds differed significantly in how close they had moved towards each stimulus (Figure 3.3: $F_{5,33.7}=4.33$, p=0.0038). Pairwise comparisons indicated that by the end of the trial, birds had approached Solo Female stimuli significantly more closely than Solo Male ($t_{40}=2.82$, p=0.0075), Female Second ($t_{43}=2.70$, p=0.0098), and Male First stimuli ($t_{40}=3.79$, p=0.0005). Birds also approached Female First stimuli significantly more closely than Solo Male

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$(t_{20}=2.43, p=0.0242)$, Female Second $(t_{17}=2.20, p=0.0417)$, and Male First $(t_{17}=3.05, p=0.0073)$ stimuli. In addition, birds approached Male Second stimuli more closely than Solo Male $(t_{20}=3.02, p=0.0067)$, Male First $(t_{17}=3.59, p=0.0023)$, and Female Second stimuli $(t_{17}=2.76, p=0.0134)$. Due to the small sample size, I did not perform corrections for multiple testing, but a greater number of comparisons were found significant than would be expected by chance. Although there were no significant differences in how closely birds approached the different stimuli in their first approach to the speaker $(F_{5,29}=1.47, p=0.2292)$, the trends were in the same direction as the end distance data.
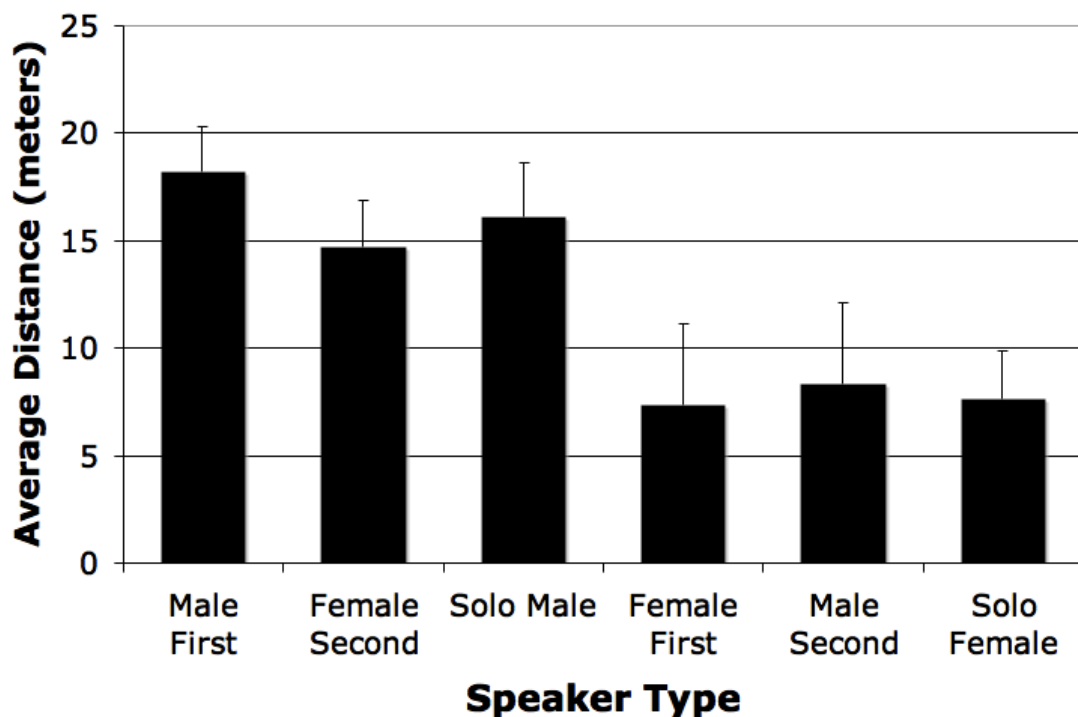
Figure 3.3. Distance to speaker at end of playback for orders 1 and 2. In paired stimulus playbacks, birds could approach either speaker independently of the other. At the conclusion of playbacks, birds were significantly closer to solo female, female-first, and male-second speakers than they were to solo male, male-first, and female-second speakers. Error bars represent standard error.

Vocal Responses

Birds were equally likely to vocalize to all four stimulus types (X^2_3=0.81, p=0.8476) and the interaction between sex and stimulus type was not significant (X^2_3=1.45, p=0.6949), indicating that neither males nor females changed their vocal behavior based on stimulus type. The number of vocalizations produced in response to each stimulus class also did not differ ($F_{54.9,3}$=0.24, p=0.8648), and once again the interaction between sex and stimulus type was non-significant ($F_{3,53.8}$=0.61, p=0.6125).

RESPONSE BY SUBJECT SEX

Approach Responses

In 24 out of 43 total trials (56%), at least one member of the focal pair approached the playback speaker. Overall, males and females were equally likely to approach a speaker playing a Scree stimulus; males approached in 21 trials and females approached in 17 trials (X^2_1=1.90, p=0.1684). Members of a pair approached or did not approach as a unit (both birds approached in 15 trials; neither bird approached in 17 trials) more often than they approached individually (male responded alone in 7 trials; female responded alone in 2 trials); the odds of birds responding together were 3.55:1 (Z=3.55, p=0.0004) indicating that birds were more likely to respond together than separately. In addition, there were no significant differences in the latency to first approach for males and females (average latency to first approach= 16.19 seconds for males, 16.58 for females; $F_{1,18.9}$=0.02, p=0.8917) indicating that male and female approaches often occurred very close together

temporally; in 13 out of 17 (76%) trials in which both birds approached, birds approached within 1 second of each other.

It is possible that this effect was caused by high levels of responsiveness in both birds at earlier orders and low levels of responsiveness in both birds at later orders, rather than a between-birds coordination of behavior; if this were the case we would expect to see the highest levels of behavioral concordance at orders 1 (often respond) and 4 (infrequently respond). However, the highest levels of concordance were at orders 1 (X^2_1=6.12, p=0.0134) and 3 (X^2_1=3.31, p=0.0691), which suggests that an overall decline in responsiveness is probably not the only factor influencing this behavioral concordance.

Although pairs frequently responded together, males initiated 71% (17 out of 24) of all first approaches to the speakers (Figure 3.4: X^2_1=4.26, p=0.0389) regardless of the order of stimulus presentation (order X^2_3=5.10, p=0.1644). There were no significant interactions between sex and stimulus type in determining the initiation of first approach (X^2_3 =4.51, p=0.2113), indicating that males were more likely to initiate the first approach regardless of the stimulus presented.

Comparison of Initiations by Sex
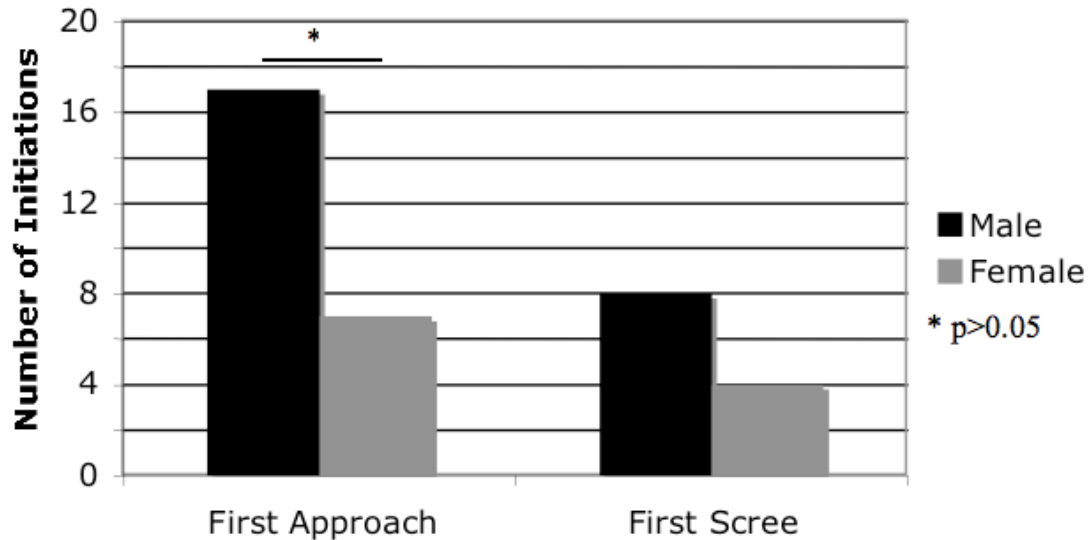
Figure 3.4. Comparison of behavioral initiations by responding bird sex. Males initiate significantly more first approaches to stimuli than do females. There is a similar but non-significant trend for first Scree initiation. Males and females are equally likely to approach a stimulus overall, and all trials in which at least one member of a pair approached are considered in this analysis (n=24). Since males give more calls overall than females, only trials in which both members of a pair give a Scree call are included in the first Scree initiation analysis (n=12).

Vocal Responses

In 28 out of 43 trials (65%) at least one bird produced a vocalization in response to the playback. When birds responded vocally, they gave significantly more Screes than any other vocalization (two-tailed t-test or matched pairs; $p<0.0001$); a subject bird gave a Scree call in 65% (28 out of 43) of total trials, and focal galahs gave a total of 155 Scree calls across all 43 trials. The next most common vocalization given was the Chewp, an alarm or alert call (Forshaw 1973). Birds gave Chewp calls in 21% (9 out of 43) of trials and gave a total of 27 Chewps across all 43

trials. It was rare for any of the subject birds to give any other vocalizations during this experiment; a total of 11 other vocalizations were given in 6 trials. I included all vocalization types in subsequent analyses of vocal behavior.

Birds vocalized more to earlier trials than to later ones ($F_{3,54}$=9.65, p<0.0001), and males were more likely to vocalize than females (X^2_1=4.26, p=0.0389) and gave more vocalizations overall ($F_{1,13.8}$=7.77, p=0.0147). However, unlike with approach behavior, males and females did not differ significantly in their likelihood of being the first to call within a trial (Figure 4: X^2_1=1.58, p=0.2087). The odds of birds both vocalizing or both not vocalizing during a trial were 2.52:1 (Z=3.07, p=0.0021), indicating that birds were more likely to behave in concordance with each other than to behave differently from each other. In 4 out of 15 (27%) trials in which both birds vocalized, members of a pair produced their first vocalization within one second of each other, and birds vocalized within 5 seconds of each other in 3 additional trials. When both birds vocalized in a trial, the average difference between their latency to first call was 9.6 seconds (SD 10.2 seconds). However, birds were most likely to do the same thing (both vocalize or both remain silent) during a trial at orders 1 (X^2_1=4.68, p=0.0305) and 4 (X^2_1=3.50, p=0.0614) which may simply indicate that both birds were very vocally responsive to initial stimuli and vocally unresponsive to later stimulus presentations. Thus, while birds showed some behavioral concordance in their vocal behavior, these similarities were less pronounced than for approach behavior.

Discussion

In this experiment, galahs responded differently to conspecific Scree calls in the vicinity of their nest based on both the sexes of the sender and receiver. Galahs demonstrated heightened responsiveness to conspecific Scree stimuli bouts that were

female-initiated, regardless of the number of birds in the interaction. In addition, while males and females tended to approach conspecific Scree stimuli in pairs, males tended to initiate these approaches, and males vocalized more than females in response to aggressive playbacks.

Typically, when animals respond differently based on the sexes or numbers of intruders, territorial animals will respond most aggressively either to conspecific intruders of their own sex (Mulder et al. 2003; Logue and Gammon 2004; Mennill 2006) or to pairs of intruders rather than single intruders (Hall 2000; Molles and Waas 2006). In some species, such as the Australian magpie-lark (*Grallina cyanoleuca*), pairs respond more strongly towards the initiator of a two-bird vocalization bout (Rogers et al 2004), but these results are not specific to one sex or the other. In this study, however, males and females responded most strongly to solo female Screes or paired Screes in which a female called before a male; that is, they responded most strongly to female-initiated Scree bouts. Thus far, a biased response towards female-initiated joint stimuli has not been documented in other species.

There are several potential explanations for why pairs of galahs may respond more strongly to female-initiated Scree interactions. My own observations suggest that males may be more likely than females to give a Scree call when they are not in the presence of their mate (Scarl, unpublished data). Thus, female Scree calls may be more reliable indicators of the presence of a pair, which often generates a heightened response from territorial conspecifics (Hall 2000). However, this does not explain why galahs respond more strongly to female-initiated paired Scree bouts over male-initiated paired Scree bouts, both of which should signal the presence of two aggressive birds. Perhaps since males initiated the majority of approach responses in this experiment, males approach females more quickly and closely for extra-pair copulation opportunities, and that their females follow them to mate-guard. Female

responsiveness to male behavior as a method of mate-guarding has been observed in some duetting species (Seddon and Tobias 2005; Rogers et al. 2006). This hypothesis seems unlikely for galahs, however, as the Scree is an aggressive vocalization given when a bird is threatened, rather than an advertisement of quality or availability per se. Also, female Screes in paired trials were always closely coupled with male Screes, which should suggest that the calling female had a mate nearby; in previous studies that suggest that females are mate-guarding against rivals, females responded most strongly only to solo invading females rather than pairs (Seddon and Tobias 2005; Rogers et al. 2006).

A third possibility for why there were stronger responses to female calls is that since females are less likely to give Scree vocalizations overall, the threshold for a female to Scree is higher than a male's threshold, and thus female Screes, or at least female initiation of repeated Scree interactions, indicate a more threatening situation than similar vocal bouts initiated by males. Similarly, since galahs give Scree calls in several situations, it is possible that females are more likely to initiate Scree bouts in qualitatively different situations than males. If females initiate Scree bouts in situations that usually have high levels of threat, galahs may develop heightened responsiveness to female-initiated Scree interactions. To investigate this possibility, the situations in which males and females initiate Scree bouts, and the levels of corresponding threat, would need to be quantified.

A second finding of this experiment is that males and females behaved in concordance with each other, as both birds approached or did not approach more often than one bird approached on its own. This behavioral concordance does not seem to simply stem from heightened responsiveness in both pair members during early trials and decreased responsiveness in later trials. Rather, these results may suggest that birds benefit from behaving together. Doing things together has been suggested as a

mechanism of reinforcing the pair bond in some species (Wickler 1980; Rowley 1983), and this behavioral concordance may be a measure of pair solidarity; Rowley (1990) suggests that joint Scree displays may serve to reinforce the pair bond. In addition, in many species, there is an increased effectiveness of defense by two individuals than by one (Robinson 1985; Seddon and Tobias 2003); two galahs may be better able to drive off intruders than one, whether the intruders be conspecific competitors or heterospecific threats.

While members of a pair behaved in concordance with each other, males were more likely to initiate the first approach towards a stimulus than females, regardless of stimulus type, which suggests that males take the lead in approaching conspecific Scree stimuli. Mathematical models predict that in a group, leaders and followers should emerge to initiate group activity (Rands et al. 2003; Dostalkova and Spinka 2007), and previous avian research indicates that in some duetting species, in which males and females coordinate vocal behavior, one sex always initiates the duet (Rogers 2005, Wickler and Seibt 1982, Langmore 1998, Wright and Dahlin 2007). However, little is known about initiation of movement in pairs of birds during territorial or threat interactions, and this experiment demonstrates that while male and female galahs are equally likely to initiate vocal behavior, and both sexes defend against threat, males seem to instigate approaches to conspecific threat stimuli, regardless of the sex of the stimulus source.

This sex difference in initiation of behavior was not present for vocal behaviors. Males were more likely to call and gave more calls overall, but males and females were equally likely to be the first member of the pair to call in response to a Scree stimulus. Pairs showed a tendency to vocalize or refrain from vocalizing together, but these concordances were most significant in the first and fourth trials

presented, which may simply reflect a high level of initial responsiveness in both birds, independently of each other, followed by a period of habituation.

These results may reflect the differing levels of risk associated with approaching and vocalizing in response to a threat stimulus as indicative of the different investments males and females put into defense. Curio and Regelmann (1985) suggest that risk of predation increases as distance to a predator decreases, and in conspecific interactions, closely approaching a competitor can lead to a physical fight (Rowley 1990). In addition, an increase in vocalization rate is often used as a measure of increased levels of aggression or competition (Dabelsteen et al. 1997; Langmore and Davies 1997). Male galahs, by vocalizing more and approaching first, thus seem to assume a more risk-prone strategy. While the sex roles of galahs in relation to breeding are less dichotomous than for many other species, males do vocalize more overall in some situations (Scarl In revision) and are on average slightly larger than females (Forshaw 1973; Rowley 1990), factors which support the idea that males may play a more active or risk-prone role in territory or mate defense (Andersson 1994). In addition, this study was conducted immediately prior to and during the laying period for most pairs, and in some species, females take fewer risks during nest defense, especially immediately after egg-laying, as a result of depleted resources (Reid and Montgomerie 1985).

This study provides additional evidence that wild parrots can identify the sex of conspecific vocalizations and respond differentially based on the sex of the caller even in response to call types that are shared by both sexes (Balsby and Scarl 2008; Scarl and Bradbury In revision), which indicates that parrots can assess the sex of a potential interaction partner without being in visual contact with that bird. More specifically, this experiment demonstrates that the sex of the galah initiating a Scree bout, rather than the number of birds in the interaction, influences the response of

paired birds at a cavity. Paired galahs respond strongly to female-initiated aggressive vocalizations near active cavities early in the breeding season, regardless of whether a male also vocalized. While males and females tend to respond to these vocalizations together, males seem to display a heightened responsiveness to these broadcast Scree calls. This experiment is the first to demonstrate that pairs of monogamous birds demonstrate joint responsiveness to female-initiated conspecific threat vocalizations, and it supports the idea that performing behaviors together may be important to the pair bond in a socially monogamous species.

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CHAPTER 4

Sex-specific responses to vocal convergence and divergence of contact calls in orange-fronted conures (*Aratinga canicularis*)[2]

Abstract

We investigated the signal function of vocal imitation of contact calls in orange-fronted conures (*Aratinga canicularis*) in Costa Rica. Orange-fronted conures live in dynamic social systems with frequent flock fusions and fissions. Exchanges of contact calls precede these flock changes. During call exchanges, the similarity between the contact calls of different individuals may either increase (converge) or decrease (diverge). We conducted a playback experiment on wild-caught, captive birds in which we simulated convergent, divergent, and no-change interaction series with male and female contact calls. Orange-fronted conures responded differently to convergent and divergent series of contact calls, but only when we considered the sex of the test birds. Males called most in response to convergent series, whereas females demonstrated high calling rates in response to both convergent and divergent interactions. Both sexes responded most to contact-calls from the opposite sex, but overall females produced more calls and had shorter latencies to calling than males. These results demonstrate that orange-fronted conures can discriminate between male and female contact calls and that subtle changes in contact call structure during interactions have signal function. The stronger overall response to convergent series suggests that convergence of contact calls is an affiliative signal.

Introduction

In vocal interactions, several species match song or call types. This matching can serve different functions ranging from escalation of a vocal conflict to the promotion of flock cohesion (Vehrencamp 2001, McGregor *et al.* 1993, Marler 2004). The mechanisms with which animals match vary by species. In some birds, song types must be acquired during a critical period and there is little augmentation of the repertoire later in life (Hultsch & Todt 2004); in these species, adults can match only those other individuals with whom they already share basic call types. Other species have the ability to modify their existing vocalizations throughout their lives. These changes generally occur gradually over the course of days or weeks (Hile & Striedter 2000; Hile *et al.*, 2000; Snowdon & Elowson, 1999; Bartlett & Slater, 1999) although there is limited evidence that certain species, such as bottlenose dolphins, can produce a new sound with little or no prior learning (Richards *et al.* 1984).

In species that form long-term stable groups or pairs, contact calls often show structural similarity within these groups. Examples include species within the passerines (Marler & Mundinger 1975, Mundinger 1979, Grooth 1993), non-passerine birds (Hile *et al.* 2000, Wanker & Fisher 2001), bats (Boughman 1997) and primates (Elowson & Snowdon 1994, Mittani & Brandt 1994). In groups of unrelated individuals, these similarities may develop through a learned convergence of contact calls. This convergence may serve an affiliative function, as it often accompanies group or pair formation (Mundinger 1979, Mammen & Nowicki 1981, Nowicki 1989, Saunders 1983, Farabaugh *et al.* 1994, Bartlett & Slater 1999, Hile & Striedter 2000). Generally, such convergences in long-term groups seem to take a minimum of two weeks (Mundinger 1979, Nowicki 1989, Bartlett & Slater 1989). The resulting contact-call similarity among group members functions as a group tag that allows

flock members to discriminate between group and non-group members (Boughman 1997).

In social species that form unstable or transient groups, such as the fission-fusion societies of bottlenose dolphins (*Tursiops truncatus)*, spider monkeys (*Ateles geoffroyi*), and orange-fronted conures (OFCs), an exchange of contact calls precedes and may mediate the formation of groups (Connor *et al*. 2000, Fernandez 2005, Bradbury *et al*. 2001). Both bottlenose dolphins and OFCs demonstrate very rapid convergence of contact calls, with individuals changing their calls over the course of a single interaction (Janik 2000, Balsby & Bradbury in prep.). These rapid convergences may function as a declaration of intended affiliation by the callers within a transient group, and/or they may allow individuals to address specific other individuals (Janik & Slater 1997, Janik *et al.* 2006). However**,** the signal function of these fast contact call convergences has not yet been demonstrated experimentally.

Orange-fronted conures live in a fission-fusion social system with daily changes in flock composition (Bradbury *et al.* 2001). During flock encounters, OFCs exchange contact calls which may converge or diverge (i.e. increase or decrease in overall similarity) relative to the calls of other interactants; these vocal modifications occur within a few seconds (Vehrencamp *et al.* 2003, Balsby & Bradbury in prep.). In this paper we address two questions. First, we investigate whether signal convergence and signal divergence elicit different responses from OFCs, indicating that these communication methods have different meanings for the birds. Second, we test whether the sex of either the sender or the receiver influences how birds perceive convergent and divergent stimuli. Many animals discriminate between similar vocalizations produced by males and females (Miller *et al.* 2004, Vicario *et al.*, 2001), and some call or song matching mediates sex-specific interactions such as male-male competition (Vehrencamp 2001) or mate affiliation (Moravec *et al.* 2006).

Methods

We conducted this experiment between June 27 and July 28 2005 in Santa Rosa National Park, Area de Conservacion de Guanacaste, Costa Rica (10°, 52.63´ N, 85°, 34.18´ W). We mist-netted 16 orange-fronted conures from two different locations that were approximately 3 km apart. Each subject bird was individually housed for 4-7 days in one of three aviaries (dimensions 3.5x1.8x1.8 m) located at least 300 m apart in habitat used daily by orange-fronted conures. During this time all birds had *ad libitum* access to water and their natural food at this time of year (Nancite fruits *Byrsomia crassifolia*). We banded all birds housed in the aviary to ensure that no birds were tested twice. Because OFCs are sexually monomorphic (Juniper & Parr 1998) we determined sex using molecular techniques at the conclusion of the experiment (Griffiths *et al.* 1998, Balsby *et al*. submitted); we did not know the sex of any of the subject birds during the experiment. The molecular sexing indicated that we used 10 males and 6 females as subjects for playbacks.

The vocalization that we used exclusively in this experiment was the "chee," the main contact call used by OFCs (Bradbury 2003). For each subject bird we recorded baseline chees to define a standard call for that bird. Because OFCs modify their chees substantially during interactions (Vehrencamp *et al.* 2003), baseline chees could only be recorded when the subject bird was not interacting with other birds. We used a Marantz PMD 670 or PMD 690 hard disk recorder and a Sennheiser MKH 816T to record the subject birds' baseline chees as well as their responses to playback; these vocalizations were recorded 1 m from the aviary. We computed the overall similarity of the subject bird's own chees by performing spectrographic cross-correlations on 20-40 of the subject's bird's baseline chees using SpecX (Cortopassi & Bradbury 2000, 2006); this program compares each call to every other call, and for

each pair, determines a cross-correlation similarity index that ranges from 0 (no similarity) to 1 (identical). An average similarity measure for each call was defined as the average of the cross-correlation of that call with all the other solo calls. We then selected the 10 baseline chees from each subject bird that had the highest overall average similarity measures as the standard set for that bird.

The stimulus calls were recorded from 8 known-sex captive individuals at our study site using "Chickadee" acquisition software (John Burt www.syrinxpc.com) on a PC (Sony VAIO PGRX 770) with a Nidaq acquisition card (model 6062E) and an omnidirectional microphone (designed by R. McCurdy at the Bioacoustic Research Program, Cornell Lab of Ornithology) placed 1.5 m from the aviary. The contact calls from a source bird of a given sex were first cross-correlated with the 10 baseline chees of the subject. This allowed us to divide stimuli into "divergent" (average similarity values between 0.15 and 0.25 in relation to the subject bird's calls), "convergent" (average similarity of between 0.55 and 0.65) and "no-change" calls (average similarity of between 0.35 and 0.45.).

Each subject received playbacks of the three levels of similarity using calls from one male conspecific and one female conspecific. All broadcast stimuli were played back interactively using the sound program "Syrinx" (Burt www.syrinxpc.com) from a PC (Sony VAIO PGRX 770) amplified by a Harman Kardon CA212 12 W amplifier and broadcast from a JBL Control 1x 50 W loudspeaker. Each subject bird received six playback treatments with two sections each. In the first section of each treatment, we presented the subject bird with 3-5 calls from the stimulus bird that were of average similarity (0.35-0.45) to the subject's own baseline calls. If the subject bird vocally responded to the first section of the playback, we presented the second section of the treatment, in which we presented four divergent, convergent, or no-change calls from the same stimulus bird. Each subject

91

bird received three treatments from a male stimulus bird and three treatments from a female stimulus bird. However, in 5 trials we could not find playback calls that converged (2 trials) or diverged (3 trials) relative to the test birds, which resulted in a total of 91 trials. We played back the male and the female stimuli for each of the treatments in pairs separated by 15 min, whereas pairs of treatments were separated by at least 3 hours. By comparing birds' responses to convergent and divergent stimuli produced by male and female stimulus birds, we hoped to determine whether subject birds perceived convergent and divergent series of calls differently, and whether the sex of either the stimulus or the subject bird was relevant to the interaction trajectory.

Each playback was preceded by a 3 minute pre-playback period and followed by a 3 minute post-playback period in which we recorded the vocal behavior of the subject bird. During playback, subject birds never interacted with sources other than the playback. If wild birds appeared near the aviary and interacted with the subject bird during the post-playback period, the duration of the post playback period was shortened, so only the undisturbed part was used for calculations of the post-playback vocal activity. We shortened the post-playback period in 6 out of 72 trials.

These playbacks were interactive in the sense that if the subject bird responded to a playback call, we played the next call after four seconds, but if the bird did not respond, we waited 15 seconds to play the next call. Once we had broadcast three calls of average similarity in section 1, we progressed to the test section of the playback if the subject bird responded with at least one chee. If the subject bird did not respond during the first three call presentations, we played an additional two section 1 chees: if the bird still did not respond we aborted the trial. We aborted 19 out of 91 trials due to lack of response in the baseline section. The initial baseline playback section had a duration of 38± 3 sec (average ±SE) and the test section on average lasted 32±2 sec

(average ±SE). In all but 4 out of 91 trials, the same chee was not used more than once in a treatment.

Data Analysis

We counted the number of chees in each of the periods and then calculated the rate of calling per minute. Playback of the first stimulus started the baseline section. The first treatment call demarcated the end of the baseline section and the start of the test section. The test section ended 15 sec after the last playback call, at which point the post-playback period started.

To determine how well the subject birds matched our playback, we cross-correlated each subject bird's chees with the specific stimulus chee preceding that particular response chee. We analyzed cross-correlation data using mixed models, which enabled us to block the data for individual and trial in order to account for the random effects in the data set. We used Poisson and binomial distributions when data were not normally distributed. We used generalized linear mixed models (glimmix) assuming a Poisson distribution for the call rates and latency data, and a binomial distribution for the likelihood of response in the test section. The tests assuming Poisson distributions were corrected for over-distribution to avoid an increase in type 3 errors (Littell *et al.* 2005). The generalized linear model also blocked for individual and trial. All models consisted of the three main factors (sex of subject bird, sex of stimulus bird, and type of change) and the second order interaction effects. We used least significant differences (LSD) to test specific post hoc pairwise differences. However, all test subjects only responded to a subset of the six trials they participated in. This results in many missing values, which make the pairwise comparisons weak. We chose not to use further corrections for multiple testing, because significantly more of the post hoc tests are significant than would be expected by chance. All

statistics were calculated using proc glimmix and proc mixed (Littell *et al.* 2005) in

SAS 9.12 (SAS Institute Inc., Cary, North Carolina, USA).

Results

Sex of subject bird

      Females had higher calling rates than males in both the baseline and test

sections of the playback, although this result was not quite significant for the test

section (figure 4.1a, table 1 column A). Female subject birds also responded faster to

playback than male test birds in both baseline and test sections (figure 4.1b, table 1

column A). In general, test subjects produced few contact calls in the post-playback

period, and in this males and females did not differ (table 4.1 column A). Male and

female subject birds did not differ in how closely their contact call responses imitated

the playback (figure 4.1c, table 1 column A).

Figure 4.1a. Sex differences in call rate (mean ±SE) of subject birds. The baseline section is represented by grey bars and the test section is represented by hatched bars. Subj: subject bird. Significant differences relevant to the study are indicated with *.

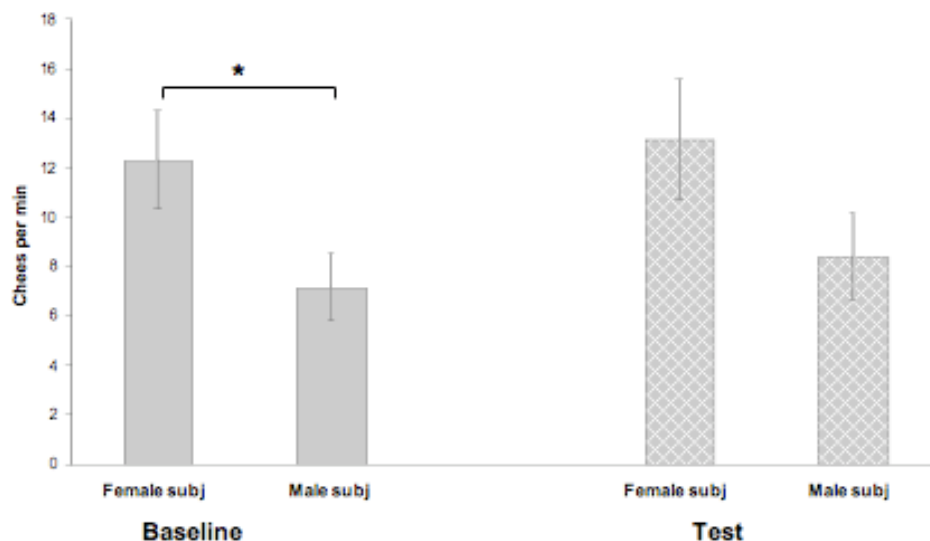**Figure 4.1b.** Sex differences in latency to response (mean ±SE) of subject birds. The baseline section is represented by grey bars and the test section is represented by hatched bars. Subj: subject bird. Significant differences relevant to the study are indicated with *.
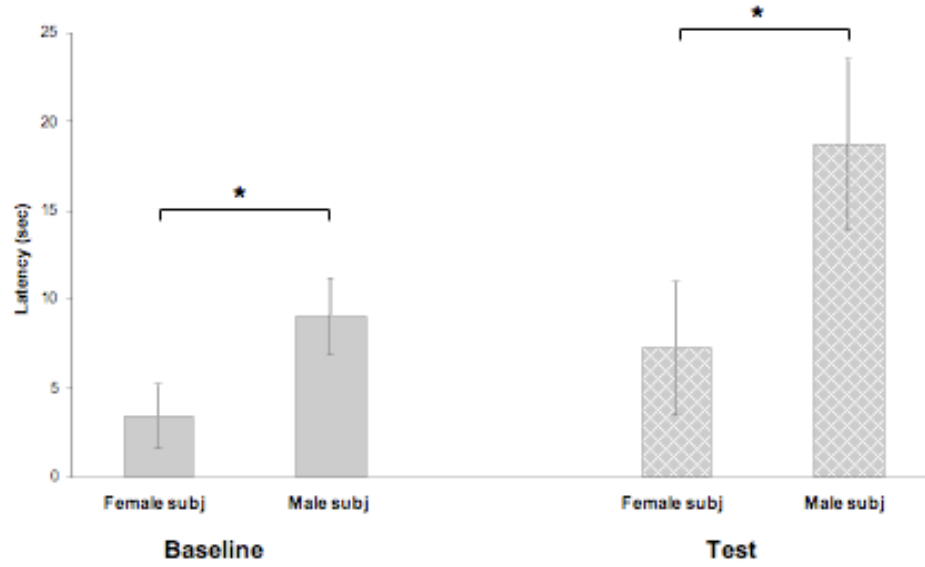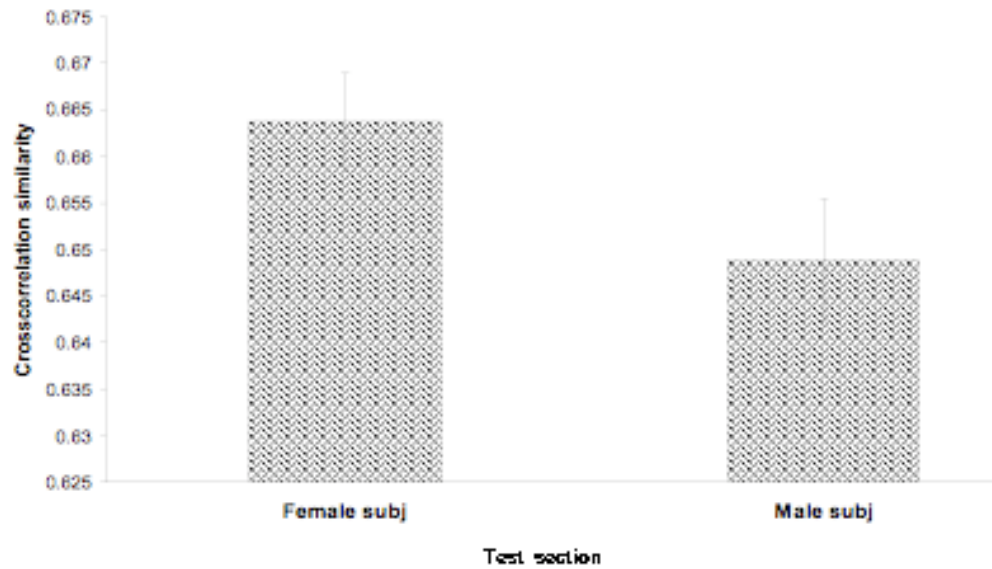

Figure 4.1c. Sex differences in cross-correlation similarity (mean ±SE) of subject birds in the test section. Subj: subject bird.

Sex of stimulus bird

When the sex of the playback stimulus bird was considered alone, it did not seem to affect the rate of calling or the latency to response directly (table 4.1 column B), except that during the post-playback period female stimuli elicited more contact calls than male stimuli (table 4.1 column B). However, when treatment or subject bird sex were considered together with the sex of the stimulus bird (see below), this factor did affect the contact call rate and the latency to calling (table 4.1 columns D & E). The cross-correlation comparing each response call to the stimulus that elicited it showed that birds imitated male and female stimuli equally well (table 4.1 column B).

Sex of subject bird * sex of stimulus bird

There were several significant interactions between the sex of the stimulus and the sex of the subject bird, indicating that males and females responded differently to male and female calls. The interaction between the sex of the stimulus and the sex of the subject bird was significant with regard to latency during both the baseline and test sections (figure 4.2a, table 1 column D). Male subject birds responded more quickly to female stimuli than to male stimuli in both baseline (LSD $t_{27}=3.45$, $p=0.002$) and test sections (LSD $t_{18}=5.28$, $p< 0.001$). Female subject birds also responded more quickly to the opposite sex in baseline (LSD $t_{27}=2.77$, $p=0.010$) and test sections (LSD $t_{18}=4.41$, $p<0.001$). Female subjects responded more quickly to female stimuli than males did to male stimuli, but only during the test section (LSD $t_{18}=2.64$, $p=0.017$).

Table 4.1. Generalized linear mixed model on subject bird's sex, stimulus bird's sex, treatment and the second order interactions for 5 response variables: chee rate in baseline, treatment, and post playback sections and latency in baseline and treatment sections. The mixed models blocked for individual and experiment number, by using these as a random variables. Each line in the table represents one of the response variables. We tested each response variable in a model with 3 factors and 3 interaction effects. For each factor or interaction effect we list the F-value and the p-value (*italics, in parentheses*). P-values significant at the $p<0.05$ level are in bold. The df for chee baseline: $df_{error}=39$, latency baseline: $df_{error}=27$, chee treatment: $df_{error}=28$, latency treatment $df_{error}=18$, chee post-playback $df_{error}=27$, similarity $df_{error}=327$.

Independent variables / Response variables	A Subject birds' Sex	B Stimulus birds' sex	C Treatment	D Subject birds' sex * Stimulus birds' sex	E Subject birds' sex *treatment	F Stimulus birds' sex * treatment
Df	1	1	2	1	2	2
Chee Baseline	4.38 (*0.043*)	0.15 (*0.702*)	0.05 (*0.955*)	10.6 (*0.002*)	0.21 (*0.813*)	2.85 (*0.070*)
Latency Baseline	4.24 (*0.049*)	2.08 (*0.161*)	1.06 (*0.360*)	4.58 (*0.042*)	1.27 (*0.298*)	1.35 (*0.276*)
Chee Test	3.95 (*0.057*)	0.03 (*0.855*)	0.68 (*0.515*)	7.38 (*0.011*)	4.19 (*0.026*)	1.45 (*0.252*)
Latency Test	8.10 (*0.011*)	0.01 (*0.919*)	1.34 (*0.287*)	21.9 (*>0.001*)	1.51 (*0.247*)	4.66 (*0.023*)
Chee post-playback	1.72 (*0.200*)	5.44 (*0.027*)	0.06 (*0.946*)	2.51 (*0.125*)	0.29 (*0.753*)	1.02 (*0.372*)
Similarity Test	0.01 (*0.927*)	2.30 (*0.130*)	0.54 (*0.586*)	11.2 (*0.001*)	4.80 (*0.009*)	2.30 (*0.102*)

Figure 4.2a. Latency to call (mean ±SE) of male and female subject birds to male and female stimulus birds. The baseline section is represented by grey bars and the test section is represented by hatched bars. Subj: subject bird. Significant differences relevant to the study are indicated with *.

Call rate showed a similar pattern with significant interactions between sex of stimulus and subject bird during both baseline and test section (figure 4.2b, table 1 column D). Birds exhibited higher call rates to opposite-sex stimuli than to same-sex stimuli during baseline (LSD female subject bird t_{39}=2.65, p=0.012; male subject bird t_{39}=2.01, p=0.052) and during test sections (LSD female subject bird t_{28}=2.04, p=0.051.; male subject bird t_{28}=2.07, p=0.048). Thus, intersexual call exchanges resulted in stronger responses than intrasexual call exchanges.
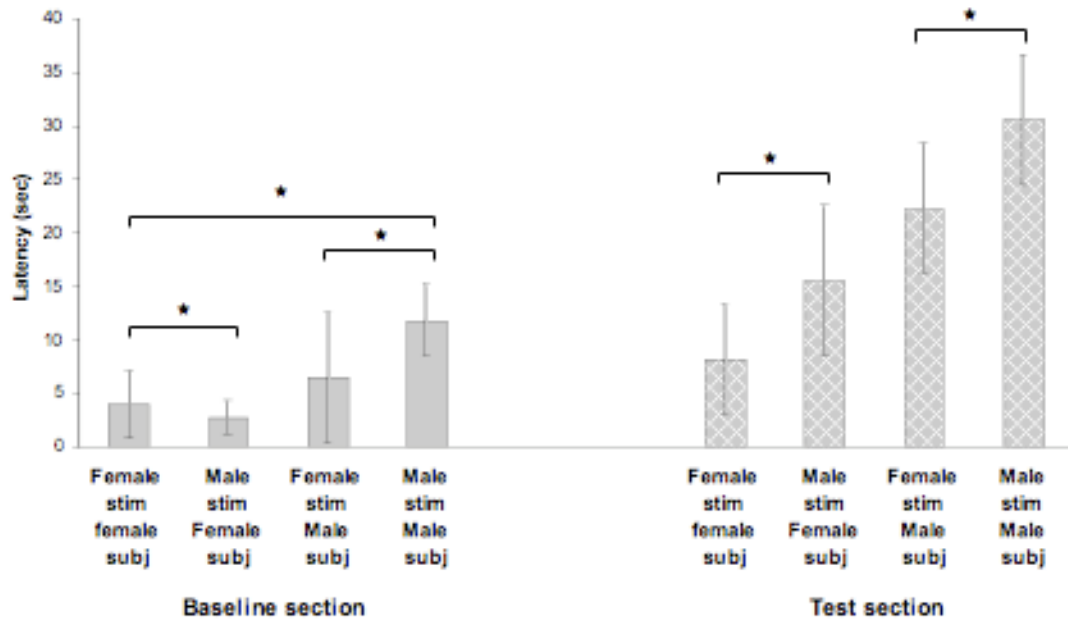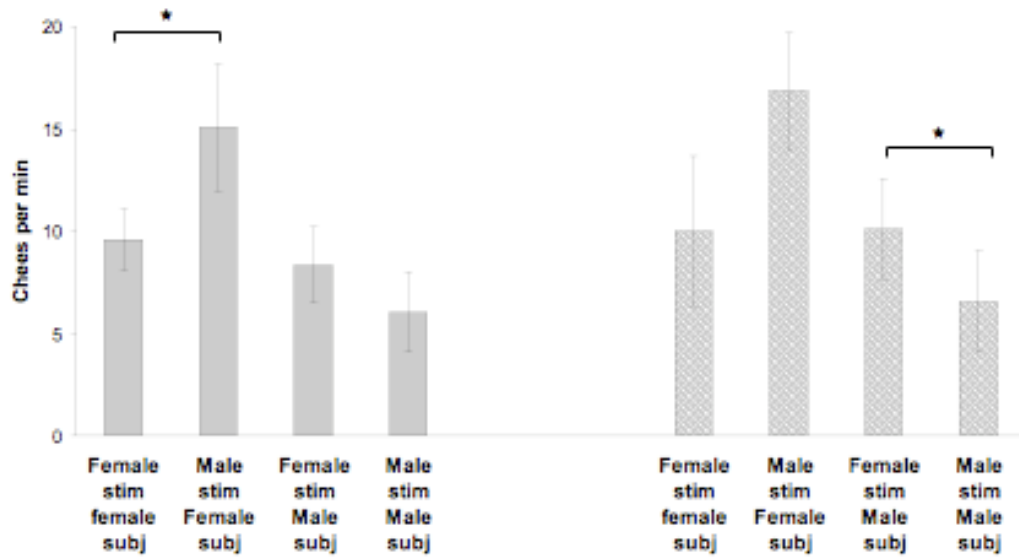
Figure 4.2b. Call rate (mean ±SE) of male and female subject birds to male and female stimulus birds. The baseline section is represented by grey bars and the test section is represented by hatched bars. Subj: subject bird. Significant differences relevant to the study are indicated with *.

Although birds called more and responded more rapidly to opposite-sex stimuli, there was a significant interaction between stimulus sex and subject sex for cross-correlation similarity (table 4.1 column D, figure 2c), indicating that birds imitated same-sex playback stimuli more closely than opposite-sex stimuli. Post-hoc tests indicated that this interaction was driven by female subject birds imitating female stimulus birds more closely than they imitated male stimulus birds (LSD t=3.46, p=0.006); male subject birds did not imitate one sex more closely than the other (LSD t=1.43, p=0.1550).

Treatment

The responses to the baseline section did not differ between treatments or interactions with treatments, indicating that no bias existed prior to the start of the test

section (Table 4.1 columns C, E & F). In the test section, treatment alone did not elicit different responses for call rate and latency time (table 4.1 column c). The cross-correlation similarity between a stimulus and the response call of subjects did not differ significantly between treatments (table 4.1 column c), indicating that subjects were capable of imitating convergent, divergent, and no-change call sequences equally well.

Treatment * sex of subject bird

The convergence, divergence and no-change treatments only differed significantly for any response variable when the sex of the subject bird or the sex of the stimulus was taken into account (table 4.1 columns E & F). Male and female subject birds differed in their calling rates during both convergent and divergent test sections, as indicated by the significant interaction between treatment and the sex of the subject bird (table 4.1 column D, figure 4.3a). Males had the highest calling rates in response to the convergent treatment and the male calling rate in response to no-change was higher than to divergent treatments. Post-hoc tests gave results in the direction of these findings but were only approaching significance (LSD no-change vs. convergence $t_{28}=0.36$, p=0.722, divergence vs. convergence $t_{28}=1.70$, p=0.101 and no-change vs. divergence LSD $t_{28}=2.00$, p=0.055, respectively). Females gave more contact calls to divergent than to no-change treatments (LSD $t_{28}=2.18$, p=0.038). Females also gave more contact calls to convergent than no-change treatments, although these differences were not significant (LSD $t_{28}=1.64$, p=0.112), and females did not differ in their response to convergent and divergent treatments (LSD $t_{28}=0.53$, p=0.602) (figure 4.3b). Thus, overall, females responded more to the changing treatment trials than to no-change trials. The interaction between sex of subject bird and treatment for latency was not significant (table 4.1 column E).

Figure 4.3a. Call rate (mean ±SE) for the interaction between treatment and sex of subject bird to convergent, divergent and no-change treatments in the test section. Stim: stimulus bird, Subj: subject bird. Significant differences relevant to the study are indicated with *.
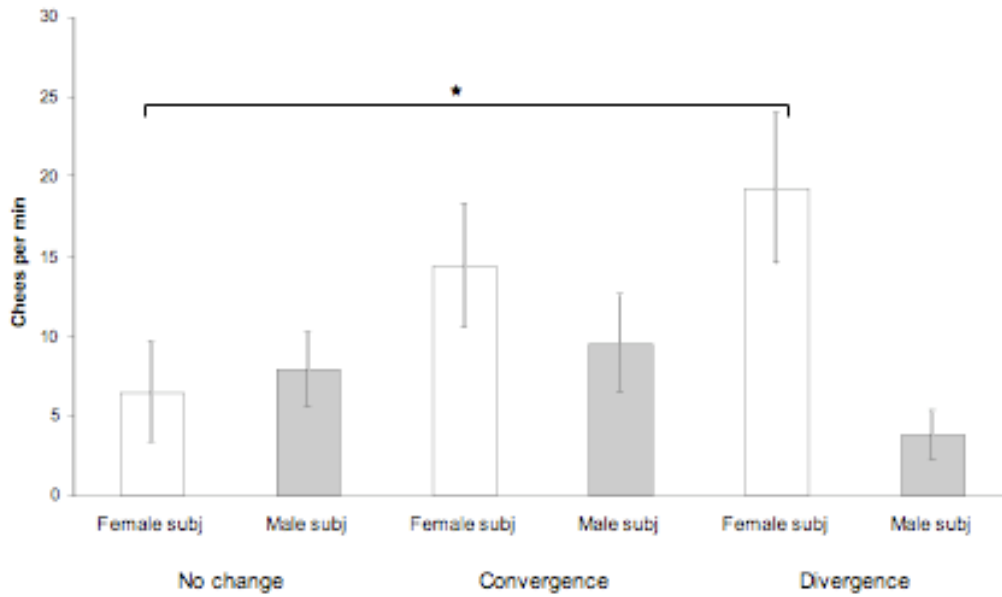

Figure 4.3b. Cross-correlation similarity (mean ±SE) for the interaction between treatment and sex of stimulus bird to convergent, divergent and no-change treatments in the test section. Stim: stimulus bird, Subj: subject bird. Significant differences relevant to the study are indicated with *.
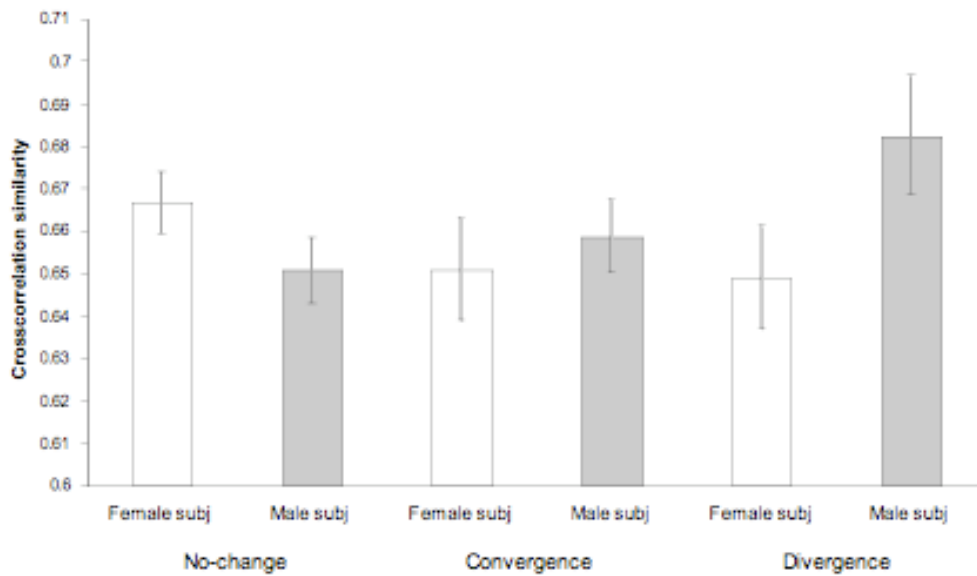
Males and females differed in how closely they imitated the 3 treatments, as indicated by the significant interaction effect between treatment and sex of subject birds (table 4.1 column E). Female subject birds imitated convergent and divergent treatments less closely than the no-change treatment (LSD convergence: t=2.30, p=0.022; divergence: t=2.07, p=0.039), whereas male subject birds did not imitate the treatments differently (figure 4.3b).

Males and females also differed in the way they conducted interactions with convergent and divergent playback; this is reflected in the significant interaction between treatment and sex of the subject bird on the likelihood of response to the treatments part: (Glimmix model, binomial distribution $F_{2, 24.4}=3.46$, p=0.048). More females than males responded to the test section of convergent and divergent treatments (Glimmix model, binomial distribution: $F_{17.24}=7.68$, p=0.012). When females responded during the baseline section of the playback they continued to interact with the playback during the test section in 87% (26 of 30) of the trials; females ceased responding only in 4 (13%) of the trials, and these were all no-change treatments. Thus, females responded to all convergent and divergent treatments if they responded during the baseline. On the other hand, males only responded after the baseline section in 68% (26 out of 38 trials). Males did not respond in 29 % (4 out of 14) of the convergent trials and in 41 % (5 out of 12) divergent trials, and in 25% (3 out of 12) no-change trials.

Treatment * sex of stimulus bird

There was a significant interaction between treatment and sex of the stimulus bird for the latency to response (figure 4.3c, table 1 column E), indicating that the sex of the stimulus bird influenced how subject birds perceived the three treatments. Birds

responded significantly sooner to convergence and divergence from female stimuli
than to no-change treatments from female stimuli (LSD convergence t_{18}=2.42,
p=0.026; divergence t_{18}=2.36, p=0.030), but they did not show this trend when
presented with male stimuli (LSD convergence t_{18}=0.08, p=0.940; divergence
t_{18}=0.02, p=0.988). In comparing birds' latency of response to male and female
stimuli, no-change treatments from female stimulus birds elicited a slower response
(i.e. longer latency) compared to those from a male stimulus bird (LSD t_{18}=2.49,
p=0.023). The interaction between treatment and sex of the stimulus bird was not
significant with regard to the call rate and similarity between the subject's response
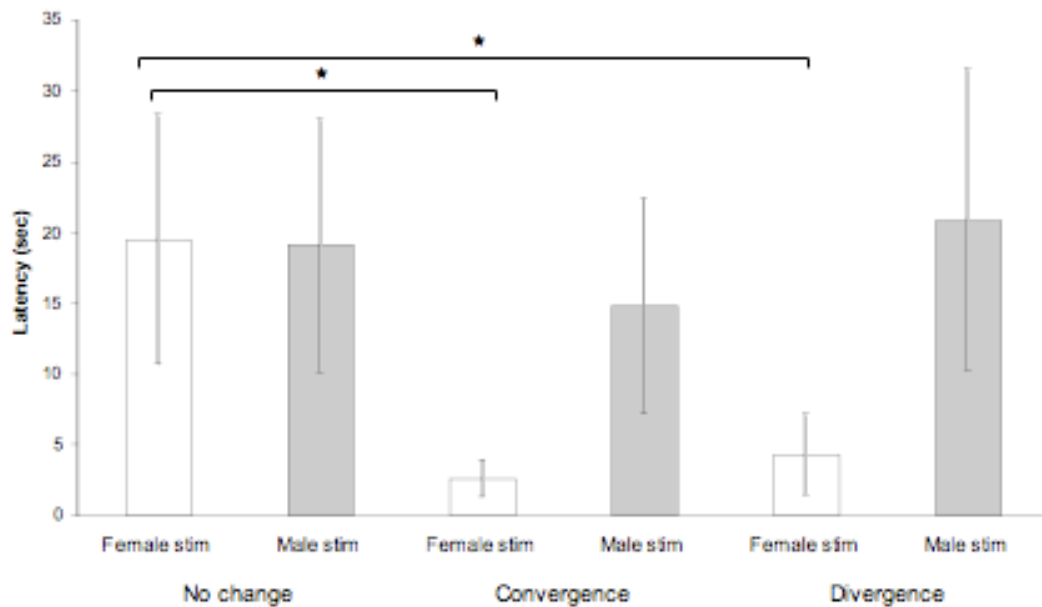calls and the stimulus (table 4.1 column E).

Figure 4.3c. Latency (mean ±SE) for the interaction between treatment and sex of
stimulus bird to convergent, divergent and no-change treatments in the test section.
Stim: stimulus bird, Subj: subject bird. Significant differences relevant to the study are
indicated with *.

Discussion

Both the sex of the stimulus and the sex of the subject influenced vocal responses in this experiment. Overall, females seemed more responsive to our treatments than males; females responded more quickly and with more calls. Subject birds discriminated between male and female calls, as indicated by the stronger and faster response to female calls. This suggests that birds can perceive the acoustic difference between male and female contact calls. Although sex differences in calls in species where both sexes give the same vocalization have been documented in several species of primates and birds (Seyfarth *et al.* 1980, Weiss *et al.* 2001, Ballintijn & ten Cate 1997), perception of such subtle sex differences has to date only been demonstrated in zebra finches, Bengalese finches and cotton-top tamarins (Vicario *et al.* 2001, Ikebuchi *et al.* 2003, Miller *et al.* 2004).

Call rate and latency to calling represent two aspects of the response in this experiment; however, when birds vocalize in response to the playback, they can also choose whether or not to increase or decrease the similarity between their response and the playback stimulus. Overall, male subject birds that responded to the test section of the playback imitated the stimulus calls of all the treatments equally well. On the other hand, when presented with stimuli that changed from the baseline (i.e. convergence and divergence), females imitated these calls less closely than the no-change stimuli. Also, female subjects imitated calls from their own sex more closely than opposite-sex playbacks, whereas males imitated both sexes equally well.

Signal function of vocal convergence and divergence

Convergent, divergent, and no-change chee interaction types elicited different responses from orange-fronted conures in our experiment. This discrimination

between treatments, however, only emerged when either the sex of the playback stimulus, or more often, the sex of the subject bird, was taken into account. Convergence elicited high calling rates both in male and female subject birds. Divergence elicited high calling rates in females but low calling rates in males, while conversely the no-change treatment elicited low calling rates in females but high calling rates in males. Convergent and divergent treatments resulted in shorter latency times than the no-change treatment in response to female stimulus birds.

The sex of the playback stimulus also influenced the response to the treatments. The no-change female stimuli resulted in shorter latencies to response than the changing (convergent and divergent) female stimuli. For male stimuli the latency did not differ between no-change and convergence, but divergence resulted in longer latencies. The different responses to convergent, divergent and no-change treatments demonstrate that the subtle variations in the contact calls and how birds vary their contact calls in vocal interactions have a signal function for OFC. The low calling rates of males to divergent stimuli indicate that at least for males, interacting with a bird whose calls diverge from their own is somewhat undesirable. On the other hand, convergence seems to be an affiliative signal for both males and females, as indicated by the high call rates and short latency times to this treatment type.

One hypothesis for how vocal matching may enhance a signal is that call convergence is used to address specific individuals in the communication network (Janik 2006). Addressing may be important in complex communication networks, such as flocks, in which multiple individuals can act as senders or receivers in a single interaction. Most bird species that use vocal matching employ discrete song- or call types during interaction (McGregor *et al.* 1992, Vehrencamp 2001). Vocal matching using discrete vocalization types could be hindered in complex communication networks due to the potential costs of sharing vocal types with large numbers of

individuals, whereas dynamic vocal matching results in calls uniquely adapted to each interaction. Our convergent playback simulates dynamic vocal matching, which has only been found in bottlenose dolphins (Janik 2000) and orange-fronted conures (Vehrencamp *et al.* 2003, Balsby & Bradbury in prep), species that both live in fission-fusion societies. Dynamic vocal matching may, therefore, represent an adaptation for communication with specific individuals in large, fluctuating groups. Given this interpretation, our convergent stimuli may represent an interest in or an investment in an interaction with a specific individual, namely, the subject bird. On the other hand, divergence may indicate that the stimulus bird is willing to invest in an interaction, but was not communicating directly with the subject bird. In our experiment, therefore, females may be willing to interact with individuals seeking contact with any individual; they would thus engage less with individuals who are not investing in a targeted interaction (the no change treatment). Under this interpretation, the differential responsiveness of males might imply that they are less interested in establishing interactive links with other birds.

A slightly different interpretation of our results is also possible. In natural interactions between wild flocks of orange-fronted conures, one can usually identify a "leader" that modifies its chee irrespective of the acoustic features in the chees of the other birds, and one or more "followers" that attempt to modify their chees to imitate that of the leader; these back and forth interactions may continue for several vocal exchanges. Often, the roles of leader and follower can shift multiple times throughout an interaction (pers. obs.). The leader-follower role in the interaction may be used to resolve dominance roles in a newly fused flock, or in later foraging and roosting activities. In this experiment, our playback is always the leader in divergent treatments, forcing the subject to assume a follower role if that bird chooses to engage in the divergent interaction. Conversely, convergent treatments place the subject bird

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in the role of leader. By responding more strongly to convergent rather than divergent interactions, males may be demonstrating that they are less likely to accept the role of follower in an interaction. Our results may thus imply that the converging stimulus bird is willing to assume a "follower" or subordinate role in subsequent interactions. As females do not discriminate between convergent and divergent interactions, females may be more willing to accept either a leader or a follower role in order to affiliate with a new group. The difference in male and female responses to the divergent playbacks may therefore reflect a social system in which females benefit more overall from being in a group, regardless of their status in the group, while males benefit most from joining groups in which they can play a leadership role. Under this explanation, convergence and divergence may still serve to address a specific individual by systematically changing acoustic features in relation to that individual's calls, but addressing is a secondary feature of the back-and-forth negotiations with that particular bird.

Conclusion

Whether imitation of contact call matching is used for selective addressing, resolution of future flock leadership status, or some other yet unconsidered function, it appears to be common in orange-fronted conures. We have advanced our understanding of these exchanges in this study by showing that a) convergent and divergent sequences of calling have different saliences to OFCs, b) these birds can identify the sex of callers by contact calls alone, and c) the interaction between the sex of the caller, the sex of the respondent, and whether a sequence is convergent, divergent, or unchanging influences the outcome of the call exchange.

The dynamic vocal system of OFCs may have evolved in response to their complex fission-fusion social system. Over the course of a day, an OFC has the opportunity to interact with a large number of individuals all with individually distinct contact calls. The fission-fusion system necessitates a method of allowing communication between two interactants in or between flocks. The current experiment demonstrated that the dynamic convergence and divergence of contact calls have different signal meanings, which may allow more subtle nuances of information to be expressed, such as which individual in a network is addressed or the negotiation of leadership between individuals.

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DISCUSSION

Many species of parrots are vocally flexible into adulthood, but compared to several members of another avian vocal learning clade, the songbirds, vocal communication in wild parrots has been the focus of very few studies. This thesis focuses on sex differences and vocal flexibility in parrot communication and investigates some of the social factors that influence parrot vocal communication.

Overall Conclusions

Sex Differences

Although male and female galahs share a repertoire of calls, sex differences in vocal behavior and behavioral differences in response to vocalizations are prevalent across several social contexts. Galahs can differentiate between male and female contact calls, and males seem to be more responsive than females to conspecific contact calls. As a subset of this behavior, males seem to more actively change their contact calls in relation to an interaction partner during vocal interactions. During aggressive interactions, also, males are more vocal, and males initiate responses to threat calls more often than do females. Taken together, these results suggest that males actively use vocalizations both to affiliate and to repel more than do females. While galahs seem to share in most aspects of nest-building and parental care (Rowley 1990), these sex differences in vocal communication most likely reflect differences in the sex roles in this species.

Male and female orange-fronted conures exhibit differences in vocal behavior, also. Birds respond more strongly to opposite-sex contact calls in this species, suggesting that contact calls may play a role in sexual affiliation. Unlike the galahs,

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female orange-fronted conures called more and called more quickly than males. However, this difference may reflect the difference in experimental setup; most galah females approached playback stimuli with their male mate, whereas the orange-fronted conures were isolated in aviaries.

Overall, experiments on both parrot species demonstrate that individuals can distinguish a caller's sex using only acoustic cues, and that these sex discriminations lead to behavioral decisions. In addition, males and females respond differently in similar social situations, which may reflect differences in the social roles of these birds.

Vocal Flexibility

These papers also help to clarify how wild adult parrots use vocal flexibility during interactions with conspecifics. Previous research has demonstrated that one species of parrot, the orange-fronted conure, can rapidly modify the acoustic features of its contact calls to become more similar to the calls of its interaction partner (Vehrencamp et al. 2003). The studies described here indicate that these rapid modifications are not unique to the conures; since galahs are so phylogenetically and geographically distant from the conures, these results are consistent with the possibility that these vocal modifications are in fact widespread within the parrot order. In addition, the final section on response to convergent and divergent call sequences by orange-fronted conures suggests that the direction of signal change has meaning to parrots. This experiment reinforces the evidence that despite sharing a repertoire, male and female parrots communicate differently, and it is a first step towards identifying the signal meaning of rapid convergence or divergence of contact calls.

Broader Implications

Animals can produce vocalizations that are acoustically similar to the
vocalizations of other individuals in several ways and in several social contexts. Vocal
copying can be divided into two categories based on whether individuals are matching
the vocalizations of conspecifics or heterospecifics (Kelley et al 2008). In both
conspecific and heterospecific matching contexts, pronounced sex differences can
exist in the manifestation of this vocal flexibility.

In a diverse array of avian species such as the Albert's lyrebird *Menura alberti*
(Putland et al. 2006*)*, gray catbird *Dumetella carolinensis* (Bailey 1912), satin
bowerbirds *Ptilonorhynchus violaceus* (Loffredo and Borgia 1986), greater racket-
tailed drongos *Dicrurus paradiseus* (Goodale et al 2006), and European starlings
Sturnus vulgaris (Hausberger et al. 1991), birds mimic the vocalizations of
heterospecific animals or other environmental sounds. In several species that
demonstrate this kind of heterospecific vocal mimicry, males produce mimicked
sounds more frequently or exclusively (Marshall 1950) and several scientists have
hypothesized that this mimicry serves to attract females or repel rival males (Marshall
1950; Dobkin 1979). However, heterospecific mimicry may serve several other
functions, such as to accentuate an alarm signal (Goodale and Kotagama 2006) or
deter potential predators (Dobkin, and magpie study cited in Kelley). Existing
evidence does not point to any one of these hypotheses as the primary purpose of
heterospecific vocal mimicry in birds (Garamszegi et al. 2007; Kelley et al. 2008).

Vocal imitation of conspecifics can be divided into several sub-categories
based on the timing and extent of vocal learning involved and, to a certain extent, the
function of imitation. In some species, vocal imitation of conspecifics involves the
immediate, one-to-one match of a signal. For example, in several songbird species,

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males match the songs of their neighbors to indicate aggression during a territorial interaction (Beecher et al. 2000; Vehrencamp 2001). Since the majority of songbirds are restricted to learning new songs during a limited juvenile period (Marler 1970a), adults can only match conspecifics' songs that are already in their repertoire. Bottlenose dolphins produce a similar one-to-one match of the signature whistles of conspecifics, and this imitation seems to address other individuals (Janik 2000). It is not known whether dolphins use signals from a pre-existing repertoire or can produce new signals to achieve these vocal matches, and it is not known whether this vocal matching is affiliative or aggressive (Janik 2000) or whether this imitation differs by sex.

In other species, individuals will gradually change their calls to produce vocalizations that are similar to those of conspecifics, rather than producing an immediate match of a partner's calls. Often this convergence occurs within a stable pair or group and yields a group signature call that identifies individuals as part of the group. For example, when black-capped chickadees (Nowicki 1989), cardueline finches *Cardeulis sp.* (Mundinger 1970), pygmy marmosets *Callithrix pygmaea* (Snowdon and Elowson 1999), and captive budgerigars *Melopsittacus undulatus* (Farabaugh et al. 1994; Bartlett and Slater 1999; Hile et al. 2000; Hile and Striedter 2000) join a new group, individuals gradually modify the acoustic features of their calls to converge on a group call. This process can take from a few days to several weeks. There is evidence that in some species, this convergence is sexually distinct; captive male budgerigars converge more quickly than females when they are introduced into a new group (Farabaugh et al. 1994; Hile and Striedter 2000), and when a new male-female pair forms, males tend to converge on the females' calls (Hile et al. 2000), and females prefer to mate with males whose calls are similar to

their own (Moravec et al. 2006). Thus, gradual convergence on a group signature call seems to serve a social or sexual affiliation function.

Parrots are renowned for their tremendous vocal flexibility, and limited evidence largely from captive birds suggests that parrots are capable of several different types of call copying, from heterospecific mimicry in African greys *Psittacus erithacus* (Cruickshank et al. 1993) to an immediate match of an interaction partner's call in captive spectacled parrotlets *Forpus conspicillatus* (Wanker et al. 2005) to a gradual call convergence that indicates group or mate affiliation in captive budgerigars *Melopsittacus undulatus* (Farabaugh et al. 1994; Bartlett and Slater 1999; Hile and Striedter 2000). One previously published study (Vehrencamp et al. 2003) and the experiments presented here suggest that parrots are capable of a potentially distinct and previously undocumented class of conspecific vocal imitation. This research indicates that parrots are using rapid vocal modification in dyads of birds in short vocal exchanges; at least two species of parrot, the galah and the orange-fronted conure, are capable of changing their calls to converge with the acoustic features of a conspecific stimulus during very brief vocal exchanges.

The ability to modify calls over the course of a single vocal exchange based on an interaction partner's calls may allow individuals to tailor their existing vocalizations to specific interactions. Parrots often communicate in large, noisy flocks, and modifying calls in relation to another bird's signal may serve to direct an interaction within a complicated communication network. However, since the vocal change itself seems to have meaning beyond simply to address a specific individual, such vocal flexibility may allow birds to increase the number or specificity of messages they can convey without an increase in the number of calls in their repertoire. This ability to flexibly tailor interactions towards specific individuals may reflect parrots' fission-fusion social system and large home ranges, in which parrots

have opportunities to interact daily with many different individuals of varying ages, sexes, social classes. Vocal flexibility may therefore allow parrots to meet the communicative needs of a frequently-changing social network.

Understanding the parrot vocal communication system may have broader comparative implications as well, not just among avian orders but also for other fission-fusion species such as dolphins and humans. In the past, songbirds have been touted as models of vocal learning, and scientists have drawn strong parallels between song learning in birds and speech learning in humans (Marler 1970b; Fitch 2005). In many ways, however, the vocal abilities and development of parrots more closely parallel those of humans than do songbirds. Like humans, but unlike the majority of songbirds, parrots are open-ended learners, which means that they can learn new sounds and modify existing sounds throughout their lives (Bradbury 2003). In addition, unlike the majority of temperate songbirds, in which only males sing, both sexes of parrots produce learned, flexible vocalizations, which means that we can directly compare vocal learning and flexibility in male and female parrots.

While heterospecific and conspecific call copying are not unusual among animals, rapid, directional call convergence has been documented only in parrots. The experiments presented here give insight into how parrots are using their tremendous vocal flexibility during interactions with wild conspecifics. In addition, these studies document how sex influences vocal communication even in species in which males and females, at first glance, seem to play similar roles in a communication system.

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