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

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We investigated the signal function of vocal imitation of contact calls in orange-fronted conures (OFCs; *Aratinga canicularis*) in Costa Rica. OFCs 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. OFCs 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 OFCs 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.

Keywords: vocal imitation; matching; sex discrimination; vocal mimicry; vocal flexibility

1. 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 (McGregor *et al.* 1992; Vehrencamp 2001; 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 (Bartlett & Slater 1999; Snowdon & Elowson 1999; Hile & Striedter 2000; Hile *et al.* 2000), although there is limited evidence that certain species, such as bottlenose dolphins (*Tursiops truncatus*), 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; Mitani & 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; Saunders 1983; Nowicki 1989; 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 1999). 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, spider monkeys (*Ateles geoffroyi*) and orange-fronted conures (OFCs; *Aratinga canicularis*), an exchange of contact calls precedes and may mediate the formation of groups (Connor *et al.* 2000; Bradbury *et al.* 2001; Fernandez 2005). 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 preparation*). 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.

OFCs live in a fission–fusion social system with daily changes in flock composition (Bradbury *et al.* 2001). During flock encounters, OFCs exchange contact calls that 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

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few seconds (Vehrencamp *et al.* 2003; Balsby & Bradbury *in preparation*). In this paper we address two issues. First, we investigate whether signal convergence and 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 (Vicario *et al.* 2001; Miller *et al.* 2004), and some call or song matching mediates sex-specific interactions such as male–male competition (Vehrencamp 2001) or mate affiliation (Moravec *et al.* 2006).

2. MATERIAL AND METHODS

We conducted this experiment between 27 June and 28 July 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 OFCs 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 3.5 × 1.8 × 1.8 m) located at least 300 m apart in habitat used daily by OFCs. During this time, all birds had access to water and their natural food *ad libitum* 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 PMD670 or PMD690 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 away 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 subjects' 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 eight known-sex captive individuals at our study site using 'chickadee' acquisition software (John Burt <http://www.syrinxpc.com>) on a PC (Sony VAIO PGRX 770) with a NI-DAQ acquisition card (model 6062E) and an omnidirectional microphone (designed by R. McCurdy at the Bioacoustics Research Programme, Cornell Lab of Ornithology) placed 1.5 m away 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 <http://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 1 × 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 three to five 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 bird received three treatments each from a male stimulus bird and 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 min pre-playback period and followed by a 3 min post-playback period in which we recorded the vocal behaviour 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 4 s, but if the bird did not respond, we waited 15 s to play the next call. Once we had broadcast three calls of average similarity in the first section, 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 first section 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 s (average $\pm$ s.e.) and the test section on average lasted for 32 ± 2 s (average $\pm$ s.e.). In all but 4 out of 91 trials, the same chee was not used more than once in a treatment.

(a) 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 s 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 analysed 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 dataset. 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.* 2006). The generalized linear model also blocked for individual and trial. All models consisted of the three main factors (sex of the subject bird, sex of the stimulus bird and type of change) and the second-order interaction effects. We used least significant differences (LSDs) to test specific *post hoc* pairwise differences. However, all test subjects responded only 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.* 2006) in SAS 9.12 (SAS Institute Inc., Cary, North Carolina, USA).

3. RESULTS

(a) 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 1a, table 1 column A). Female subject birds also responded faster to playback than male test birds in both baseline and test sections (figure 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 1 column A). Male and female subject birds did not differ in how closely their contact call responses imitated the playback (figure 1c, table 1 column A).

(b) Sex of stimulus bird

When the sex alone of the playback stimulus bird was considered, it did not seem to affect the rate of calling or the latency to response directly (table 1 column B), except that during the post-playback period female stimuli elicited more contact calls than male stimuli (table 1 column B). However, when treatment or subject bird sex was 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 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 1, column B).

(c) Sex of subject bird $\times$ sex of stimulus bird

There were several significant interactions between the sex of the stimulus and 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

Figure 1. Sex differences in response (mean $\pm$ s.e.) of subject birds. The baseline and the test sections are represented by grey and hatched bars, respectively. Subj, subject bird. (a) Call rate, (b) latency and (c) cross-correlation similarity. Significant differences relevant to the study are indicated with asterisks.

subject bird was significant with regard to latency during both the baseline and test sections (figure 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 $t_{18}=2.64$, $p=0.017$).

Call rate showed a similar pattern with significant interactions between the sex of the stimulus and the subject bird during both baseline and test section (figure 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 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.

Although birds called more and responded more rapidly to opposite-sex stimuli, there was a significant interaction between stimulus sex and subject sex for

Table 1. Generalized linear mixed model on subject bird's sex, stimulus bird's sex, treatment and the second-order interactions for five 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 random variables. Each line in the table represents one of the response variables. We tested each response variable in a model with three factors and three interaction effects. For each factor or interaction effect we list the *F*-value and the *p*-value (*italics*, in parentheses). The *p*-values significant at the <0.05 level are in bold. The d.f. for chee baseline, d.f._{error} = 39; latency baseline, d.f._{error} = 27; chee treatment, d.f._{error} = 28; latency treatment, d.f._{error} = 18; chee post-playback, d.f._{error} = 27; similarity, d.f._{error} = 327.

independent variables	A	B	C	D	E	F
response variables	subject birds' sex	stimulus birds' sex	treatment	subject birds' sex $\times$ stimulus birds' sex	subject birds' sex $\times$ treatment	stimulus birds' sex $\times$ treatment
d.f.	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)

cross-correlation similarity (table 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 $t=1.43$, $p=0.1550$).

(d) 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 1 columns C, E and F). In the test section, treatment alone did not elicit different responses for call rate and latency time (table 1 column C). The cross-correlation similarity between the stimulus and the response call of subjects did not differ significantly between treatments (table 1 column C), indicating that subjects were capable of imitating convergent, divergent and no-change call sequences equally well.

(e) Treatment $\times$ 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 1 columns E and 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 the treatment and the sex of the subject bird (table 1 column D, figure 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 divergent treatments. *Post hoc* tests gave results in the direction of these findings but were only approaching significance (LSD no-change versus convergence: $t_{28}=0.36$, $p=0.722$; divergence versus convergence: $t_{28}=1.70$, $p=0.101$; and no-change versus 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 3b). Thus, overall, females responded more to the changing treatment trials than to no-change trials. The interaction between the sex of the subject bird and the treatment for latency was not significant (table 1 column E).

Males and females differed in how closely they imitated the three treatments, as indicated by the significant interaction effect between the treatment and the sex of the subject birds (table 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 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 the treatment and the sex of the subject bird on the likelihood of response to the treatments (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 out of 30) of the trials; females ceased responding only in 13% (4) 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 responded only after the baseline section in 68% (26 out of 38) of the trials. Males did not respond in 29% (4 out of 14) of the convergent trials and in 41% (5 out of 12) of the divergent trials, and in 25% (3 out of 12) of the no-change trials.

(f) Treatment $\times$ sex of stimulus bird

There was a significant interaction between the treatment and the sex of the stimulus bird for the latency to

Figure 2. Response (mean $\pm$ s.e.) of male and female subject birds to male and female stimulus birds. The baseline and the test sections are represented by grey and hatched bars, respectively. Subj, subject bird. (a) Call rate, (b) latency and (c) cross-correlation similarity. Significant differences relevant to the study are indicated with asterisks.

response (figure 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 with those from a male stimulus bird (LSD $t_{18}=2.49$, $p=0.023$). The interaction between the treatment and the 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 1 column E).

Figure 3. Response (mean $\pm$ s.e.) to convergent, divergent and no-change treatments in the test section. (a) Call rate and (b) cross-correlation similarity for the interaction between treatment and sex of the subject bird. (c) Latency for the interaction between the treatment and the sex of the stimulus bird. Stim, stimulus bird; Subj, subject bird. Significant differences relevant to the study are indicated with asterisks.

4. DISCUSSION

(a) Sex differences in response and vocal discrimination

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; Ballintijn & Ten Cate 1997; Weiss *et al.* 2001), perception of such subtle sex differences has to date only been demonstrated in zebra finches (*Taeniopygia guttata*), Bengalese finches (*Lonchura striata* var. *domestica*) and cotton-top tamarins (*Sanguinus oedipus*) (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.

(b) Signal function of vocal convergence and divergence

Convergent, divergent and no-change chee interaction types elicited different responses from OFCs in our experiment. This discrimination between treatments, however, emerged only 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 in both 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 *et al.* 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 OFCs (Vehrencamp *et al.* 2003;

Balsby & Bradbury in preparation), 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 OFCs, 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 (T. J. S. Balsby, A. Goldstein & J. W. Bradbury 2006, personal observation). 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 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.

5. 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 OFCs. We have advanced our understanding of these exchanges in this study by showing that (i) convergent and divergent sequences of calling have different saliences to OFCs, (ii) these birds can identify

the sex of the callers by contact calls alone and (iii) 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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