Individual recognition and selective response to contact calls in foraging brown-throated conures, *Aratinga pertinax*

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Foraging individuals can benefit from recruiting conspecifics to food sites, but must balance potential benefits against increased competition. Foragers in fission–fusion societies may recruit others to food resources by calling and can reduce the relative cost of this behaviour by selectively recruiting preferred conspecifics. Observational studies of the brown-throated conure on the island of Bonaire showed that overflying groups were much more likely to settle in the area when a foraging group called to the overflying group. However, foraging groups did not call to every overflying group, and food abundance alone did not determine whether foraging groups would call. Playback experiments indicated that conures can respond preferentially to social partners. Observational and experimental data suggest that brown-throated conures may use loud contact calls selectively to recruit conspecifics to currently available foraging sites.

Foraging in groups can decrease the risk of predation or enhance food finding, but may reduce individual intake through either competition or direct stealing (Pulliam & Caraco 1984; Valone 1996; Bradbury & Vehrencamp 1998; DiBitetti & Janson 2001). Foragers in flexible societies, such as fission–fusion groups, can maximize benefits and minimize costs through selective associations with preferred social partners. Foragers may choose to avoid foraging with dominant or aggressive individuals (Chapman & Lefebvre 1990), or preferentially forage with social group members who can aid in resource defence (Wilkinson & Boughman 1998). Foragers may also actively recruit others to forage with them. In doing so, they may offset the costs of sharing through benefits such as reduced predation risk through increased group size (Elgar 1986; Newman & Caraco 1989; Caine et al. 1995), increased opportunities to mate (Evans & Marler 1994), assistance with resource defence (Heinrich & Marzluff 1991; Wilkinson & Boughman

1998), enhanced ability to find food (e.g. Brown et al. 1991) and a reduction in punishment for not sharing (Hauser 1992). Recruiters may also benefit from the recruitment of kin (Judd & Sherman 1996) or reciprocal partners, who have the potential to recruit the caller at a future time. Reciprocal sharing requires advanced cognitive abilities to factor in future discounting and thus is probably limited to a small number of species that are able to maintain long-term social memories (Stevens & Gilby 2004).

The dynamic nature of fission–fusion societies poses challenges for maintaining social bonds while foraging. Individuals need to locate mates and other preferred social partners amid shifting group associations. In long-lived species, individuals may meet for only brief periods but need to remember previous contacts. To facilitate such social accounting, many species rely on signals that convey individual-specific information. In species with large, overlapping home ranges, this information is often contained in long-distance contact calls (Bradbury & Vehrencamp 1998). Individuals may use the information in these calls in deciding whether to forage with others.

Most species of parrot (Psittaciformes) are nonterritorial, with dynamic fission–fusion societies in which group

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composition shifts frequently throughout the day (Bradbury 2003). Parrots are predominantly seed predators and as such are unwelcome visitors to plants. Many plants have responded-to parrots and other seed predators by making their fruit hard to spot or by adding toxic secondary compounds to the fruit or seeds (Bradbury 2003). Other plants rely on unpredictable phenologies or actively attract seed dispersers that can compete with the seed predators. These coevolutionary adaptations make foraging a daily challenge for wild parrots (Bradbury 2003). Given these challenges, the sharing of public information (Valone 1996) and coarse-level local enhancement (Poysa 1992) could be very valuable for parrots. However, although the green coloration and quiet foraging habits of many parrot species conceal individuals from aerial predators while foraging in foliage (Juniper & Parr 1998; Bradbury 2003), they also probably conceal foraging groups from overflying conspecifics.

Nearly all species of parrot have a loud contact call, used to maintain contact between visually separated individuals (Forshaw 1989; Farabaugh & Dooling 1996; Bradbury 2003). Given its function in generating and/or maintaining contact between separated individuals, this signal is likely to provide individual-specific information. In fact, the loud contact calls of several parrot species contain information that indicates individual identity. Laboratory studies have shown that domestic budgerigars, *Melopsittacus undulatus*, can discriminate between the contact calls of over 30 different individuals (Dooling 1986; Ali et al. 1993). Captive spectacled parrotlets, *Forpus conspicillatus*, also have individually distinct contact calls (Wanker & Fischer 2001), and laboratory experiments have shown the ability of the parrotlets to discriminate between mates and siblings (Wanker et al. 1998). Wild-caught orange-fronted conures, *Aratinga canicularis*, have an individually distinctive dominant contact call type (Bradbury et al. 2001; Cortopassi & Bradbury 2006). Based on this accumulated evidence for individual recognition in parrot contact calls, it has long been posited that parrots may use contact calls to form selective associations in foraging groups (Bradbury 2003). Vehrencamp et al. (2003) found an increased approach and vocal response in orange-fronted conures to calls from the local area. They also noted that the strength of response to a local contact call varied widely between groups and suggested that some form of recognition of or attraction to calls of known individuals may have played a role in the strength of response to the stimuli. However, with the exception of playbacks involving mate (Rowley 1980) and parent–offspring (Saunders 1983) recognition, evidence for discrimination between and preferential responses to contact calls of particular individuals in wild parrot populations is lacking.

We studied contact call interactions between foraging and overflying groups of brown-throated conures, *Aratinga pertinax xanthogenesis*, on the island of Bonaire, Netherlands Antilles. The brown-throated conure is a medium-sized (80–100 g), sexually monomorphic parrot species. The conures roost in large groups (several hundred individuals) at night and move throughout the habitat in small groups, most often of two to four individuals, that fuse and break apart frequently throughout the day. The loud contact call of the brown-throated conure is usually a two-part call, although one-part, three-part, and four-part variants occur. The second syllable is usually lower in amplitude and separated from the first syllable by a few to one hundred milliseconds (Fig. 1). Most of the energy is contained within 2–5 kHz. Brown-throated conures utter these loud contact calls as they fly through the habitat. Foraging groups in the canopy either respond or remain silent. Overflying groups may join the foragers or continue on.

We used observational and experimental studies of interactions between overflying and foraging groups in the wild to look for selectivity in association based upon contact call interactions. Due to the difficulty of obtaining repeat recordings of individuals and conducting controlled experiments in the wild, we used studies of wild-caught individuals to determine if brown-throated conure contact calls are individually distinctive and to test for individual discrimination based on contact calls in this species.

METHODS

Foraging Group and Overflying Group Interactions

Observations of natural foraging group and overflying group interactions

We conducted the observations in June–July 2002 and March–May 2003 in a popular foraging area with high rates of overflying parakeet flocks in the southern part of Bonaire. Bonaire is a xerophytic island, with patchily distributed resources (Buhrman-Deever 2007) that probably make searching for food difficult for conures. The
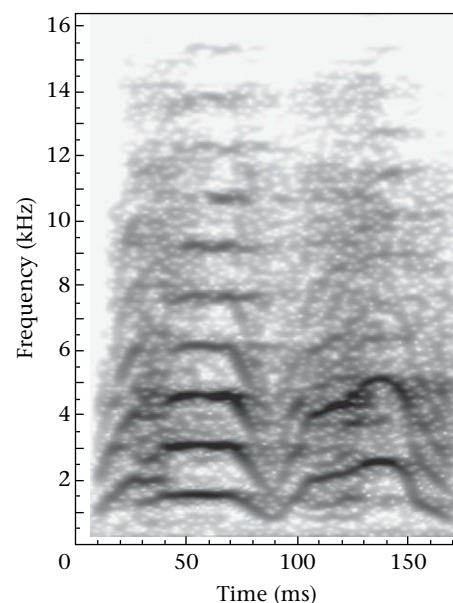

Figure 1. Contact call of the brown-throated conure on Bonaire. Spectrogram parameters: Hanning window, FFT size 1024, overlap 90%.

vegetation is low (2−3 m), allowing for better observations of natural foraging and direct assessment of the amount and quality of food patches. The observed foraging area was part of a former goat ranch with relatively open habitat, permitting observations of multiple trees at a time. In two areas, separated by approximately 100 m, with 20 and 14 food trees, respectively, we identified the species of each tree and marked each with flagging and an individual identification. We concurrently monitored each area from dawn to 1030 hours and from 1530 to 1830 hours, times of peak flight and foraging activity. We estimated each food tree's fruit abundance twice daily after each observation period, by counting the number of fruit on one-quarter of the canopy and multiplying by 4. We verified the accuracy of this method by counting all of the fruit on selected trees and comparing those counts to our routine quarter-canopy estimates.

During each observation period, we noted when foraging groups landed on and left the counted trees and the group size. For each foraging group, we recorded when every overflying group approached, the vocalizations of the approaching overflying groups, whether there was a vocal response and, if so, the type of vocal response from the foraging group. The possible responses of overflying groups that we recorded included landing in the same tree; landing within 25, 50 or 75 m; or not stopping. We interpolated the amount of food present on the tree during the visit of each foraging group using the twice-daily counts.

Experimental playbacks

We chose, as stimuli, 14 clean two-part brown-throated conure contact calls from 14 foraging or perched individuals recorded in previous years at four different locations on Bonaire, none of which was the playback site. We made recordings with a Sennheiser ME67K6 shotgun microphone onto an HHB Portadat DAT recorder or the audio track on a Canon GL-2 mini-DV recorder. Calls were high-pass filtered at 500 Hz to remove low-frequency background noise. We digitized the calls using Raven 1.2 (Bioacoustics Research Program, Cornell University) at 16 bits, 48 000 Hz; saved them as .wav files; and loaded them onto a Yamaha SU200 portable sound sampler. We played calls through a Targus A-2CH 100 amplifier and a Radio-Shack (no. 40-1352) omnidirectional speaker. All calls were played at 85−90 dB at 2 m, equivalent to natural sound levels (Buhrman-Deever 2007).

We conducted the playback trials at three sites in the central region of the island in September−December 2004. We conducted playbacks from dawn to 1030 hours and from 1530 to 1800 hours. We placed the speaker in a potential food tree approximately 1−2 m off the ground (in the middle of typical foraging heights for the conures), and positioned ourselves 30 m away from the speaker under the canopy. We waited until the immediate area (within 100 m) was clear of conures before conducting the trials. If an overflying group landed in the area, we waited until at least 5 min after they departed before proceeding with the next trial. When we heard an overflying group approach, we played one contact call exemplar

one to three times in response to the overflying group's calls (similar to natural foraging/overflying group interactions). We called to every other approaching overflying group, using the non-called-to groups as controls. We noted the size of overflying groups, whether they landed in the area, how close to the speaker they landed and how long they remained in the area. We used the same distance scale for playbacks to overflying groups as for the observational study. We completed 39 trials (14 each at two sites and 11 at the third) and used no call more than once per site.

Statistical analyses

We used Fisher's exact tests to compare overflying group settlement rates in both the experimental and the observational studies using JMP IN software (version 5.1, SAS Institute, Inc., Cary, North Carolina, U.S.A.). We tested for ecological influences on foraging group calling using logistic regression in SAS (version 9.1) Proc Genmod with autoregressive estimation (SAS Institute). We treated foraging group identity as a random factor, with each overflying group interaction as a repeated measure for each foraging group. Because the same tree was used by different foraging groups on different days, we nested the tree identification within foraging group. Although we could not reliably identify the individuals in groups from day to day, foraging group composition often shifted in as little as 10 min (Buhrman-Deever 2007), so we treated each foraging group as independent in the analysis. The presence or absence of a vocal response to overflying groups was the response variable. Groups with missing data were excluded from the analysis. The initial explanatory model included the amount of time the foraging group was on the tree before each overflying group's arrival, the size of the foraging group, the size of the overflying group, the number of fruit per bird available on the tree, the number of other groups called to previously and the number of other groups in the area. Because the timing of overflying groups' appearances did not follow a regular pattern (overflight arrivals were often temporally clumped), we treated the amount of time on the tree before an overflying group's appearance as a categorical variable. We initially created three categories: whether the overflying group appeared (1) 0−4 min after the foraging group arrived on the tree, (2) >4 to 8 min after the foraging group or (3) >8 min after the foraging group. We chose these categories so that an equal number of observations was placed in each category. An initial screen revealed no statistical difference between the second and the third category, so we combined those categories for the final analysis. After an initial run of the whole model, we sequentially removed those explanatory variables with a P value >0.15, as including too many explanatory variables in a logistic regression model may reduce the ability of the model to pull out significant factors (Tabachnick & Fidell 2001). We report here the results of the final model. A total of 35 foraging groups with one to nine overflights each were used in the statistical analyses. To control for the potential effect of differing food types, we included only those groups foraging on *Acacia tortuosa* trees.

Short-term Captive Studies

Capture and housing

We captured individuals and groups in mist nets as they flew from the night roost at dawn in the autumn of 2004. All were caught near the same roost at the southern part of the island, which has been active for at least 4 years (Harms & Eberhard 2003; Buhrman-Deever 2007). As the conures flew into the nets, we noted the group size and whether we had captured a complete group. We measured each individual's mass at capture, tarsus and wing length; rated fat deposits; and took a brachial vein blood sample for later genetic analysis. We gave captured individuals an individually distinctive facial marking with a Sharpie marker to aid identification in the aviary.

Short-term captives were housed in an aviary measuring $3 \times 1.5 \times 1.5$ m. A waterproof roof covered half of the aviary for shelter. We placed several tree branches inside the aviary for perches. One wall of the aviary was covered with a sheet with an observation window, through which the conures were observed and recorded. We provided water ad libitum in two small water dishes on either side of the aviary. Food was also available ad libitum; we placed several fruit-bearing branches inside the aviary and replenished the supplies several times a day throughout the captive period. All provided branches were of species commonly consumed by the conures (Buhrman-Deever 2007). We housed the conures for 2−3 days and then released them back at the site of capture. If a conure showed any sign of distress (e.g. not eating after a few hours, extreme agitation, conflicts with other captives), we immediately released it at the site of capture. No more than four individuals captured together were housed in the aviary at any one time.

Recording and analysis of short-term captives' contact calls

We recorded the contact calls uttered by the captive individuals with a Sennheiser ME67K6 shotgun microphone as .wav files at 48 kHz, 16 bits, sampling onto a Marantz PMD 670 or PMD 690 hard-drive recorder. We were able to identify the caller by beak movements and narrated the caller's identity (as determined by the individually specific dye markings) on the recording. We used only those calls that could be attributed to an individual with 100% confidence in subsequent analyses.

We analysed only two-part contact calls, the most common call variant. We compared the 30 calls from each of 16 individuals using a spectrographic cross-correlation (Clark et al. 1987) and principal coordinates (PCO; Legendre & Legendre 1998) analysis in a specially designed Matlab (Mathworks, Natick, Massachusetts, U.S.A.) routine. The routine cross-correlated each pair of calls, generating a symmetrical similarity matrix, followed by a PCO analysis on the matrix (Vehrencamp et al. 2003; Cortopassi & Bradbury 2006). Because we were interested in how the spectral and temporal structure of each syllable varied with each individual, we separated each contact call into syllables and analysed each separately. We used the first five PCO coordinates for the comparisons, as they explained 87.7% (syllable 1) and 81.1% (syllable 2) of the variation of the data. We then performed a MANOVA and linear discriminant analysis on the coordinates for each of these PCO axes, testing for significant differences between the calls of individuals. We transformed all data and excluded outliers as necessary to conform to the assumptions of the test. The MANOVA was run in JMP IN 5.1 (SAS Institute) and the linear discriminant analysis with cross-validation was run in SAS version 9.1 Proc DISCRIM (SAS Institute).

Sexing of the individuals and assignment of individuals to pairs

Because the brown-throated conure is sexually monomorphic, we molecularly sexed all captured individuals. We extracted DNA from the blood samples using an Eppendorf gDNA extraction kit. We then amplified the CHD locus with the polymerase chain reaction using primers P2 and 1237L (Griffiths et al. 1998; Dyrcz et al. 2004) in 10-μl reactions: 25 mM $MgCl_2$, 1 μl of each 10 mM primer, 1.8 μl of Sigma Jumpstart Taq polymerase, 2 μl of template DNA, 1 μl of 2 mM dNTPs and double-distilled H_2O to volume. We used the following amplification protocol: 94 °C for 2 min, 50 °C for 1 min, 72 °C for 1 min, and then 30 cycles of 94 °C for 45 s, 50 °C for 1 min, 72 °C for 1 min, with a final annealing step of 72 °C for 5 min. We ran the amplified samples out on a 2% agarose gel at 35 V for 4−6 h to obtain the best separation of bands.

We classified captured individuals as mated pairs in the field if two individuals performed duetted warbles in the aviary. Such vocalizations have been observed only in presumed pairs in the wild and never observed between same-sex individuals in the aviary (S. C. Buhrman-Deever, personal observation). These initial assignments were later corroborated with the molecular sexing; mated pairs had to be a male and female captured together.

Tests for preferential response to mates and group members

We tested each individual singly in the aviary. We chose only clear two-syllable calls that were free of background interference for stimuli. We high-pass filtered all stimuli at 600 Hz to remove low-frequency background noise. We played back the stimuli to the subjects from a laptop computer through a Targus (A-2CH 100) amplifier and a Soundsphere Q6 omnidirectional speaker placed 0.5 m off the ground and 15 m from the aviary. All calls were played at 85−90 dB at 2 m (see above). We videorecorded the trials onto mini-DV tape with a Canon GL-2 camcorder. We recorded the trial audio onto two channels of the tape: the subjects' responses, with a Sennheiser ME67K6 shotgun microphone, on one channel and the trial annotations, with a lapel microphone, on the second channel. If a trial was interrupted by a suspected interaction with a wild bird outside of the aviary, we excluded that trial from further analyses. We also excluded a trial if a subject did not respond to any of the stimuli, as we could not determine whether the bird did not respond because of a lack of desire or because of excessive stress due to the testing conditions.

We used an interactive playback protocol (Vehrencamp et al. 2003) to measure the subject's responses to the stimuli, allowing the subject to control the length of the interaction with the playback stimuli. Each subject was presented with each stimulus at least three times, but the total number of presentations was determined by the number of subject responses, given the following protocol. We began the trial by playing a two-part contact call from one individual to the subject. If the subject responded with a contact call, we immediately replied with the same contact call stimulus and continued to reply immediately until the subject stopped responding. If the subject did not respond, we waited 10 s and played the first stimulus a second time. If the subject responded, we immediately responded. If the subject still did not respond, we waited another 10 s before presenting the same contact call again; thus, each individual had a least three opportunities to respond to a stimulus. Once a subject stopped responding, we waited for a 2-min quiet period before presenting the next stimulus. We continued with the above protocol until all contact call stimuli had been presented to the subject. No contact call stimulus was used in more than one successful trial, and we randomized the order of presentation for each stimulus category (see below).

Stimuli for mate trials

Each subject was tested with one call each from five individuals: one call from a conspecific on a different island (Aruba, Curacao or Isla Margarita), ensuring no previous interactions between the subject and that individual; one call each from three individuals captured from the same roost, with whom no relationship could be assigned a priori; and one call from its mate. Given the highly selective nature of conure responses to contact calls in the wild (S. C. Buhrman-Deever, personal observation), we were concerned that testing responses to a call from a bird's mate versus responses to a randomly chosen individual from the same roost would be very likely to lead to a positive bias towards the mate's response. This could be due simply to a preference for a familiar individual's call. Therefore we made the test 'harder' by giving each subject a chance to respond to three different same-roost individuals, increasing the chance that one of those individuals was also familiar to the subject. We used calls from other islands to control for these potential effects of previous social contact; extra-island calls were from individuals with which there was no possibility of previous social interaction with experimental birds. We controlled for subject as a random effect in the statistical analyses (see below).

Stimuli for group-member trials

We presented the subject with one call each from five individuals. For most of the subjects, these were one group member and four other individuals captured at the same roost. In three cases, we were able to capture entire groups flying off of the roost. Thus, for three trials, we presented the subjects with calls from two group members and three roost members. Again, we presented the subjects with more than one same-roost individual to attempt to compensate for a presumed high probability of ignoring a randomly chosen same-roost individual.

Statistical analyses

We compared the response strength of the subjects to each of the stimuli by examining the likelihood of response to a stimulus category, the number of vocal responses to each stimulus and the latency to the first response. We used logistic regression analyses in JMP IN 5.1 (SAS Institute) for the comparisons. Subject was treated as a random factor in all analyses. The number of vocal responses included the number of loud zips (preflight calls) and loud contact calls. Because the number of responses was not normally distributed, we divided the number of responses into the following categories: (1) 0 responses, (2) 1−5 (inclusive) responses, and (3) >5 responses. We also compared the latency to the first response to each stimulus given by the subject. We measured this response latency to the nearest 10 ms in Raven 1.2 (Bioacoustics Research Program, Cornell Lab of Ornithology). We coded response latency as one of two possibilities: 1 = response within 1 s, and 0 = no response or response after 1 s.

Ethical Note

All observational and experimental protocols were approved by the Institutional Animal Care and Use Committee of Cornell University (IACUC Protocol no. 98-102-1) and the government of the Netherlands Antilles, DROB and STINAPA (Permit no. 23002924).

RESULTS

Observational Study: Overflying Group Behaviour When Called To

Overflying groups were much more likely to settle in the immediate area when they were called to than when they were not (55.8%, $N = 86$, versus 22.6%, $N = 137$, $P < 0.0001$, Fisher's exact test). Local settlement by overflying groups was not different when the birds were silent

Table 1. The influence of ecological (non-call-based) parameters on contact call response by foraging groups

Parameter	Estimate	SE	Odds ratio	χ^2	P
Fruit per bird (FPB)	0.01	0.003	1.01	0.89	0.34
Time before flyby (TBF)	3.04	0.72	20.99	7.37	0.007
FPB*TBF	−0.01	0.005	0.99	2.29	0.13

Logistic regression model of ecological (non-call-based) parameters influencing response by foraging groups. This is the final model, with all nonsignificant factors (the size of the foraging group, the size of the overflying group, the number of other groups called to previously and the number of other groups in the area) sequentially removed from the analysis. $N = 35$ groups foraging on *A. tortuosa*, with one to nine potential overflying group interactions each. The calculated odds ratio of 20:1 indicates that foraging groups were almost 20 times more likely to call to overflying groups that passed during the first few minutes of the foraging group's arrival on the tree.
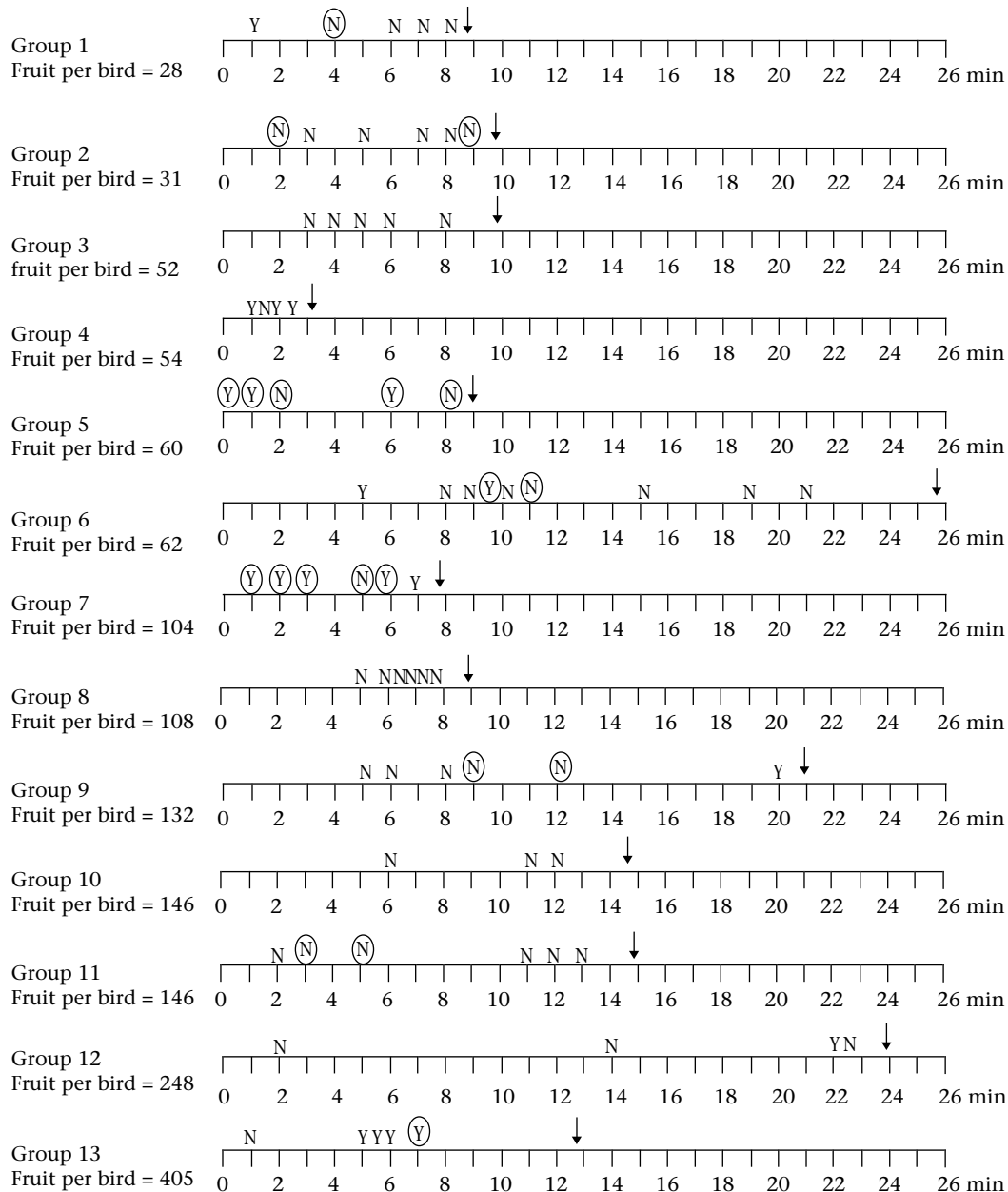
Figure 2. Foraging group calling patterns for those groups foraging on *A. tortuosa* with three or more overflying groups each. Y: foraging group called to the overflying group; N: foraging group ignored the overflying group. Circled letters indicate those overflying groups that landed in the area. Each line indicates a timeline for a different foraging group, and the time of departure of each foraging group is indicated by the arrow.

compared to when no other birds were in the area (22.6%, $N = 137$, and 25.8%, $N = 720$, $P = 0.46$, Fisher's exact test). There was no evidence of aggression (displacement interactions, physical fights, aggressive vocal interactions) regardless of whether new arrivals were or were not called to. All responded-to overflying groups uttered one or two loud contact calls as they approached before the response from a foraging group. No quiet overflying groups were called to ($N = 39$).

Joining groups did not always land in the same tree as the foraging group. In 12 of 22 cases (54.5%) in which responded-to groups landed in the area, the new arrivals did not join the current foragers, but instead landed and foraged in nearby trees. In 10 of 22 cases, however (45.4%), the initial foraging groups' sizes increased upon departure. These new members came from the same tree ($N = 3$) or from neighbouring trees ($N = 7$).

Playback Study: Overflying Group Behaviour When Responded To

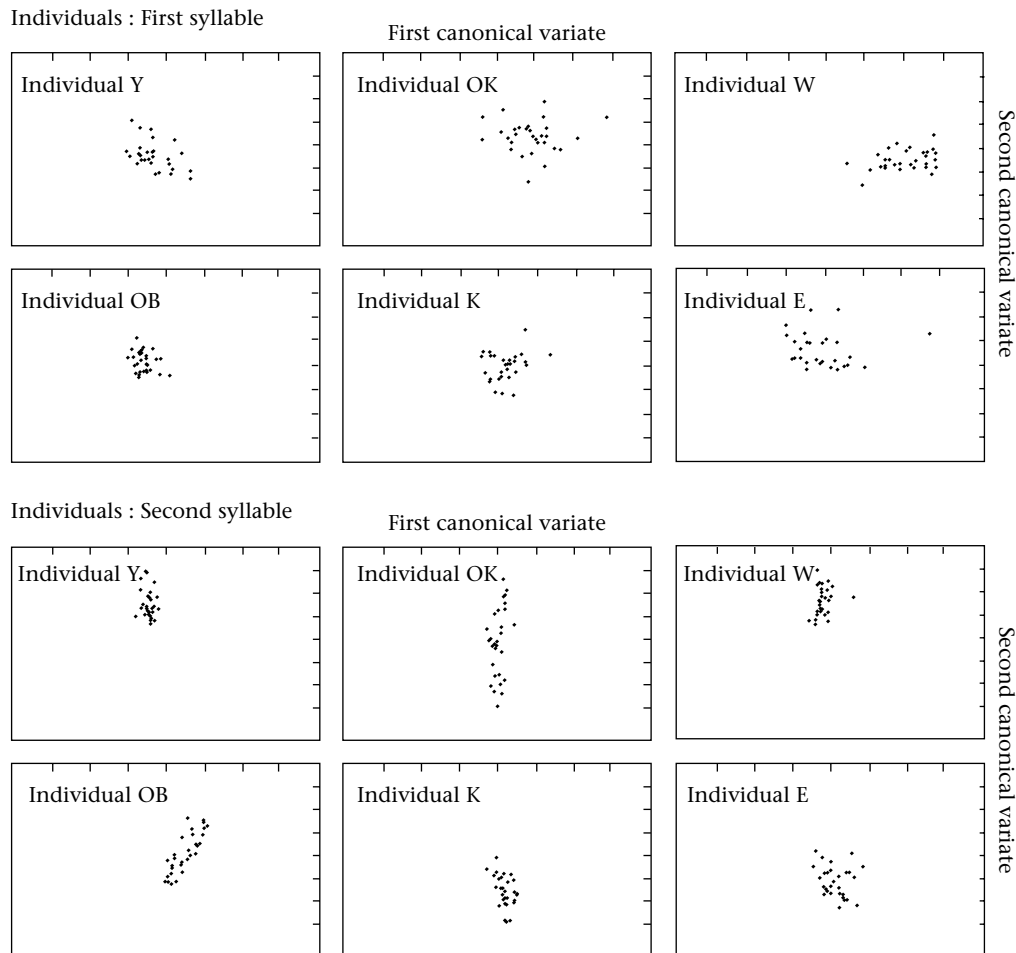Birds in the called-to treatment were much more likely to settle in the immediate area than those in the quiet

Individuals : First syllable

First canonical variate

Second canonical variate

Individuals : Second syllable

First canonical variate

Second canonical variate

Figure 3. Canonical plots of contact call separations for six individuals. Plots of the 30 calls on the first two canonical variates (as generated by the MANOVA) for six of the 16 compared individuals are presented. Each plot is on the same scale. Better separation is obtained with more canonical variates.

treatment (70%, $N = 39$, versus 28.9%, $N = 39$, $P = 0.0006$, Fisher's exact test). Thus, calling alone, without any visual stimulus, is sufficient to induce local settlement. The settling percentages were not significantly different from those in the observational study ($P = 0.11$).

Do Ecological or Call-based Factors Drive Calling by Foraging Groups?

The initial model screen indicated that there is no effect of group size (foraging or overflying group), the number of other groups in the area or the number of other overflying groups the foragers had already called to on the probability of recruitment calling. The results of the final model are listed in Table 1. There was no effect of the amount of available food on the likelihood of foragers replying to flyby groups. The only significant variable was the amount of time spent on the tree before an overflying group approached; foragers were more likely to call if an overflying group approached in the first few minutes of their residence on the tree.

However, further examination of the calling patterns (Fig. 2) of foraging groups to overflying groups shows that timing is not the sole factor influencing the foragers' decision. Even given the effect of timing on calling behaviour (see above), there still is some apparent selectivity within the first few minutes of the foraging group's time on the tree (e.g. group 4, Fig. 2). In addition, for those foraging groups that had the opportunity to call to several groups, it was clear that not all overflying groups were treated the same; foraging groups would not call to all groups, regardless of whether or not the overflying group landed in the area (Fig. 2). For example, the sixth listed group (Fig. 2) called to the first overflying group, but not to the next two groups, even though the first group did not land. Similar calling selectivity regardless of subsequent joining can be seen in groups 1, 4 and 12. This again suggests that the number of birds in the area does not influence calling by a foraging group. Rather, the foragers seem to be choosing which groups to recruit. This selectivity is evident even early in a foraging group's residence on a tree. Thus it does not appear that ecological factors such as food abundance, number of individuals, and even the timing of the overflying group's arrival are the dominant factors in the foraging group's decision to call.
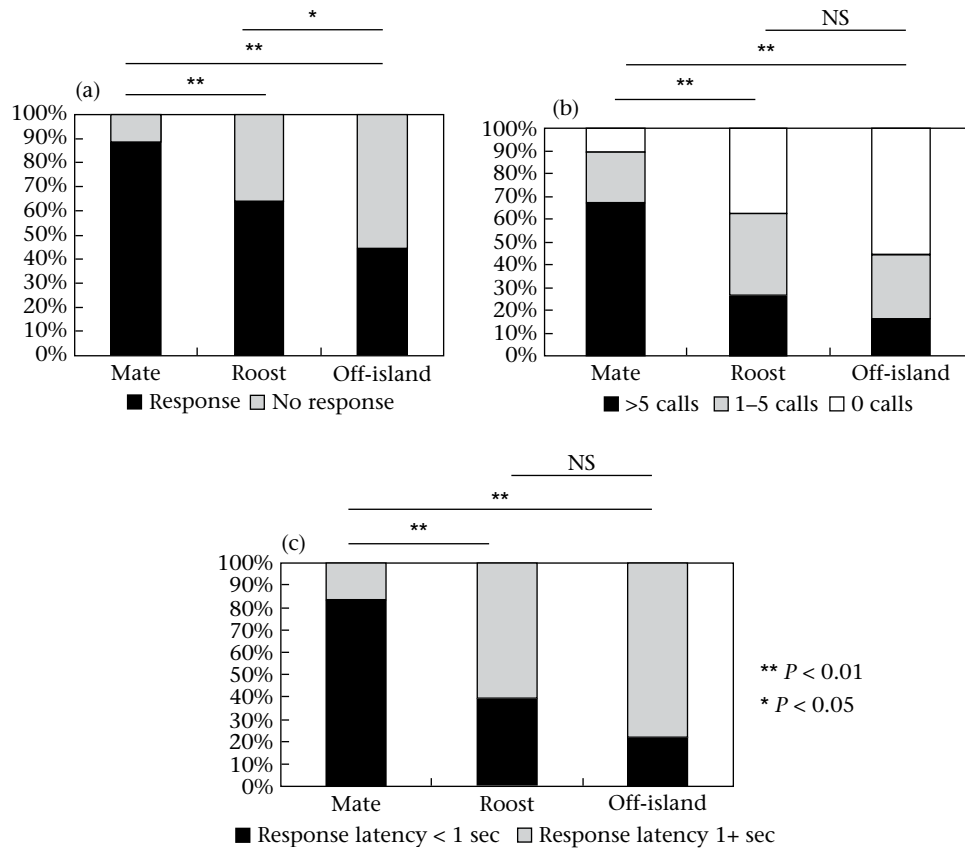
Figure 4. Results of the preferential response experiment for pairs: mate versus all stimuli. (a) Effect on the likelihood of response. Logistic regression overall model: $P = 0.002$, L-R $\chi^2 = 12.5$, off-island versus mate estimate 3.4 ± 1.1, roost versus off-island estimate -1.4 ± 0.8. Comparison tests: mate versus roost estimate 2.5 ± 1.0, odds ratio 12.2, L-R $\chi^2 = 7.5$, $P = 0.006$; roost versus off-island estimate -15 ± 0.8, odds ratio 0.2, L-R $\chi^2 = 3.8$, $P = 0.05$; mate versus off-island estimate 4.4 ± 1.5, odds ratio 81, L-R $\chi^2 = 14.7$, $P = 0.0001$. (b) Effect on the number of calls in response. Logistic regression overall model: $P = 0.0001$, L-R $\chi^2 = 17.8$, off-island versus mate estimate 3.1 ± 0.8, roost versus off-island estimate -0.9 ± 0.6. Comparison tests: roost versus mate estimate 2.5 ± 0.7, L-R $\chi^2 = 14.1$, $P = 0.0002$; mate versus off-island estimate 6.0 ± 1.7, L-R $\chi^2 = 28.2$, $P = 0.0000$; roost versus off-island estimate -1.0 ± 0.6, L-R $\chi^2 = 2.6$, $P = 0.1$. (c) Effect on the latency to response. Logistic regression overall model: $P = 0.0001$, L-R $\chi^2 = 18.6$, off-island versus mate estimate 3.4 ± 1.0; roost versus off-island estimate -0.9 ± 0.7. Comparison tests: mate versus roost estimate 2.8 ± 0.9, odds ratio $= 15.7$, L-R $\chi^2 = 13.9$, $P = 0.0002$; mate versus off-island estimate 5.0 ± 1.5, odds ratio 144, L-R $\chi^2 = 21.9$, $P = 0.0000$; roost versus off-island estimate -0.9 ± 0.7, odds ratio 0.4, L-R $\chi^2 = 2.1$, $P = 0.1457$.

Individual Differences in Contact Calls

We tested 30 calls each from 16 individuals. We found significant differences among the 16 different individuals' calls in both the first (MANOVA, Wilk's $\lambda = 0.316$, $\eta^2 = 68.4\%$, $P < 0.0001$) and the second syllable (MANOVA, Wilk's $\lambda = 0.027$, $\eta^2 = 97.3\%$, $P < 0.0001$) (Fig. 3). Discriminant function analysis correctly classified calls according to individual in 28.6% (27.1% with cross-validation) of the cases for syllable 1 and 57.3% (56.2% with cross-validation) of the cases for syllable 2 (a priori correct classification: 6.3%). Thus, the potential for recognition of individuals by their contact calls exists.

Preferential Response Trials: Responses to Mates

We completed 18 trials looking for differences in response to the call of a mate and calls from other individuals. There were significant differences in the number of calls

produced, the likelihood of a response and, additionally, the likelihood of responding within 1 s of the stimulus presentation to the different stimulus categories. In all cases, the call of the mate received the strongest response (Fig. 4). In addition, comparing the response to the mate's call versus the strongest response to a roost-member's call (as determined by fastest response and/or most number of responses), we still found significantly stronger responses to the mate's call (Fig. 5).

Preferential Response Trials: Responses to Group Members

We completed 11 successful trials testing for preferential response to individuals caught from the same group flying out of the roost. We found no evidence for a stronger response (likelihood of response, response latency or number of responses) to those caught within the same group than to randomly selected roost mates (Fig. 6). Thus
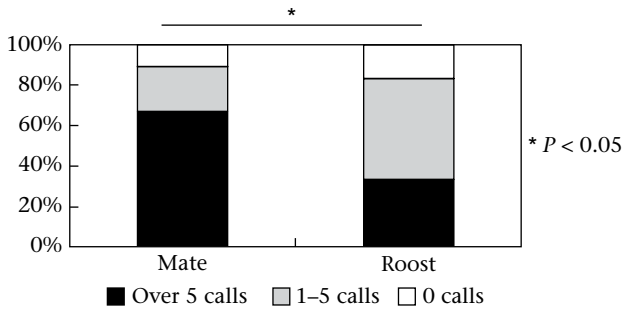
Figure 5. Preferential response experiment. Comparison of the number of calls in response for pairs: mate versus strongest roost response. Logistic regression: estimate 2.0 ± 0.9, L-R $\chi^2 = 5.3$, $P = 0.02$.

there was no evidence that simply travelling in the same group per se was sufficient to elicit a preferential response.

DISCUSSION

The results of this study suggest that brown-throated conures could use loud contact calls to form selective associations at foraging sites. Calling by foraging groups in response to overflying groups significantly increased the local settlement of overflying groups. Playback studies confirmed that overflying groups are attracted to the contact calls of conures from the canopy, suggesting that it may be difficult for overflying groups to detect quiet foraging groups. The contact calls of the approaching groups also seem to be important in the foragers' decision to call. Foragers responded only to overflying groups that

were calling, and the patterns of those who were called versus ignored suggest that the foragers were not using resource availability, or other non-call-based factors, as the dominant factor in their decision to call. Our studies of the short-term captives show that the conures can use contact calls to discriminate between individuals and preferentially respond to particular social partners. There were individual differences in contact calls in wild brown-throated conures. The conures also displayed a strong preferential response to the calls of their mate. These results, taken together, suggest that brown-throated conures may use characteristics of the approaching contact calls to determine whether to call.

Interestingly, despite the observed preference for the calls of a mate, no preference could be determined for group members per se—not all group members' calls elicited strong reactions from the test subjects. One possible explanation is that individuals flying off the roost together are not necessarily members of preferred social groupings. We thus may not have consistently tested subjects with calls from individuals they chose to fly and forage with, but rather used calls from other individuals who had simply left the roost at the same time.

How might the foragers benefit from responding to the overflying groups? Calling for mating advantage in this species seems unlikely, as brown-throated conures most often travel as (presumed) mated pairs. It also does not seem likely that the foragers are responding to others to avoid aggression or physical punishment (Hauser 1992). The evidence presented here suggests that foraging conures are difficult to detect by overflying individuals, which would make discovery and punishment by aggressive or dominant
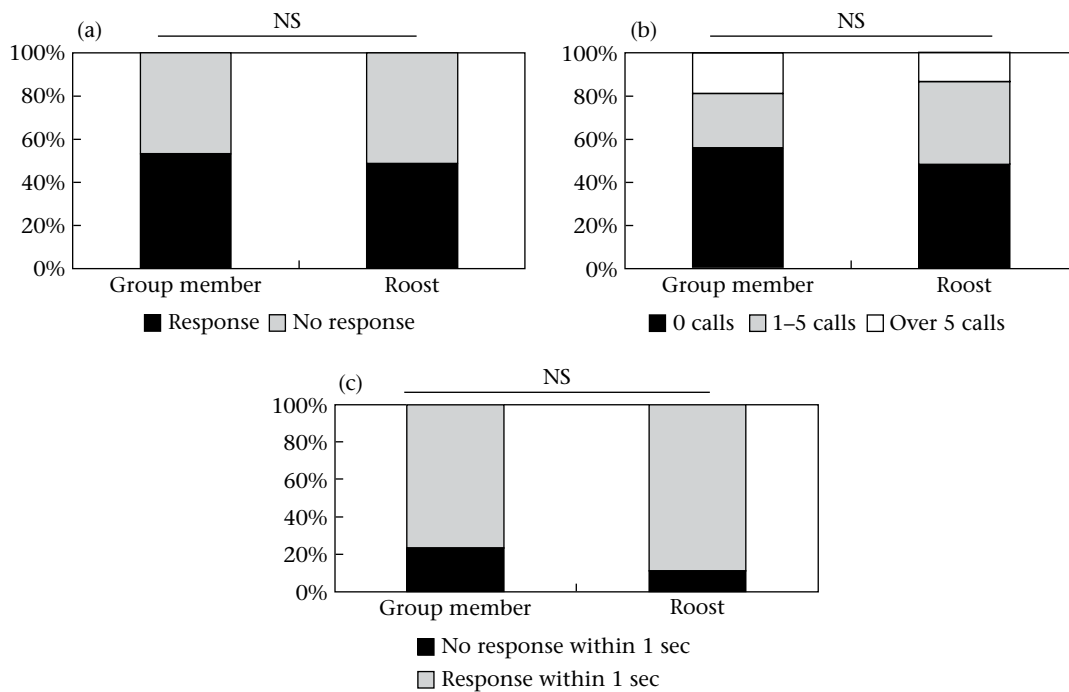

Figure 6. Preferential response experiment: group member versus roost. (a) Effect of likelihood of response. Logistic regression: estimate 0.1 ± 0.3, L-R $\chi^2 = 0.1$, $P = 0.76$. (b) Effect on number of responses. Logistic regression: estimate 0.2 ± 1.0, L-R $\chi^2 = 0.3$, $P = 0.56$. (c) Effect on latency to response. Logistic regression: estimate -0.8 ± 0.5, L-R $\chi^2 = 2.4$, $P = 0.12$.

conspecifics unlikely. In addition, there was no evidence of aggression between foraging groups and overflying groups that settled without being responded to; thus, there is no physical punishment for withholding information.

Recruiting others to reduce predation risk through 'selfish herd' dilution (Hamilton 1971) or increased antipredator vigilance effects (Pulliam et al. 1982) is a possibility, but is not likely to be the dominant factor in the selectivity of the interactions. If the foraging conures were recruiting additional individuals to either help scan for predators or dilute predation risks, they would probably not be so selective in their calling. Perhaps most telling, even if not joined by called-to groups, they still ignored some subsequent groups, suggesting that the identity of the approaching group was important in the decision to call. Risk of predation seems low on the island. Although merlins (*Falco columbarius*) and peregrine falcons (*Falco peregrinus*) do stop over on the island during spring and fall migrations, the only resident raptors are crested caracaras (*Caracara cheriway*) (J. Ligon, personal communication), which present little risk to the conures. In addition, although the presence of feral cats probably carries some risk, there are no native terrestrial predators on the island.

The conures may respond to overflying groups to enhance their foraging efficiency at the resource. Although food abundance (characterized as available fruit per bird) had no significant effect on the likelihood of calling, the conures were more likely to call to groups that arrived in the first minutes of their residence on a tree. By observing additional foragers, they could obtain information about the location of currently ripe fruits within a particular tree through local enhancement (Pulliam & Caraco 1984). Foragers may also gain information about food availability on neighbouring trees, as overflying groups landed in neighbouring trees about half the time. Because we could not easily observe conures foraging within the canopy and determine if successful foragers were approached and copied within a tree, this remains a potential benefit. However, it does not seem likely that this is the only benefit to responding to the contact calls of overflying groups, as local enhancement alone would not necessitate the observed selectivity in response.

Foragers may benefit through the recruitment of individuals with local knowledge and respond to others who could guide them to new food resources. Newly joining individuals did depart with the original foragers approximately half the time. This may also be a reason foragers were more likely to respond to overflying groups when they were recent arrivals themselves. Later-joining birds may be less likely or willing to coordinate their departure with foragers who have had many minutes to exploit the resource. Foragers also may be recruiting recently separated group members to the foraging site. If this is the case, then this could be an additional explanation for the increased likelihood of calling early on the time of the tree; early overflying individuals are more likely to be part of the group 'catching up' to the others.

There is some evidence that individual recognition could be based upon frequent interactions with particular individuals in this species. Radiotracking studies of six individuals revealed that some consistently settled in the same location in the night roost for up to a month at a time (J. R. Eberhard & S. C. Buhrman-Deever, unpublished data). At least one conure roost on Bonaire has remained in the same location for 4 years (Harms & Eberhard 2003; Buhrman-Deever 2007). This leaves open the possibility that the conures are able to establish long-term relationships with other individuals foraging within the same home range. Further study with marked individuals is needed to address this possibility and to determine to what extent long-term relationships may influence preferential calling in this species.

Due to the difficulty of obtaining quality recordings of rapidly approaching overflying groups, we were unable to obtain high-quality recordings of contact call interactions in the wild. Thus, although our captive studies show that the conures can recognize individuals based on their contact calls, we cannot say definitively that the conures are using individual recognition alone in their decision to call. Indeed, geographic variation and local dialects have been found in many parrot species (Wright 1996; Bradbury et al. 2001; Baker 2003; Kleeman & Gilardi 2005; Bond & Diamond 2005). We examine the possibility that similarity may also play a role in selective response in a separate study (Buhrman-Deever 2007).

Most parrot species, brown-throated conures included, utter loud contact calls in many contexts, including when gathering at and departing from night roosts, between foraging and overflying groups, and in long-distance interactions between perched individuals (Bradbury 2003; Buhrman-Deever 2007). This study has suggested the possibility that individual recognition may be important in the formation of selective foraging associations. Given the many contexts in which contact call exchanges apparently mediate selective social interactions in wild parrots, further studies examining the information contained in contact calls and how they are used in the wild should yield important insight into the potential benefits of social exchanges in parrots.

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