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Call Convergence within Groups of Female Budgerigars
(Melopsittacus undulatus)

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Abstract

The budgerigar (Melopsittacus undulatus) is a promising model species for the study of adult vocal learning. To date, several studies have confirmed the existence of vocal plasticity and, more importantly, rapid imitation of contact calls by adult male budgerigars. Vocal learning has not been investigated in female budgerigars, however. Since one likely function of the contact call is to denote group affiliation, we tested the hypothesis that female budgerigars, when placed into groups, would develop a shared contact call. We recorded the contact call repertoires of eight adult female budgerigars that were unfamiliar with one another, then placed them into two groups. Each group was deprived of visual contact with other birds. Recording sessions continued for the subsequent 8 wks, and behavioral observations were also conducted during this time. Within 4–7 wks, females in both groups converged on a common call type. This rate of convergence is slower than that observed in prior experiments limited to male birds, and much slower than vocal imitation by male budgerigars paired with females. Therefore, while our study documents vocal plasticity in adult female budgerigars, it also suggests that female budgerigars learn new vocalizations more slowly than males do.

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Introduction

The budgerigar (Melopsittacus undulatus), a small parrot native to Australia, has emerged as a promising subject for the study of vocal learning in adult animals. Budgerigars possess several vocalizations, the most well-studied of which is the
contact call. Because contact calls are readily produced by captive budgerigars and brief in duration, they have been used as convenient stimuli for perception studies (Dooling et al. 1987; Brown et al. 1988). Contact calls have also been identified as a type of learned vocalization that is highly stereotyped, yet varies among individuals (Dooling 1986). Contact calls probably play a role in individual recognition, as budgerigars are able to distinguish among the contact calls of other birds, especially cage-mates (Brown et al. 1988).

Several studies have concluded that vocal plasticity and, more importantly, vocal imitation continues into adulthood in budgerigars. Farabaugh et al. (1994) first documented call convergence, probably through mutual imitation, in small groups of adult male budgerigars. More recently, Bartlett & Slater (1999) found that males introduced into all-male budgerigar flocks learned the flock’s dominant call type within 2–4 wks. Hile et al. (2000) discovered that male budgerigars consistently and rapidly (on average in 2 wks) imitated the contact call of the female with whom they were paired. What has not been studied to date, however, is vocal plasticity in female budgerigars. The literature contains no evidence for female vocal plasticity, and Hile et al. (2000) found little change in the females’ calls in their study of budgerigar pairs. It is possible, however, that females may change their calls in settings other than when they are paired with a single male, or that their calls change much more slowly than do those of males. Therefore, it is important to test for female vocal plasticity in other social contexts. Because contact call convergence is likely to signal group membership, we tested the hypothesis that female budgerigars will, when placed into a new social setting, exhibit vocal convergence within their group. In order to determine whether this intra-group convergence occurs more slowly in females than in males, we designed our study to be similar to that of Farabaugh et al. (1994) on intra-group convergence among males.

Methods

Subjects

Eight young adult (based upon plumage and iris color) female budgerigars were obtained from a local wholesaler, two birds at a time, with 2 wks between each purchase. Because the wholesaler buys and sells approximately 500 birds per week, the birds obtained at different times could be assumed to be unfamiliar with one another. Next, at least 100 of each bird’s contact calls were obtained by recording the birds for 3–4 h every other day. Individuals generally had one dominant call type (more than 50% of all calls), and one or two call types that were uttered infrequently. Birds purchased at different times were housed in separate locations so that no visual or vocal contact was possible among subjects destined to be placed into the same group. Once the initial repertoire of contact calls was recorded, subjects were divided into two groups of four birds each, separating the birds that were purchased together. Each group was housed in a cage (61 cm high × 61 cm wide × 46 cm deep) and placed in a room containing other female budgerigars. A plywood barrier was placed between each group’s cage and any other cages. Thus, the different cages were in acoustic but not visual contact. The groups
were kept together for the next 8 wks, and weekly recordings were made of their contact calls. Birds were maintained on a 14 h : 10 h light : dark cycle, and fed a standard seed mixture, supplemented with nesting diet, seed sprouts, mineral grit, cuttlefish bone, and millet.

Call Recording

For each recording session, two birds were transferred to a cage located within a sound isolation chamber (Model AC-3; Industrial Acoustics Inc.). Prior to group formation, each bird was recorded along with the bird that had been purchased at the same time. Following group formation, each bird was recorded with the same individual for 4 wks, then the assignment was changed for the subsequent 4 wks.

A CD recording of sounds from a budgerigar colony (not containing the prospective cage-mates) was played at barely audible levels (below the data collection trigger point) in the background to encourage the birds to vocalize. The two birds in the recording apparatus were separated by a sheet of transparent Plexiglas (1.2 cm thick) and a microphone (PRO 7a, Audio Technica) was placed on each side of the barrier, which provided 4–6 dB of signal attenuation between the two microphones. The audio signals were digitized at 20 kHz with 16-bit resolution (ITC-16, Instrutech Inc.). Data acquisition was controlled with the Pulse Control software additions to the Igor Pro software package (WaveMetrics Inc. 1994; Bookman & Newton 1996). With this combination of hardware and software, two vocalizations could be recorded in a sound-activated manner, with specifiable pre- and post-trigger periods, and on two channels simultaneously. Signal intensities were compared across the two audio channels to confirm caller identity. All recorded vocalizations were transferred to CDs for long-term storage.

Call Classification

To determine whether or not call convergence had occurred within groups, as well as to classify calls objectively, we performed similarity comparisons followed by cluster analyses. All recorded vocalizations were displayed as sound spectrograms with a sliding step time of 2 ms and a frequency resolution of 156 Hz (FFT size = 128 points; Hanning window applied). All sound spectrograms were bandpass filtered (1.5–5.5 kHz, with smoothed filter corners) and multiplied by a Gaussian image filter (3 x 3 pixels). For each week, as well as for the pre-group period, up to 50 calls were randomly chosen from each bird in a group and compared using the normalized cross-correlation method (Clark et al. 1987), which essentially involves sliding two sound spectrograms across one another in the time domain to determine their maximum percentage similarity. The resulting similarity scores were converted into distances, and this matrix of distances subjected to a hierarchical clustering algorithm. We chose Ward’s agglomerative method, which minimizes variation within clusters (Hair et al. 1998). The clustering algorithm yielded nine dendrograms of calls from each group, one for each week that the groups were housed together, and one for the calls collected prior to group forma-
tion. The size of each dendrogram was scaled to the distance scores, and the same arbitrary cutoff point along the branches of each dendrogram was used to determine which calls were placed within the same cluster. This method yields clusters of similar calls, which, when used to construct averages, can be displayed as sound spectrograms that appear nearly as sharp as single calls (Hile et al. 2000). In some dendrograms, this method also yields an entropic cluster, containing a few rarely produced calls. Although calls that fell into entropic clusters were not classified as a separate call per se, they were retained for more in-depth analyses.

**Measurement of Call Plasticity**

Calls from within each cluster were used to construct call averages for each bird, which in turn served as references for further comparison of calls among birds. For calls collected prior to group formation, all of each bird’s averages were compared to all of the single calls collected from each of the other birds, including calls not used in the cluster analysis. Comparing every bird to each of the others resulted in six columns of similarity scores, and from these we extracted the mean and maximum values. This represented a measure of the baseline similarity among the birds’ calls when these individuals were unfamiliar with one another.

The dendrograms were then inspected to determine whether or not calls from all four birds in a group could be found within the same call cluster in a given week. When such multi-bird clusters were found, separate call averages from those clusters were constructed for each individual. The averages obtained in this manner were then used as references and, as for the pre-group data, compared to all of the calls collected from other group members during the same week. These measures reflect the degree of similarity among birds with respect to the calls contained within the shared cluster. The baseline pre-group similarity scores among birds were contrasted with those obtained from the post-grouping, multi-bird cluster references. Student’s t-tests were employed to determine whether there were changes in mean and maximum similarity scores between baseline and after birds were placed into groups.

Once birds within a group had developed a shared call cluster, we hypothesized that the level of similarity among birds might continue to increase. Additionally, previous work had suggested that shared call types might continue to change following convergence (Farabaugh et al. 1994). In order to address the first question, we measured the degree of call convergence at 4 and 8 wks for the birds in group 1 (data from group 2 were not analyzed in this manner as one of the birds died during week 8). Specifically, we compared each bird’s shared call average to the shared call averages of every other bird in the group at 4 wks (when a shared cluster was first observed) and at 8 wks after group formation. We then compared the within-week 4 and within-week 8 similarity scores using a paired, two-tailed t-test. To determine whether call types continued to change, we tested whether the shared call averages from weeks 4 and 8 sorted out by week or by bird in a second, meta-cluster analysis (again using Ward’s method).
Results

During the 8 wks of the group housing, both sets of birds developed a shared call, albeit more slowly than previously noted within all-male groups (Farabaugh et al. 1994). The cluster analysis revealed that groups 1 and 2 developed a shared call type within 4 and 7 wks, respectively. The visual appearance of the sound spectrograms confirmed this subjectively (Fig. 1). The more detailed statistical analysis indicated that there were significant increases in both mean (paired t-test, \( t_{22} = 5.01; p < 0.0001 \)) and maximum (\( t_{22} = 3.32; p = 0.003 \)) similarity scores among birds at the time when shared clusters appeared, when compared to the pre-group baseline values (Fig. 2). Mean ± SE similarity scores changed from 46.5 ± 2.5 to 63.1 ± 2.2%, while the maximum values increased from 67.3 ± 1.4 to 76.3 ± 2.3%. It was critical to document the change in the maximum values, since this rules out the possibility that birds had ‘pre-existing’ shared calls, and also shows that the change in mean similarity scores was not merely due to a shift in the frequency with which each call type was produced.

The similarity scores between call averages during weeks 4 and 8 were compared using a paired, two-tailed t-test. During week 4, the shared calls were 74.4 ± 1.7% similar, while in the 8th week this figure increased to 84.6 ± 1.9%. This is a statistically significant increase (paired, 2-sided t-test, \( t_{10} = 2.70; p = 0.04 \)). In addition, the shared calls recorded from group 1 during week 4 appeared subjectively to be slightly different from those recorded during week 8. To test this hypothesis, averages for each bird obtained from calls within the shared clusters for weeks 4 and 8 were subjected to the clustering algorithm. Because the call averages from the two weeks fell into two separate clusters, we conclude that there was a measurable change in the shared call, over time.

Behavioral observations (two 1-h sessions during which we observed birds from behind a partial blind) suggested that the all-female group members behaved strikingly different from either all-male groups or heterosexual pairs (Hile et al. 2000). While both bonded pairs and males typically engage in affiliative behaviors such as allopreening, females in this study were never observed to interact at all, showing a total lack of either affiliative or agonistic interaction. Each group’s behavior was, on a whole, marked both by a lack of interest among its members and a general lack of activity.

Discussion

This study is the first to demonstrate that female budgerigars are capable of vocal learning as adults, just as male budgerigars are (Farabaugh et al. 1994). However, some important differences in vocal plasticity may nonetheless exist between the sexes. The results of our study suggest that female and male budgerigars learn new vocalizations at different rates, and that this may be due to differences in the way in which they interact with conspecifics.

In the current study, the two groups converged upon a common call type in 4–7 wks, and the shared call did not appear to resemble any of the pre-existing
Fig. 1: Sample sound spectrograms of four birds from group 1, documenting call convergence at week 4, continued convergence at week 8, and subtle changes in the shared call type over time. Pre-group sound spectrograms are calls taken from the cluster containing each bird’s most commonly produced call type. Week 4 and 8 sound spectrograms are calls of each bird that fell into the shared cluster. Sliding step time = 2 ms; FFT size = 128 points.
calls. Groups of male budgerigars develop a shared call type within a period of 3–4 wks, probably by mutual imitation of portions of calls (Farabaugh et al. 1994). More dramatically, when a male is paired with a female, he generally imitates her call in its entirety within 2 wks (Hile et al. 2000), and often in less than 1 wk (Hile unpubl. data). It is difficult to compare these data to those reported here, however, because the experimental designs were not identical. However, a separate line of evidence is also consistent with a sex difference in vocal learning rate: female budgerigars that are paired with males change their calls very little, and do not imitate the males’ calls (Hile et al. 2000).

A difference in the rate of vocal learning between male and female budgerigars may be due to a sex difference in vocal learning ability. Alternatively, or perhaps in addition to this sex bias, females may be less likely, for functional reasons, to share calls with other birds. In the wild, breeding female budgerigars remain in the nest hole during laying, incubation, and the early portion of the nestling period, while males form small flocks whose members forage together (Wyndham 1980). Breeding females may therefore have little reason to learn the calls of social partners, apart from those of their mate. In our experiment, females did not have access to a nest box and were not in breeding condition (based on cere color, Baltz & Clark 1996), although they were exposed to a breeding season photo-period. This leaves open the interesting possibility that call convergence by females could vary with the reproductive cycle and hormonal state.
In the laboratory, males are inclined to interact with their companions in positive ways in either the all-male or the male–female social setting. Females, on the other hand, often exhibit agonistic behaviors during initial contact and are generally much more aggressive towards males than vice-versa (Trillmich 1976; Hile et al. 2000). Interactions with other females can also be violent, particularly when females compete for nest boxes (Baltz & Clark 1999; Hile pers. obs.). In the present study, the lack of a nest box may explain why birds were not observed to exhibit agonism towards one another. Neither did they seem to have any interest in affiliative social interactions; for example, allopreening was never observed.

Farabaugh et al. (1994) previously noted that social interactions are important in adult vocal learning in budgerigars, pointing out that birds learn from birds that they can both hear and see in preference over birds that they can only hear. Likewise, individual birds in the current study came to share calls with conspecifics housed in the same cage, and no calls were shared between groups. Learning from companions regardless of the nature of the social interaction suggests that group membership alone can influence which calls are learned. Our behavioral observations did not indicate that the nature of the social interactions differed between the two groups, so we could not account for the large amount of variation in latency to convergence which we observed. We have suggested in the past that vocal imitation may play a role in courtship behavior (Hile et al. 2000), which may explain the sex difference in the pair setting. We also acknowledge, as others have, that contact calls also function in group cohesion and individual recognition. There could be strong selective pressure on birds within groups to develop a shared call, perhaps even in the absence of social exchange.

There is little evidence for song learning in female birds, but call plasticity has been observed in some songbirds (Nowicki 1989), and call sharing within groups may not be uncommon (Brown & Farabaugh 1997). Little has been done to determine whether there are sex differences in call learning. Some work with cardueline finches followed the process of call convergence in captive pairs, finding that either males or females may imitate their partners (Mundinger 1970). Nowicki (1989) arranged adult and juvenile black-capped chickadees (Parus atricapillus) into a small, mixed-sex flock, and several portions of the birds’ calls began to converge upon one another within a week. However, there did not appear to be any sex differences in vocal plasticity in this species. Thus, budgerigars are the only species in which a sex difference in call learning has been reported.

The behavioral sex difference in budgerigar call learning is likely to reflect sex differences in brain organization or physiology. There have been some reports of sex differences in the size of some vocal control nuclei in budgerigars (Nespor et al. 1996a, 1998), but these differences are likely to be quite minor in comparison to the well-known sex differences in the vocal control system of songbirds. This suggests that behavioral sex differences in budgerigars may be related to sex differences in micro-circuitry and/or physiology. One intriguing possibility is that the rate of call learning may be under the influence of hormones, as testosterone or estradiol treatments can induce female budgerigars to sing warble song (Brockway 1969; Nespor et al. 1996b). For the moment, the evolutionary and mechanistic
bases of the observed behavioral differences between the two sexes remain unknown.

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