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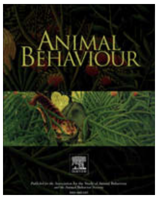

Rapid vocal convergence in an Australian cockatoo, the galah *Eolophus roseicapillus*

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There are several mechanisms for producing vocalizations that are similar to those of a conspecific, including song type matching during a vocal contest, group convergence on a signature call over time, or one-to-one matching of another individual's signature call. A novel category of conspecific matching has been described in a parrot, the orange-fronted conure, *Aratinga canicularis*, which shows rapid and directional modification of vocalizations over the course of a single vocal interaction. We examined whether a geographically and phylogenetically distant parrot, the galah, *Eolophus roseicapillus*, uses similar rapid call modifications during contact call exchanges, and sought to better define the conditions under which wild parrots directionally modify their contact calls. In each trial, we interactively broadcast a single call exemplar recorded from wild galahs and recorded the vocal responses of nearby galahs. Temporal parameters of response calls converged on the stimulus over the course of an interaction. Frequency measures also showed convergence, although this effect was less pronounced. Male galahs were more vocally responsive overall, and birds tended to converge more closely on male stimuli over the course of an interaction. This experiment confirms that other parrots, in this case galahs, are capable of rapid, directional call modification, and we suggest that this vocal technique may be an efficient mechanism for mediating the fission–fusion social system that is characteristic of many parrot species.
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Producing a vocalization with acoustic features similar to another individual's call is a vocal technique used by several avian and mammalian species. Behavioural mechanisms of such conspecific vocal imitation divide into four major categories. In many species of passerine, territorial males match the song types produced by their neighbours during aggressive interactions (Beecher et al. 2000; Vehrencamp 2001). This matching is discrete and variable, since a bird with a similar repertoire can choose to produce either a matching or a nonmatching song from its repertoire at any point in the interaction (Vehrencamp 2001). Since most passerines learn their songs during a sensitive period in development (Marler 1970), adults are limited to matching neighbours' songs that are already in their repertoire. Black-capped chickadees, *Parus atricapillus* (Nowicki 1989), cardueline finches, *Cardeulis* sp. (Mundinger 1970), pygmy marmosets, *Callithrix pygmaea* (Snowdon & Elowson 1999), and captive budgerigars, *Melopsittacus undulatus* (Hile & Striedter 2000; Hile et al. 2000) show a second category of vocal imitation in which changes in semipermanent group affiliations are accompanied by progressive changes in vocalizations over days or weeks that lead to a shared call type between individuals. A third type of conspecific vocal imitation exists in bottlenose dolphins, *Tursiops truncatus* (Janik 2000) and captive spectacled parrotlets, *Forpus conspicillatus* (Wanker et al. 2005), in which individuals match the features of a conspecific's individually unique contact calls during a single vocal interaction; this matching may serve to address (Janik 2000; Tyack 2003) or name (Wanker et al. 2005) a specific interaction partner. It is not known whether these interactions serve an aggressive or affiliative function (Janik 2000), and it is not clear whether this matching is caused by individuals discriminatingly producing existing signals in specific contexts, or whether they are modifying signal features at the time of the interaction.

There is some evidence that a Central American parrot, the orange-fronted conure, *Aratinga canicularis*, may use a fourth type of vocal modification that is characterized by continuous, directional call changes that rapidly and systematically lead to increased (Vehrencamp et al. 2003) or decreased (T. J. S. Balsby & J. W. Bradbury, unpublished data) similarity to an interaction partner's calls over the course of a single interaction. Unlike the one-to-one matching of calls shown by songbirds, dolphins and captive spectacled parrotlets, orange-fronted conures produce sequences of

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calls that have trajectories of increasing or decreasing similarity. Systematic convergence and divergence of acoustic features may have different signal meanings to conures, and it has been suggested that such rapid modification may serve either to mediate transient affiliation with an individual or a group, or to negotiate dominance or group decisions (Balsby & Scarl 2008).

Many species of parrots are nonterritorial, have large home ranges and live in fission–fusion flocks whose composition may change daily. Constantly changing social groups may necessitate a mechanism for rapidly mediating affiliations or social hierarchies within a group, and the production of contact calls accompanies flock formation and reunification of individuals in many species of parrots (Bradbury 2003). We thus wanted to determine whether other parrot species use rapid vocal modifications of contact calls during interactions with conspecifics in a manner similar to that of orange-fronted conures. The galah, *Eolophus roseicapillus*, an Australian cockatoo, is geographically far removed from the Central American orange-fronted conure, and these two species of parrots are from different families within the parrot order (Brown & Toft 1999; Wright et al. 2008). However, both species are nonterritorial, have large home ranges, share a fission–fusion social system, and use contact calls to mediate interactions between individuals and flocks (Rowley 1990; Bradbury 2003). Therefore, social pressures that might necessitate rapidly mediating affiliations with changing groups of individuals exist in both species. Although galahs seem to use contact calls to recognize specific individuals (Rowley 1990) and to discriminate between the sexes (J. C. Scarl, unpublished data), we have noted that the double chet contact calls in interactions between two birds can be quite similar. Thus, the purpose of this study was to determine whether galahs rapidly modify double chet call features to become more similar to a conspecific's calls over the course of a single interaction. In addition, since galah vocal behaviour varies by sex (J. C. Scarl, unpublished data), we tested whether male and female galahs change their calls differently based on whether they are interacting with a male or a female.

METHODS

Study Site

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

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

Stimulus Selection and Processing

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

We eliminated the majority of background noise from each stimulus by high-pass filtering at 500 Hz; as the majority of energy in the double chet call is above 2000 Hz (see Fig. 1), this did not affect the acoustics of the stimulus. We then amplified the stimulus using Syrinx (www.syrinxpc.com) so that the peak amplitude of the call was at 90% of the maximum amplitude possible without overloading the signal. All stimuli were broadcast using either a Sony VAIO PCG-8H1L notebook computer or a Dell Latitude C540 laptop computer connected to a Pioneer GM-3000T power amplifier and a JBL Control speaker.

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

Playback Protocol

Individual playback sites were interspersed throughout the study area, separated from each other by at least 75 m, and were within acoustic range of both foraging sites and nest cavities. The speaker was elevated at least 1.5 m by hanging it from a tree branch. During the playback, one person (J.C.S.) sat within 20 m of the speaker and interactively broadcast a playback stimulus. Two additional observers with Sennheiser MKH 816 or ME67 microphones and Marantz PMD690 recorders moved to record and sex galahs as birds came into the playback arena and vocalized. Untagged responding birds were visually sexed by eye colour; adult females have red irises whereas adult males have dark brown irises (Rowley 1990). If we could not determine the sex of a responding bird during a playback, we followed that bird after the playback until we could reliably see the bird's eyes.

Parrots may react differently based on whether they perceive themselves as a leader or a follower in a vocal interaction (Balsby & Scarl 2008), so to ensure that our playback stimulus initiated all vocal interactions, we commenced playbacks only when no other bird had given a double chet call in the area for at least 30 s prior to playback. This method increased the chances that calling birds were directing their calls at our stimulus, or at least were aware of the stimulus when they started calling. However, if no birds responded to the stimulus, it was impossible to tell whether this was due to a lack of interest or a lack of birds within hearing range of the playback. Thus, trials in which no birds came into the area or vocalized during the playback were disregarded. If any bird responded to the stimulus during the trial, that stimulus was never used in another trial, and once a response was achieved at a playback site, that site was not used for additional trials that year. If no birds responded to a stimulus during that trial, the stimulus and playback location could be used again in a future trial.

In each trial, one experimenter (J.C.S.) repeatedly broadcast a single double chet call at 5 s intervals with minor (<1 s)

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