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Mechanisms of heterospecific recognition in avian mobbing calls

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Abstract

Some birds emit special calls, referred to as mobbing calls, when they detect a predator in their area. These calls are easily localisable and function to rally other individuals to help chase out a threatening intruder. Interestingly, individuals may respond to the mobbing calls of other sympatric species. To understand the mechanism underlying interspecific recognition it is essential to determine whether birds also respond to the mobbing calls of allopatric species. If, as has been suggested, learning is important for call recognition, then calls from allopatric species should not evoke mobbing. If, however, there are intrinsic (and possibly convergent) characteristics of mobbing calls, then novel calls from allopatric species should evoke mobbing. We conducted two playback experiments with apostlebirds (*Struthidea cinera*, Family Corcoracidae), Australian mud-nesters, to understand mechanisms underlying mobbing-call recognition. The first demonstrated that allopatric mobbing calls could elicit a response significantly greater than control stimuli, but less than that elicited by playback of conspecific calls. The second demonstrated that the dominant frequency was critical for eliciting mobbing, rather than the commonly assumed broad bandwidth. Taken together, these results suggest that experience with a particular species' call is not essential to elicit mobbing; rather, intrinsic aspects of the calls themselves may explain heterospecific recognition.

Introduction

Alarm calls are given by many birds to warn others of the presence or approach of a predator (Marler 1955, 1957; Klump and Shalter 1984). One special type of alarm call is the mobbing call. Mobbing calls and mobbing behaviour are generally used to announce the presence and immediate location of a terrestrial predator or a perched bird of prey (Marler 1955; Curio *et al.* 1978). The calls in turn attract nearby birds to the site of the disturbance (Marler 1955; Jurisevic and Sanderson 1994). The function of the call may be to alert predators to 'move-on' from the area, because its detection impairs successful predation, or the predator may be harassed by the caller and others until it is driven away from the site (Curio *et al.* 1978; Klump and Shalter 1984; Jurisevic and Sanderson 1994).

Species often respond to heterospecific alarm and mobbing signals (Marler 1955, 1957; Nuechterlein 1981; Hurd 1996; Shriner 1998). There is a mutual advantage in responding to heterospecific calls because animals may collectively profit from increased vigilance or group defense against predators (Marler 1957; Morse 1977). Such mobbing works. For instance, Pavey and Smyth (1998) showed that the powerful owl (*Ninox strenua*) preys 8.75 times more frequently on non-mobbing species than on mobbing species.

Heterospecifics routinely respond to mobbing calls. In a study site where black-capped chickadees (*Poecile atricapilla*) were common, 24 non-chickadee bird species responded to black-capped chickadee mobbing calls (Hurd 1996). Mobbing calls of willow tits (*Parus montanus*) and redwings (*Turdus iliacus*) attracted more heterospecifics than either species' territory song (Forsman and Mönkönnen 2001). A study in Queensland, Australia,

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found that 9 of 35 mobbing bouts observed had multiple species mobbing a powerful owl together (Pavey and Smyth 1998). Jurisevic and Sanderson (1994) found that heterospecifics were attracted to the sites where mobbing was occurring. As far as we know, all previous studies that have reported on heterospecific attraction to mobbing calls have studied the response to calls of sympatric species.

Three hypotheses have been suggested to explain avian recognition and response to heterospecific mobbing calls. The first is that specific recognition must be learned. Using playback experiments, Curio (1971) found a lack of interspecific response to mobbing calls broadcast in regions where the species was not commonly heard. His interpretation of this result was that birds occupying the same area have mutual predators and learn to associate heterospecific mobbing calls with a detected predator. Shriner (1999) also found associative learning of antipredator response in golden-mantled ground squirrels (*Spermophilus lateralis*). By repeatedly exposing squirrels to a model predator together with a previously neutral sound, he showed that antipredator behaviour increased compared with their pre-exposure responses. The second is that mobbing calls are acoustically similar and therefore facilitate heterospecific recognition (Marler 1957; Stefanski and Falls 1972; Hurd 1996). Mobbing calls across many related and unrelated species have convergent acoustic properties: they often consist of rapidly repeated, short-duration broad-bandwidth pulses of sound (Marler 1955, 1957; Stefanski and Falls 1972). These properties allow a call to be more easily locatable by nearby animals, as suggested by Forsman and Mönkkönen (2001). The third hypothesis combines both previous ones: Hurd (1996) suggested that interspecific recognition results from both associative learning and common acoustic properties. Clearly, experiments are needed to distinguish among these hypotheses.

We conducted two playback experiments to study mechanisms underlying heterospecific recognition of mobbing calls in an Australian mud nester, the apostlebird (*Struthidea cinera*). Our first experiment controlled for the possibility of learned heterospecific mobbing-call recognition. We played a mobbing call of a North American bird, the Carolina wren (*Thryothorus ludovicianus*) to eliminate the possibility that the apostlebird might have learned to recognise the call. To properly interpret our experiment we also included a North American bird song control to ensure that the response was not due to call novelty. Our second experiment included the manipulation of an apostlebird mobbing call to study the acoustic mechanism underlying heterospecific recognition.

Methods

The two experiments were conducted between 20 April and 5 May 2002 at the Fowler's Gap research station, 112 km north of Broken Hill, New South Wales, Australia (31°S, 142°E).

Subjects

Apostlebirds are medium-sized, highly social birds living in arid inland regions of Queensland and New South Wales, Australia (Baldwin 1974). The birds are cooperative breeders and usually live in family groups of ~12 individuals. Chapman (1998) observed non-breeding season 'flocks' of ~50–100 apostlebirds drawn to a common food or water supply. These birds did not behave as true flocks and instead maintained strong familial units of ~9 birds. We did not capture or mark individuals for our study. We estimate that there were 50–100 individuals wintering in our study site and assume that the focal groups of 5–30 birds observed during this experiment came from different family groups.

Apostlebird recordings

Mobbing calls were elicited and recorded from small groups of apostlebirds perched in trees using a model great-horned owl (*Bubo virginianus*) (Dalen Products Inc., Knoxville, TN). While this species is not native

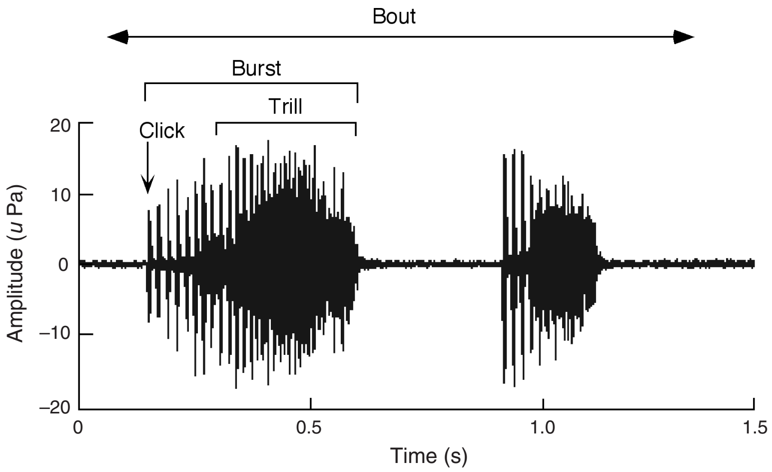

Fig. 1. Waveform of an apostlebird mobbing call. The call consists of a series of sound bursts, or a bout, each composed of many rapidly paced clicks, average (±s.d.) = 8.13 ± 1.79 ms in duration, followed by a short trill. The average (±s.d.) interval between clicks was 11.5 ± 3.9 ms.

to Australia, it is morphologically similar to sympatric species such as the southern boobook owl (*Ninox novaeseelandiae*) and the barking owl (*Ninox connivens*). The model was placed on the ground ~1 m from the base of the tree. Two other methods to elicit vocalisations included throwing a frisbee into the tree, and by having a human approach the birds on foot. Calls were recorded using a Sennheiser ME-88 unidirectional microphone and Sony TC-D5M cassette recorder onto high-bias tape. Calls were then digitised at 44.1 kHz into Canary 1.2.4 (Charif *et al.* 1995) using the 16-bit A/D board in a Macintosh Powerbook G3.

Experiment I: *Allopatric call recognition*

Call description

The mobbing call of the apostlebird has been described as a ‘ch-kew ch-kew’ sound (Pizzey 1980) or a ‘kreech’ sound (Baldwin 1974). The call consists of a series of sound bursts, each composed of many rapidly paced clicks averaging (±s.d.) 8.1 ± 1.8 ms (n = 80 clicks), followed by a short trill (Fig. 1). Silence between clicks lasted an average of 11.5 ± 3.9 ms (n = 80 intervals). Calls (n = the 3 exemplars) contained frequencies of 0–15 kHz, with a dominant frequency at 5.0 ± 0.5 kHz, but often with two dominant frequencies at 4.5 ± 0.3 kHz and 6.3 ± 0.6 kHz.

We obtained a single exemplar of a mobbing call of a Carolina wren from the internet (http://www.math.sunysb.edu/~tony/birds/wrens.html). The wren mobbing call was similar in structure to the apostlebird call: it consisted of bouts of short, repeated, broad-band bursts of noise (Fig. 2). Frequencies ranged up to 11.1 kHz, with a dominant frequency at 6.0 ± 0.8 kHz, but pulses often had two dominant frequencies at 4.8 ± 1.2 kHz and 6.7 ± 0.03 kHz.

Exemplars (16 bit, 44.1 kHz) of the songs of North American birds [Townsend’s solitaire (*Myadestes townsendi*), sage thrasher (*Oreoscoptes montanus*), and American robin (*Turdus migratorius*)] were obtained from the Peterson Field Guide to Western Bird Songs CD series and were used as controls (Fig. 2).

Playback procedure

We selected three mobbing-call exemplars from single apostlebirds with little background noise. Each exemplar, of 10–15 s, was normalised to match peak amplitudes using SoundEdit 16 (Macromedia Inc. 1995) and then copied and pasted to create 30-s playback stimuli. These exemplars, along with one 30-s mobbing-call exemplar from the Carolina wren, and three 30-s exemplars of North American bird song were burned onto a compact disc for playback.

Using a sound-level meter (Realistic model 33-2050, A-weighting, slow response) at a distance of 12 m, apostlebirds were observed to elicit mobbing calls with an average amplitude of 76 dB SPL and an average peak at 80 dB SPL. Recorded calls were played back using a Kenwood DPC-451 personal compact disc

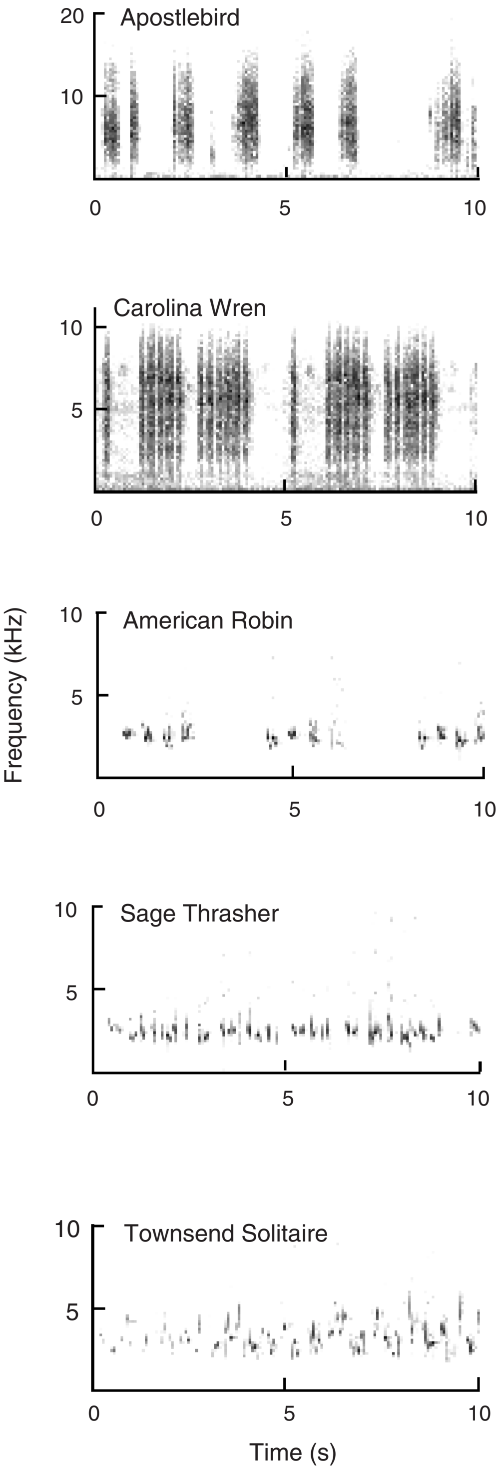

Fig. 2. Spectrograms (analysis bandwidth = 349.7 Hz, temporal resolution = 11.61 ms, clipping level = –80 dB below peak amplitude) of 10-s segments of playback stimuli used in the first experiment.

player through a Sony SRS-77G powered speaker. The playback setup would not allow for playbacks with amplitude above 58 dB SPL at 12 m from the speaker. Recorded exemplars were standardised for amplitude at 1 m from speaker to 78–80 dB SPL peak.

Playbacks were performed in a predetermined randomised order to birds in groups with more than five individuals. Playback trials were carried out between 0630 and 1000 hours, or between 1600 and 1730 hours, as these were the cooler times of day when birds were most active. The speaker was placed ~12 m from the birds and was covered in eucalyptus branches to obscure it from sight. When the animals had resumed normal behaviour we began the playbacks. Successive playbacks of the different treatments to the same group of birds were separated by at least 10–20 min.

Response measurements

We focused on the group and scored mobbing-related responses using a series of binomial (i.e. yes/no) questions. The proportion of positive responses during each trial was our measure of response intensity. We noted whether at least one bird within the group exhibited any of the following: looking toward the speaker, tail flaring, rocking, mob calling, chattering (contact calling within immediate group), and movement toward the speaker. These behaviours are recognised responses to the 'kreech' mobbing call of the apostlebirds (Baldwin 1974) and we saw apostlebirds engage in these behaviours during natural bouts of mobbing. We placed equal value on each response and summed the positive scores to determine the total proportion of response for that trial.

Experiment II: *Recognition mechanisms*

The same three exemplars of apostlebird mobbing calls were used as control stimuli in Experiment II. We created synthetic mobbing calls (Fig. 3) by generating bursts of white noise ranging from 0 to 10 kHz using SoundEdit 16 (Macromedia Inc. 1995). The temporal patterns of the first 10 s of each of the three apostlebird exemplars were mimicked using white noise, and then copied and pasted twice to create 30-s exemplars. These synthetic calls were termed 'broad-band' calls. 'Narrow-band' calls were also created by filtering the broadband calls below 4.5 kHz and above 5.5 kHz, thus creating a stimulus with the same tempo that was centered on the dominant frequency found in apostlebird calls. By design, the synthetic calls matched the tempo of the apostlebird calls; thus, the only difference in the stimuli was in the bandwidth.

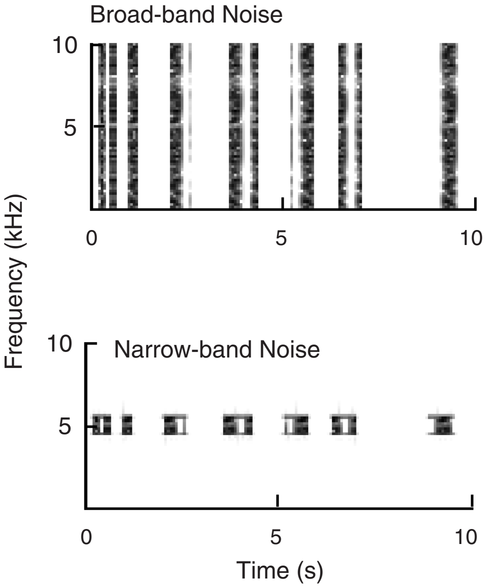

Fig. 3. Spectrograms of 10-s segments of the two synthesised playback stimuli used in the second experiment. Analysis bandwidth, temporal resolution and clipping level is the same as in Fig. 2.

Treatments were again presented to the birds in a pre-determined, randomised order and we scored the same response behaviours used in the first experiment.

Statistical analysis

We used Statview 5.01 (SAS Institute Inc. 1999) for all statistical analyses. The dependent variable for both experiments was the proportion of binary responses elicited in each trial to the playbacks. In the first experiment we used a Kruskal–Wallis non-parametric ANOVA to determine the main effect between treatments, because variable distribution was not normal, and the variances were not equal. Mann–Whitney U *post hoc* tests were then performed to detect significant differences between treatments. To test for habituation we regressed playback order on response. We found no effect of habituation in the first experiment, but found a significant effect of playback order on response in the second experiment. We therefore fitted an ANCOVA that included playback order and playback stimulus to analyse the results from the second experiment. Residuals from this ANCOVA were examined and appeared not to violate the assumption of normality. Throughout, we interpret significant results as those with P-values less than 0.05.

Results

Experiment I: *Allopatric call recognition*

Apostlebirds responded differently (Kruskal–Wallis: $H = 16.82$, d.f. = 2, $P < 0.001$) to the three treatments in the first experiment (Fig. 4). *Post hoc* analyses revealed significant differences in responses elicited by the apostlebird mobbing call and the birdsong control (Mann–Whitney $U = 5.50$, $Z = -3.42$, $P = 0.001$), the Carolina wren mobbing call and the birdsong control (Mann–Whitney $U = 11.00$, $Z = -2.99$, $P = 0.003$) and the apostlebird mobbing call and the Carolina wren (Mann–Whitney $U = 20.50$, $Z = -2.34$, $P = 0.019$). There was no evidence that birds responded less as the experiment proceeded (regressions of playback number on total responses: $R^2_{\text{Apostle}} = 0.018$, $P = 0.313$; $R^2_{\text{Wren}} = 0.002$, $P = 0.900$; $R^2_{\text{Birdsong}} = 0.040$, $P = 0.579$). Taken together, our results show that Carolina wren mobbing calls elicited a response, although it was not as great as the response elicited by the apostlebirds' own mobbing call.

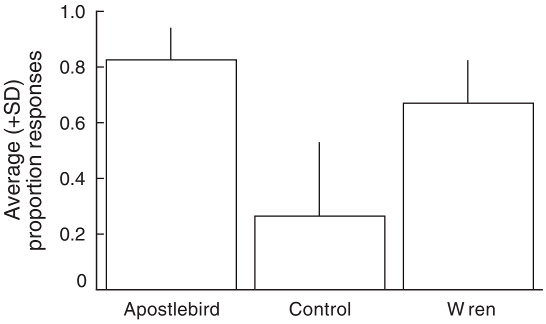

Fig. 4. Average (+s.d.) proportion of binary responses elicited from each treatment in the first experiment.

Experiment II: *Recognition mechanisms*

Regressions of experiment order on the proportion of dichotomous responses suggested that the birds habituated selectively to the broad-band playbacks, but not to the apostlebird or narrow-band playback ($R^2_{\text{broad}} = 0.530$, $P = 0.017$; $R^2_{\text{Apostle}} = 0.089$, $P = 0.403$; $R^2_{\text{narrow}} = 0.006$, $P = 0.837$). Therefore, we analysed responses using ANCOVA that included trial order. There was no main effect of treatment ($F_{2,24} = 2.24$, $P = 0.128$) or trial order ($F_{1,24} = 1.86$, $P = 0.185$), but there was a tendency toward a significant interaction ($F_{2,24} = 3.15$, $P = 0.061$). *Post hoc* pairwise comparisons of the interaction demonstrate that, compared with apostlebird mobbing calls, the birds selectively habituated to white noise ($F_{1,16} = 8.18$,

$P = 0.011$), but not to narrow-band noise ($F_{1,16} = 0.39$, $P = 0.542$). There was no significant difference in the narrow-band and wide-band comparison ($F_{1,16} = 2.55$, $P = 0.130$).

Discussion

In the first experiment we found that apostlebirds responded to their own mobbing call and the mobbing call of a North American bird, the Carolina wren. However, the response to the Carolina wren's mobbing call was less intense than to their own call. This is somewhat expected, as natural selection might favour the strongest response to their own call. Because the North American songbird playbacks controlled for novelty as well as response to any sound, we know that the birds did not respond simply to a novel sound. Moreover, the apostlebirds could not have learned the allopatric Carolina wren call, indicating that recognition of mobbing calls reflects some intrinsic acoustic characteristic.

The second experiment revealed that apostlebirds did not differentially respond to their own calls compared with narrow-band pulses of noise played back at the same tempo. We found, however, a difference between the birds' responses to their own call and to broad-band noise. Apostlebirds selectively habituated to broad-band noise, suggesting that band-width alone is not the only factor that elicits a response from apostlebirds.

Previous interpretations of heterospecific mobbing-call recognition suggested that a learned association of accompanying predation risk is necessary for an alarm or mobbing response to occur (Curio 1971; Nuechterlein 1981; Ramakrishnan and Coss 2000). Nuechterlein (1981) invoked learning to explain why western grebes (*Aechmophorus occidentalis*) flew immediately from their nest when alarm calls of the sympatric Forster's terns (*Sterna forsteri*) were broadcast. Curio (1971) invoked learning to explain why pied flycatchers (*Ficedula hypoleuca*) and collared flycatchers (*F. albicollis*) responded to playbacks of heterospecifics in some regions and not others. And Ramakrishnan and Coss (2000) found that heterospecific alarm recognition by bonnet macaques (*Macaca radiata*) occurred only in individuals that had frequently encountered the heterospecifics in their lifetimes.

Our results demonstrate that learning is not a necessary component of heterospecific recognition because it was impossible for an apostlebird to have learned the mobbing call of the allopatric Carolina wren. Nonetheless, a learned association may still be important. For instance, Busnel (1963) demonstrated that while the distress signals of the sympatric carrion crows (*Corvus corone*), jackdaws (*C. monedula*) and rooks (*C. fugilegus*) differed in their acoustic structure, each species was attracted to the distress calls from all three species. Although a learned association might elicit a stronger response in apostlebirds, our results indicate that experience with mobbing calls is not necessary for heterospecific recognition in apostlebirds.

A more complex view of learning is that the apostlebirds first learned their own mobbing call, and then generalised it to other similar-sounding calls. This alternative hypothesis to 'simple' associative learning may occur in these birds since the mobbing call of the Carolina wren is similar to their own in both bandwidth and dominant frequency.

Marler (1955, 1957) first suggested that the convergent features themselves would facilitate interspecific mobbing. Like the mobbing calls of many birds, the calls of both the apostlebird and the Carolina wren consisted of short, repeated broad-band notes (Marler 1955, 1957; Jurisevic and Sanderson 1994; Hurd 1996; Ficken and Popp 1996). The repetition of short notes is what accounts for the easy locatability of mobbing calls (Marler 1955, 1957; Curio 1978; Jurisevic and Sanderson 1994; Ficken and Popp 1996).

Interestingly, however, Ficken and Popp (1996) found that fewer than 50% of the mobbing calls from 52 species contained sharp onset and broad frequency range.

The results of our second experiment show that apostlebirds did not respond simply to broad-band white noise, nor to short, repeated pulses of sound. Thus, neither tempo nor bandwidth alone are the acoustic properties underlying heterospecific recognition. Rather, there may be certain frequencies, i.e. the dominant frequencies, that are particularly evocative. Although the same frequencies are contained in the broad-band white noise, the relative amplitude of certain frequencies in the natural apostlebird calls may be a more important feature than the broad frequency range. At this point it is premature to conclude that pulse rate is an unimportant mechanism in mobbing-call recognition because pulse rate and bandwidth were not manipulated simultaneously. Further study of the effects of mobbing-call pulse rate are necessary to better understand its role in interspecific recognition.

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