

A predator-elicited vocalisation in the Variegated Fairy-wren (*Malurus lamberti*)

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Abstract. We document a previously undescribed vocalisation in the Variegated Fairy-wren (*Malurus lamberti*), the Type II song, which is given in response to the calls of a specific avian predator. We used playbacks of five species of both predators and non-predators to determine which species most commonly elicit Type II songs. Calls of Grey Butcherbirds (*Cracticus torquatus*) were the only stimuli to elicit Type II songs. Two other species in the genus *Malurus*, the Splendid Fairy-wren (*M. splendens*) and the Superb Fairy-wren (*M. cyaneus*), are also known to sing Type II songs in response to the calls of specific avian predators. In all these species, Type II songs may function as displays to conspecifics. This study highlights the possibility that predator-elicited display behaviour may be more widespread in the genus *Malurus* than was previously recognised.

Additional keywords: alerting signals, anti-predator calls, *Cracticus torquatus*, display songs, Type II song.

Introduction

Bird vocalisations have many functions, ranging from attracting mates to alarming others of danger (Catchpole and Slater 1995). Vocalisations that function in mate-attraction or territorial defence are often elaborate and conspicuous displays (Catchpole and Slater 1995), whereas vocalisations that function as alarms are typically brief and simple signals that draw minimal attention to the location of the signaller (Marler 2004). Remaining inconspicuous in the presence of predators is generally advantageous, but exceptions to this are seen in species that give conspicuous mobbing calls and pursuit-deterrent signals that either facilitate formation of mobs or signal to the predator that pursuit is likely to fail (e.g. FitzGibbon and Fanshawe 1988; Cresswell 1994; Hurd 1996; Murphy 2006). Thus, producing easily detected displays in the presence of predators occurs in some species, but these displays are usually thought to have some anti-predator function.

Males of two species in the genus *Malurus*, the Splendid Fairy-wren (*M. splendens*) and the Superb Fairy-wren (*M. cyaneus*), regularly sing in response to the calls of avian predators, using a vocalisation labelled Type II song (Langmore and Mulder 1992; Zelano *et al.* 2001; Greig and Pruett-Jones 2008, 2009). Splendid Fairy-wrens most often sing in response to calls of Grey Butcherbirds (*Cracticus torquatus*), but despite being closely associated with the presence of a predator, Type II songs do not appear to function in alarm, mobbing or pursuit deterrence. Splendid Fairy-wren males do not give Type II songs in response to silent, mounted Grey Butcherbirds,

females respond to Type II songs as if they are displays, and nestlings ignore Type II songs given at the nest (Greig and Pruett-Jones 2009). An analogous vocalisation (labelled Type II song or trill song) given primarily in response to Australian Ravens (*Corvus coronoides*) and Pied Currawongs (*Strepera graculina*) has been described in Superb Fairy-wrens (Langmore and Mulder 1992). In both these species of *Malurus* it is thought that Type II songs are sexual or territorial displays directed towards conspecifics (Langmore and Mulder 1992; Dalziel and Cockburn 2008; Greig and Pruett-Jones 2009). One explanation for why males sing after predator calls may be because conspecific receivers are alerted by predator vocalisations and are thus more likely to detect and respond to subsequent Type II songs (Langmore and Mulder 1992; Greig and Pruett-Jones 2009). This behaviour of singing to conspecifics in response to predator calls has previously been considered an anomaly, but little is known about the details of signal function in other members of the genus *Malurus* so it is possible that predator-elicited songs are not unique to Superb and Splendid Fairy-wrens.

Using the calls of a predator to aid signal detection in conspecifics is a strategy that any species could use if having alerted receivers enhances signal detection. One prerequisite for this strategy is that the alerting calls are obvious to receivers by being consistently recognisable and acoustically conspicuous (Richards 1981). Although, in practice, the conspicuousness (or ease of detection) of vocal signals is influenced by their acoustic properties, the environment and the sensitivity of the receiver (Wiley 2006), for the purposes of this paper we use

the term conspicuous to refer to fairly stereotyped, long-range signals. We know from experimental work that the vocalisations of Grey Butcherbird are readily detected and recognised by Splendid Fairy-wrens (Zelano *et al.* 2001; Greig and Pruett-Jones 2009), and if Butcherbird vocalisations are an effective alerting signal then we might expect other birds with similar perceptual tendencies to use them for this purpose as well. Here we describe the acoustic properties of a vocalisation in the Variegated Fairy-wren that is given in a context similar to Type II songs in Splendid and Superb Fairy-wrens. We refer to it as the Type II song to be consistent with previous literature on *Malurus*. We use playback experiments to test the hypothesis that Grey Butcherbirds are particularly effective stimuli of Type II songs in Variegated Fairy-wrens and we speculate about possible functions of this vocalisation.

Methods

Field site and study species

We conducted work at the Brookfield Conservation Park, South Australia, 100 km north-east of Adelaide, in arid scrub and woodland habitat during the breeding season of October–December 2008. We did not band individuals, but the approximate size of territories is known (Tidemann 1990) so we were able to map the general locations of the groups using an eTrex Legend Cx GPS (Garmin International Inc., Olathe, KS, USA). Based on mapping locations where Variegated Fairy-wrens were consistently present, we considered groups to be separate and independent if they were ~400 m apart, unless they were discovered consecutively (one immediately after the other, on the same day) and we were thus certain that two distinct groups were in the area. We considered 400 m to be an appropriate distance for two reasons: first, groups found consecutively were as near to one another as ~100 m, so our distance requirement for groups discovered on different days is likely to be conservative; and, second, our main concern was not to identify all groups, but simply to identify different groups for the purposes of conducting independent playback experiments, so having an exceptionally large distance criterion made our playback data less subject to accidental pseudoreplication. We revisited groups several times to verify their predictability of presence, and we were confident in the identity of 33 distinct groups. The observed size of groups ranged from two to six birds.

Playback experiment

We created a series of playback audio files of five avian species. These consisted of our treatment of interest, the Grey Butcherbird, which is a predator of fairy-wren nests (Gardner 1998) and is likely to be a predator of adults (Tarburton 1991), and four control species that we chose because they are fairly common at the Brookfield Conservation Park and produce conspicuous, easily identifiable vocalisations. We used vocalisations of two predators and two non-predatory species for the control playback audio files. The non-predatory species were the Willie Wagtail (*Rhipidura leucophrys*) and Galah (*Cacatua roseicapilla*), and the predator species were Grey Currawongs (*Strepera versicolor*), a known predator of fairy-wren nests (Colombelli-Négrel *et al.* 2009), and Nankeen Kestrels (*Falco cenchroides*), which are potential predators of adults (Olsen *et al.* 1979;

Aumann 2001). We used a combination of recordings taken from a published collection of bird calls (Stewart 2005) and recordings made in the field using a Marantz PMD 660 solid-state digital recorder (D&M Professional, Itasca, IL, USA), with 44.1 kHz sampling rate, and a Sennheiser ME66 shotgun microphone capsule and K6 power module (Sennheiser Electronic Corporation, Old Lyme, CT, USA). We used recordings from the published CD because we were not able to record a sufficiently large sample of every test species to use recordings made exclusively at Brookfield Conservation Park and we wanted to have a different example recording for every playback. Because we were only able to acquire seven Nankeen Kestrel calls, we supplemented this category with three calls of Collared Sparrowhawk (*Accipiter cirrhocephalus*) because this species also represents a threat to adult fairy-wrens (Aumann 2001) and therefore functions as an appropriate non-butcherbird predator control.

We used a total of 50 different recordings and conducted 50 playback trials, 10 for each of the five test species. We chose playback recordings randomly when we encountered groups of Variegated Fairy-wrens unless we had already conducted a playback to that group, in which case we randomly chose a recording of one of the test species not played to that group previously. Two of the 32 groups of Variegated Fairy-wrens used in the experiment received more than two playbacks over the course of the season (a total of three and five playbacks each), and we never tested groups more than once in a day.

For all playback trials we used a SME-AFS amplified field speaker (Saul Mineroff Electronics Inc., Elmont, NY, USA) and an iPod mini (Apple Inc., Cupertino, CA). Playbacks of vocalisations were all AIFF audio files. The amplitude of all playback audio files was standardised in Raven 1.2 (Cornell Laboratory of Ornithology, Ithaca, NY, USA) and tested with the field playback equipment using a Radio Shack (model 33–2050, Radio Shack Corporation, Fort Worth, TX, USA) sound-pressure level meter, set at C-weighting, fast response (~90.0 dB at 1 m for all playback audio files). The playback audio files were judged by ear to be comparable to natural vocalisations and we checked this by recording (with the above equipment) a wild Grey Butcherbird at a distance of ~20 m and then recording Grey Butcherbird playbacks broadcast from the playback speaker at a distance of 20 m with the same recording level as the wild Grey Butcherbird. We viewed these recordings in Raven 1.2 and verified that the relative amplitude was comparable.

Two observers were present for every playback trial, one to take written notes and manage the playback equipment and one to observe the birds and record the trial. To document vocal responses of focal birds we recorded trials using the recording equipment described above. Before each playback trial, focal birds were observed until we were confident that they were not disturbed by our presence or by the presence of any predators and that there was at least one male present. We monitored birds for several minutes after each playback trial. The distance between the speaker and the focal birds was estimated after the playback trial by pacing from the speaker to the location of the birds at the time of the playback. Distances ranged from ~10 to 20 m, were randomly distributed across playback types and had no effect on Type II song response (logistic regression; $\chi^2 = 1.06$, $n = 50$, $P = 0.301$). The speaker was ~1 m above ground for all playback

trials. Playback trials were conducted between 0700 and 1700 hours and we did not conduct tests in conditions of rain or strong wind.

Measurements of vocalisations

To quantify the structure of Type II songs we used recordings accumulated from the above playback experiments. We supplemented these with recordings of Type II song responses to additional playback trials of Grey Butcherbird vocalisations to 22 focal groups that were used in the experiment for non-butterbird playback trials and one focal group that was not used in the experiment. Of these 23 additional Butcherbird playbacks, 14 elicited Type II songs. We did not consider these additional playback trials in the statistical analysis of the playback experiment because we wanted to maintain an equal sample size for every test species. We used Raven 1.2 to create spectrograms (16-bit sample format, DFT=512 samples, frequency resolution=124 Hz, time resolution=11.6 ms, frame overlap=50%) and, based on the clarity of the spectrograms, chose a total of 16 Type II songs on which to measure the following variables: length of song, number of notes, high frequency, low frequency and peak frequency. Notes were defined as a continuous tracing on a spectrogram; peak frequency was defined as the frequency at which amplitude was highest; measurements of high and low frequencies were taken on only the lowest harmonic.

Results

Playback trials

Variegated Fairy-wrens never gave Type II songs in response to the four non-butterbird playback trials ($n=40$), but they did give Type II songs in response to 70% of Grey Butcherbird playback trials ($n=10$) (two-tailed Fisher's exact test: $P=0.003$ for all four pairwise comparisons, significant after Bonferroni correction for four tests where $\alpha=0.012$). If we consider the 23 additional Butcherbird playbacks conducted to collect Type II song recordings, Variegated Fairy-wrens gave Type II songs to a total of 21 of 33 playbacks (64%). Only males were observed to give Type II songs, both in the playback experiment and in the additional Butcherbird playback trials, but in some instances the focal birds were concealed in vegetation at the time of playback so we cannot rule out the possibility that females gave Type II songs. Group members gave two other types of vocalisations in response to playback of Butcherbird calls: Seets ($n=5$) and Chatters ($n=3$) (Fig. 1). Seet and Chatter calls were usually uttered multiple times and in quick succession. Seet and Chatter calls were occasionally given in response to playback of vocalisations of Nankeen Kestrels (Seet, $n=3$; Chatter, $n=1$) and Grey Currawongs (Seet, $n=1$; Chatter, $n=1$). Although the calls tended to be given most often in response to playback of Butcherbird vocalisations, the differences were not statistically significant for either Seet call responses (two-tailed Fisher's exact test: $P \geq 0.032$ for all four pairwise comparisons, not significant after Bonferroni correction for four tests where $\alpha=0.012$) or Chatter call responses (two-tailed Fisher's exact test: $P \geq 0.211$ for all four pairwise comparisons). All vocal responses were given immediately after the playback or not at all.

Structure of Type II songs

Type II songs (Fig. 1) contained a mean of 3.44 notes (s.d. 1.79) and ranged in frequency from an average low frequency of 2.89 ± 0.33 (s.d.) kHz to an average high of 7.32 ± 1.17 (s.d.) kHz. The total length of Type II songs was 0.89 ± 0.45 (s.d.) s. The mean peak frequency was 4.95 ± 0.52 (s.d.) kHz.

Discussion

The context in which Type II songs are given by Variegated Fairy-wrens is strikingly similar to the context in which Type II songs are given by male Splendid Fairy-wrens. Type II songs were stimulated only by Grey Butcherbird calls and were only observed being given by males. During general fieldwork we rarely heard Type II songs from Variegated Fairy-wrens, but the instances in which we did hear the songs were after the vocalisations of wild Butcherbirds and during the dawn chorus. These contextual similarities suggest that Type II songs in Variegated Fairy-wrens may be functionally analogous to Type II songs in Splendid and Superb Fairy-wrens.

If Type II songs of Variegated Fairy-wrens are displays to conspecifics, as they are thought to be in Splendid and Superb Fairy-wrens, then the specificity of the songs to Grey Butcherbird vocalisations may be because Butcherbird calls make particularly effective alerting signals. Fairy-wren response to Butcherbird calls with Type II song could essentially be a form of sensory exploitation (Ryan 1990), such that males use heightened conspecific awareness in the presence of a predator to enhance detection of their own signal. The alerting ability of Butcherbird calls could be explained if their vocalisations are more easily detected acoustically than those of other species or if Butcherbirds are a particularly dangerous predator. The tendency for fairy-wrens to give Seet and Chatter calls (likely alarm and mobbing vocalisations; Marler 2004) more often in response to Butcherbirds than to other predators is consistent with this idea, although Butcherbirds (a predator of both nests and adults) do not represent a unique type of predation threat compared to Grey Currawongs (a nest predator) or Nankeen Kestrels (an adult predator). More detailed information on the probability of predation by Butcherbirds relative to other species would provide additional insight, as would work investigating the acoustic properties of calls that stimulate Type II songs.

The fact that Variegated Fairy-wrens often accompanied Type II songs with Seet and Chatter calls suggests that, unlike in Splendid and Superb Fairy-wrens, Type II songs of Variegated Fairy-wrens functioned as an anti-predator response, either as an alarm call, mobbing call or pursuit-deterrent signal. This interpretation is weakened, however, by the observation that Variegated Fairy-wrens gave Type II songs only in response to Butcherbirds, whereas they gave Seet and Chatter calls in response to playback of vocalisations of other predatory species as well (although to a lesser extent). If Type II songs had an anti-predator function then we might expect Variegated Fairy-wrens to give the vocalisation in response to any predatory species. It may be that Type II songs are temporally associated with anti-predator responses yet have some other function, or it may be that Grey Butcherbirds present a specific predation threat

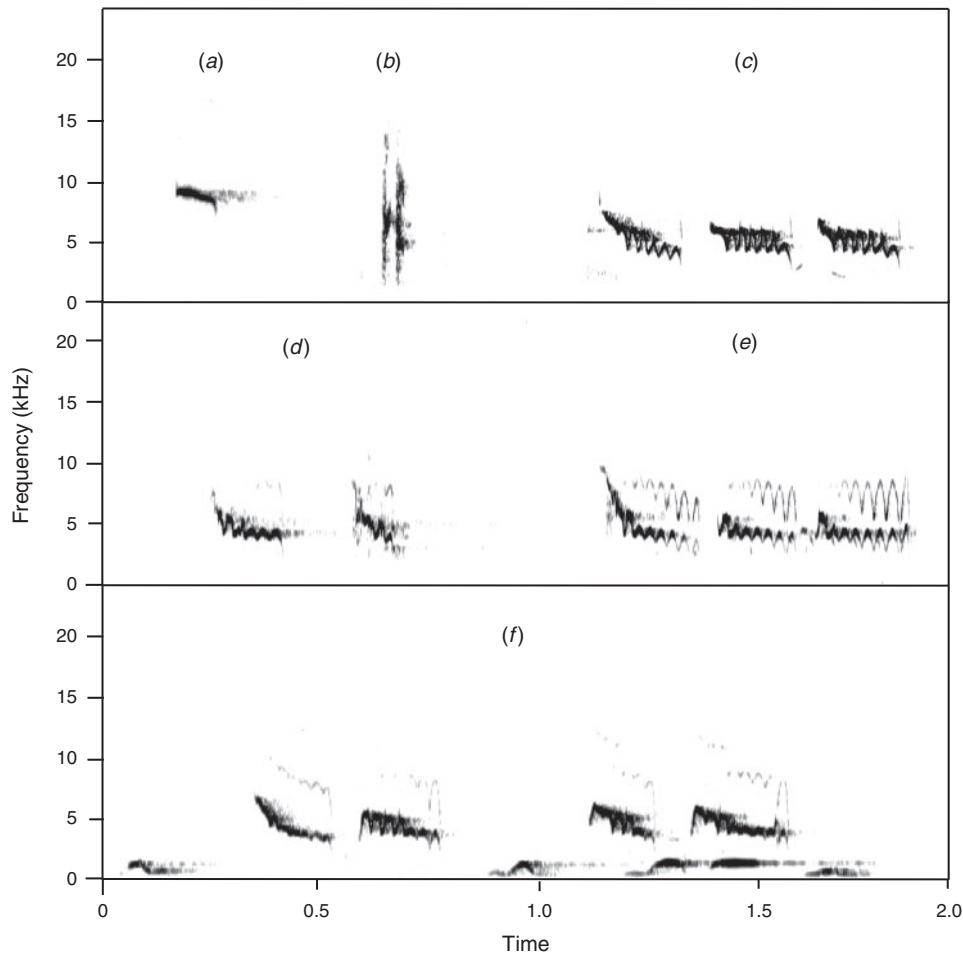


Fig. 1. Spectrograms of vocalisations of Variegated Fairy-wrens heard in response to playback of predator vocalisations. (a) Seet call; (b) Chatter call; (c) three-note Type II song; (d) two-note Type II song; (e) three-note Type II song; and (f) four-note Type II song. In (f) the four higher frequency notes (>2.0 kHz) are the Type II song and the lower frequency notes (<2.0 kHz) are the Grey Butcherbird call that prompted the Type II song.

that requires a unique vocal response by fairy-wrens. If Type II songs function as an anti-predator response, rather than as displays to conspecifics, then the contextual similarity of Type II songs of Variegated Fairy-wrens to those of Splendid and Superb Fairy-wrens hints at a possible evolutionary path for predator-elicited displays to conspecifics: vocalisation given in response to predators that function as an anti-predator response may be co-opted to be displays if conspecifics begin to use those vocalisations to extract information about the quality or status of the singer.

Since its discovery (Langmore and Mulder 1992), the Type II song has only been found to occur in the blue fairy-wren clade (Christidis and Schodde 1997) and has been thought to be an especially unusual vocal behaviour. Documenting the occurrence of contextually similar Type II songs in Variegated Fairy-wrens, which are in the chestnut-shouldered fairy-wren clade (Christidis and Schodde 1997), suggests that Splendid and Superb fairy-wrens may not be as unusual as previously thought. Although we did not determine the function of Type II songs in this study, exploratory playbacks of Type II songs to Variegated Fairy-wrens

in the absence of Grey Butcherbirds elicited vocal responses in four of five trials (responses were display songs; see Rowley and Russell 1997 for a description of the display reels of Variegated Fairy-wrens), which suggests that conspecifics may generally pay attention to Type II songs. A playback series of display songs, Type II songs and alarm vocalisations to Variegated Fairy-wrens would help to evaluate the relative importance of anti-predator and display functions for Type II songs. We hope that this paper highlights the need for additional research on the function of predator-elicited vocalisations in Variegated Fairy-wrens and other species of *Malurus*, as well as the importance of multi-species comparisons when investigating seemingly anomalous behaviours.

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