

A predator-elicited song in the splendid fairy-wren: warning signal or intraspecific display?

Emma I. Greig*, Stephen Pruett-Jones

Department of Ecology and Evolution, University of Chicago

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Predator-elicited vocalizations are typically thought to function as alarms to conspecifics or as deterrents to predators. In splendid fairy-wrens, *Malurus splendens*, 'Type II song' is commonly elicited in response to vocalizations of the grey butcherbird, *Cracticus torquatus*, a potential predator of both nestlings and adults. We examined the context of Type II songs and investigated possible antipredator functions of this vocalization using mount presentations of predators at nests, playbacks of Type II songs to females in the field and playbacks of Type II songs to nestlings. Males did not give Type II songs in response to silent mount presentations of predators at the nest, females ignored Type II songs played in the field and nestlings ignored Type II songs played at the nest. Using playbacks of butcherbird calls to males in the presence of predator and nonpredator mounts, we found that males were not more likely to give Type II songs when a predator was near the nest. Despite being commonly uttered in response to predator calls, this vocalization does not appear to be an alarm or predator deterrent. We suggest that the song is a form of male advertisement.

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Many antipredator vocalizations benefit both the signaller and conspecifics by functioning as alarms or predator deterrents (Altman 1956; Sherman 1977; Klump & Shalter 1984). While antipredator vocalizations are typically given in the presence of a predator, courtship behaviours are, in contrast, typically given when there is no immediate threat of predation (e.g. Magurran & Seghers 1990; Godin 1995; Simon 2007). The reason for this is not surprising; courtship behaviours are often elaborate displays that increase the conspicuousness of the signaller and therefore cause increased predation risk to the performing individual (Endler 1992; Andersson 1994; Zuk & Kolluru 1998). For example, the foot-drumming courtship display in wolf spiders, *Hygrolycosa rubrofasciata*, makes them more vulnerable to predation (Mappes et al. 1996), wood quail, *Odontophorus leucolaemus*, are more often depredated when they sing (Hale 2004) and male túngara frogs, *Physalaemus pustulosus*, make themselves more attractive to females and simultaneously more obvious to predatory bats by adding a 'chuck' to their calls (Ryan et al. 1982).

Courtship displays may be detrimental when performed in the presence of a predator because of increased conspicuousness and thus increased risk of predation; however, the presence of a predator may actually aid signal transmission to conspecifics and thus provide benefits in terms of increased mating success. Sensory systems in females are tuned to male traits, and females often show preferences for exaggerated forms of these traits, whether they be intricate songs, bright plumage or elaborate behavioural displays (Andersson 1994). Sexually selected male traits may be honest indicators of quality (Grafen 1990; Johnstone 1995; Gil & Gahr 2002), but they may also be amplifiers that aid the transmission of a signal without being costly themselves (Hasson 1991a). Aiding signal transmission is not trivial; the acoustic structure of many bird songs is optimized for transmission through the environment (Wiley & Richards 1978; Wiley 1991) and many species time their vocalizations to avoid overlap with other interfering sounds (Greenfield 1994; Grafe 1996; Brumm 2006). Additionally, some birds incorporate 'alerting signals' into their songs to grab the receiver's attention (Richards 1981). Although a courtship signal that exploits the presence of a predator to optimize transmission to conspecifics has not been experimentally documented for any species of which we are aware, such a signal has been hypothesized to occur in superb fairy-wrens, *Malurus cyaneus* (Langmore & Mulder 1992). In the

* Correspondence: E. I. Greig, Department of Ecology and Evolution, University of Chicago, 1101 East 57th Street, Chicago, IL 60637, U.S.A.

E-mail address: blufinch@uchicago.edu (E.I. Greig).

present study, we examined whether such a display is used by cooperatively breeding splendid fairy-wrens, *Malurus splendens*.

Splendid fairy-wrens give trills, which we refer to as Type II songs, in response to avian predators, particularly in response to the vocalizations of grey butcherbirds, *Cracticus torquatus* (Zelano et al. 2001; Greig & Pruett-Jones 2008). We have adopted the terminology 'Type II song' rather than the previously used 'Type II call' because these vocalizations are relatively long, complex, song-like trills that have individually specific acoustic structures (Greig & Pruett-Jones 2008). The response of a male splendid fairy-wren to hearing a vocalization of a grey butcherbird is so fast that the joint vocalizations appear duet-like (Fig. 1). Zelano et al. (2001) hypothesized that Type II songs are alarms directed towards kin, which provide indirect fitness benefits to the signaller. Although Type II songs are usually given in response to an already conspicuous predator vocalization, the song may function to draw attention to the predator, thus making it even more conspicuous. Alternatively, Type II songs may function as a predator deterrent by signalling that the predator has been detected and that pursuit is therefore less likely to be successful (Hasson 1991b; Caro 1995).

Superb fairy-wrens also give trills, referred to as Type II songs (Langmore & Mulder 1992) or trill songs (Dalziell & Cockburn 2008), in response to avian predators, particularly in response to the vocalizations of Australian ravens, *Corvus coronoides*, and pied currawongs, *Strepera graculina*. These trills are similar in acoustic structure to Type II songs given by splendid fairy-wrens; however, in superb fairy-wrens, Type II songs are somewhat longer and contain a greater diversity of note types (Langmore & Mulder 1992; Dalziell & Cockburn 2008). In contrast to the hypothesis proposed by Zelano et al. (2001) for splendid fairy-wrens, Langmore & Mulder (1992) suggested that Type II songs in superb fairy-wrens may be a condition-dependent handicap. They hypothesized that males give Type II songs after a predator vocalization to advertise their fitness rather than as a warning of danger to conspecifics, because only fit males can afford to sing in the presence of

a predator. Type II songs, therefore, become an honest signal of male quality.

In this study we used observational data to document the context of Type II songs in splendid fairy-wrens and we used three experimental approaches to test the hypothesis that Type II songs are a functional alarm. We predicted that if Type II songs are an alarm, then (1) males should give the call not only in response to the vocalizations of a butcherbird, but also in the presence of a silent but conspicuous butcherbird, (2) females should respond to Type II songs by becoming more vigilant or seeking cover and (3) vocalizing nestlings should respond to Type II songs by becoming silent. We also tested the hypothesis that Type II songs are a predator deterrent. We predicted that if Type II songs are a predator deterrent, then males should be more likely to give Type II songs in the presence of a predator mount than in the presence of a nonpredator mount.

METHODS

Study Species

The splendid fairy-wren is widespread throughout southern and southwestern Australia and is a cooperatively breeding, socially monogamous species that inhabits year-round territories (Rowley & Russell 1997). Although species in the genus *Malurus* are socially monogamous, they also show the highest levels of extrapair paternity known in birds (Mulder et al. 1994). In our study group of splendid fairy-wrens, *M. s. melanotus*, extrapair paternity occurs in an average of 55.3% of broods (Webster et al. 2004).

Both male and female splendid fairy-wrens produce 'Type I song', which is used in territorial encounters and during the dawn chorus (Payne et al. 1988; Rowley & Russell 1997; Zelano et al. 2001). Although males (both primary and helper) and females also both give Type II song, it is primarily a male vocalization (Greig & Pruett-Jones 2008). Type II songs are given as independent vocalizations, but they may also be incorporated into Type I songs, most often during the dawn chorus (Greig & Pruett-Jones 2008). Both sexes also give a typical passerine alarm call, the 'seet' call, in response to avian predators (Greig & Pruett-Jones 2008).

Field Site

We studied a banded population of splendid fairy-wrens at the Brookfield Conservation Park in South Australia (Van Bael & Pruett-Jones 2000; Tuttle & Pruett-Jones 2004; Tarvin et al. 2005; Webster et al. 2007) during the October–December breeding seasons of 2005, 2006 and 2007. The primary habitat in the park was mallee eucalyptus scrubland. We collected observational data each year on the context of Type II songs and we conducted experiments on the function of Type II songs in 2007. In 2005, we monitored 103 individuals from 45 family groups (five groups had one or more helpers). In 2006, we monitored 138 individuals from 55 family groups (19 groups had one or more helpers). In 2007, we monitored 120 individuals from 55 family groups (nine groups had one or more helpers).

Ethical Note

Behavioural manipulations in this study were approved by the University of Chicago Animal Care and Use Committee (ACUP permit number 71708) and the Government of South Australia Department of Environment and Heritage (Wildlife Ethics Committee approval number 21/2006, Scientific Research Permit number C25249 and animal use license number 187). During behavioural manipulations, we presented experimental stimuli for

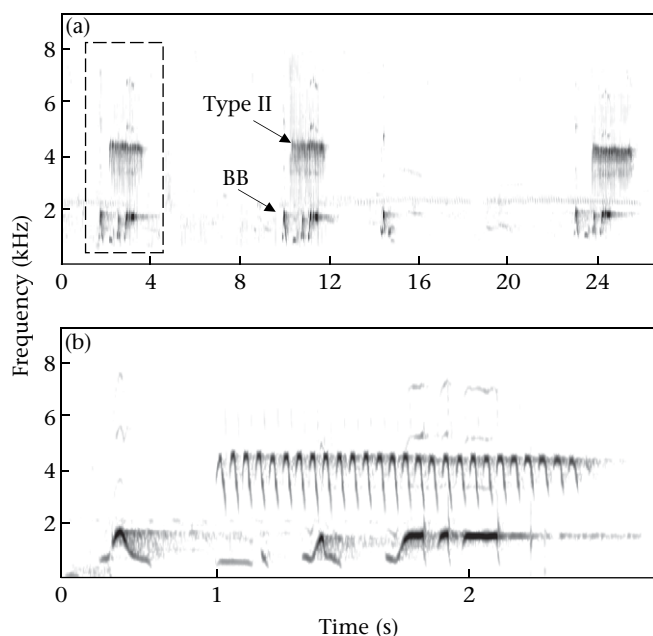


Figure 1. (a) Spectrograms of male splendid fairy-wren Type II songs (Type II) in response to grey butcherbird songs (BB). Three such pairings are displayed. (b) Expanded time axis of the pairing contained in the dotted rectangle in (a). Butcherbird calls are restricted to the lower frequency range (<2.0 kHz) and fairy-wren calls are restricted to the higher-frequency range (>2.0 kHz).

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