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## **Singing in the Face of Danger: the Anomalous Type II Vocalization of the Splendid Fairy-Wren**

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### **Abstract**

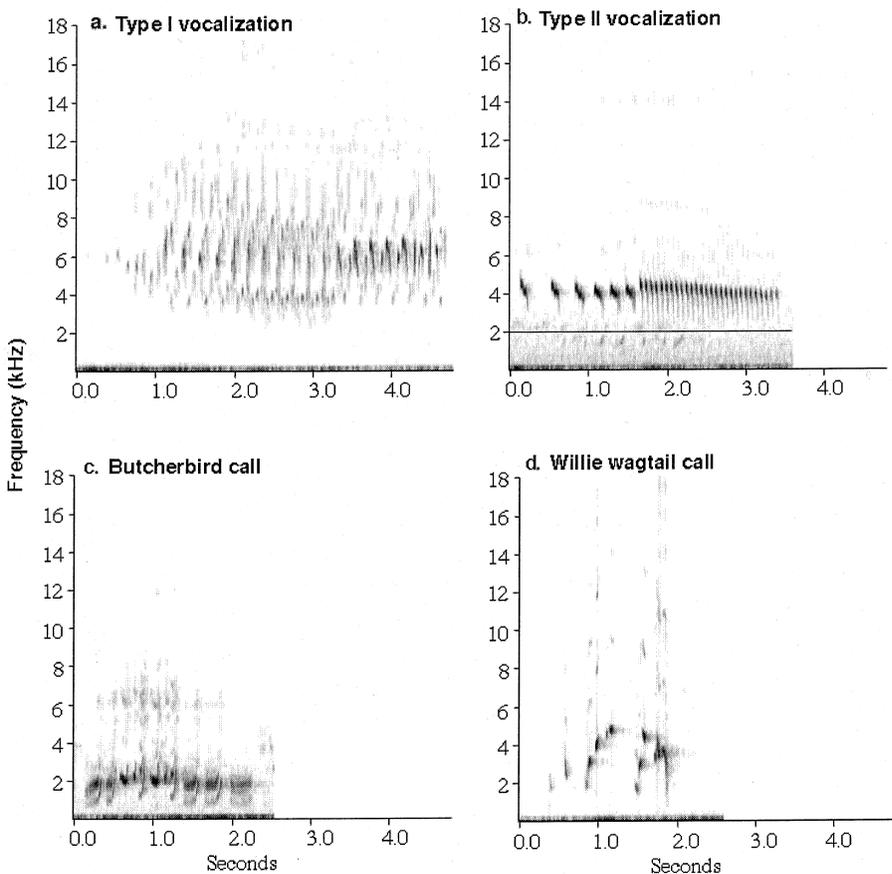
Males of certain species of fairy-wrens (Aves: Maluridae) emit a unique vocalization, the Type II vocalization, in response to the calls of potential predators. We conducted field observations and playback experiments to identify the contexts in which the Type II vocalization is emitted by splendid fairy-wren (*Malurus splendens*) males, and to examine social and genetic factors that influence its occurrence. In field observations and controlled playback experiments, Type II vocalizations were elicited most consistently by calls of the predatory gray butcherbird (*Cracticus torquatus*). Some vocalizations from other avian species also elicited Type II vocalizations, and the majority of these were vocalizations from avian predators. Splendid fairy-wrens are cooperative breeders, and males that responded with Type II vocalizations to playbacks of butcherbird calls tended to be primary rather than secondary males, had larger cloacal protuberances, and were older than those that did not respond. In addition, secondary males that were sons of resident females were more likely than non-sons to respond with a Type II vocalization. In another playback experiment, females responded similarly to the Type I song and Type II vocalizations of their mates. Although the Type II vocalization is emitted primarily in response to predator calls, it is inconsistent with an alarm call explanation. Patterns of reproductive success among Type II calling males suggest that it does not function as an honest signal of male quality. At present, the function of the vocalization remains anomalous, but indirect fitness benefits may play a role in its explanation.

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### Introduction

Animal vocalizations serve many functions, including the establishment and defense of a territory, and communication with members of a social group (e.g. Catchpole 1982; Kroodsma & Byers 1991). Call or vocalization rate, duration, or repertoire may be indicators of overall individual quality or vigor (Kroodsma & Byers 1991; Mountjoy & Lemon 1997). Additionally, an animal may vocalize in response to nearby predators, thereby alerting other members of its group (e.g. Marler 1955; Klump & Shalter 1984). Indeed, some species emit alarm calls that vary in structure depending on the specific predatory threat (Elowson & Hailman 1991; Greene & Meagher 1998).

Fairy-wrens (Aves: Maluridae) have a range of vocalizations from a complex typical reel, or Type I song (Fig. 1), to soft, brief contact calls (Rowley & Russell



*Fig. 1.* Spectrograms of (a) a male splendid fairy-wren Type I vocalization; (b) a male splendid fairy-wren Type II vocalization; (c) a gray butcherbird call; and (d) a willie wagtail call. Frequencies below the line at 2 kHz, in b, are probably from the gray butcherbird playback used to elicit the Type II vocalization

1997). The Type I song, given by both male and female fairy-wrens, is similar to the songs of many passerines in that it is used in territorial advertisement and perhaps in displays directed towards potential mates (Cooney & Cockburn 1995; Rowley & Russell 1997; pers. obs.). However, male, but not female, superb fairy-wrens (*Malurus cyaneus*) emit an additional vocalization, the Type II vocalization, that seems to be given in response to the loud calls of potential predators such as ravens, currawongs, and hawks (Langmore & Mulder 1992). The Type II vocalization seems paradoxical because male and female superb fairy-wrens have a different alarm call that they commonly use for perceived threats (Rowley & Russell 1997). In contrast to this typical *Malurus* alarm call, which consists of a loud, short, often repeated 'chit' (Rowley & Russell 1997), the Type II vocalization is a relatively long, structurally complex vocalization that is emitted only once per stimulus. Although usually given in response to predators, the Type II vocalization does not appear to be an alarm call (Langmore & Mulder 1992; see Discussion), and its function remains unclear.

Male splendid fairy-wrens (*Malurus splendens*) emit a call that is apparently homologous to the superb fairy-wren Type II vocalization (Fig. 1), and is also given in peculiar contexts. Our preliminary observations indicated that the Type II vocalization in splendid fairy-wrens was given primarily in response to calls of gray butcherbirds (*Cracticus torquatus*), and in response to other predators only infrequently. In this study, we conducted field observations and playback experiments to identify the contexts in which the Type II vocalization is given, examined social and genetic relationships that might influence the incidence of Type II vocalizations, and measured the responses of non-calling fairy-wrens to Type II vocalizations. We discuss our data in light of hypotheses suggested by Langmore & Mulder (1992) to explain the function of this unusual vocalization. Langmore & Mulder (1992) referred to the vocalization as the Type II song, but we refer to it simply as a vocalization to avoid connotations of function or structural complexity.

## Methods

### Study Population

We studied splendid fairy-wrens at Brookfield Conservation Park in South Australia from Oct. through Dec. 1998. The habitat of this park consists of mallee *Eucalyptus* scrub and chenopod shrubland. Further details of the study area and general field methods are presented in Tibbetts & Pruett-Jones (1999) and Van Bael & Pruett-Jones (2000). The color-marked fairy-wren population has been monitored since 1992, and in 1998 consisted of about 114 adult birds in 46 social groups. Splendid fairy-wrens are cooperative breeders, with groups varying in composition (Rowley & Russell 1990; Van Bael & Pruett-Jones 2000). Of the 46 groups monitored on our study site in 1998, 29 (63%) consisted of one breeding female and one male, eight (17%) consisted of one female and two males, and the

remaining nine (20%) consisted of one breeding female, one primary male and any combination of up to two secondary males or secondary females. By secondary males or females, we mean younger or behaviorally subordinate individuals that are usually the offspring of the primary males and females from previous generations and which remain within the family group as non-breeders instead of dispersing and breeding on other territories. Occasionally females, and more rarely males, may achieve secondary status by joining a group other than that into which they were born. Death of breeding females and their subsequent replacement, and to a lesser extent divorce of mated pairs, leads to groups in which secondary males or females may be unrelated to breeding females (Rowley & Russell 1990; Dunn et al. 1995). Relatedness between primary males and secondary males and females is further decoupled because the genetic mating system is promiscuous; that is, many offspring are sired by extra-group males (Brooker et al. 1990; Pruett-Jones, unpubl. data).

### Field Observations of Type II Vocalizations

We kept notes during fieldwork on the natural occurrence of Type II vocalizations. We recorded when a Type II vocalization was heard and what elicited or immediately preceded the vocalization. This method was potentially prone to bias, but was conducted to provide observations of the context of Type II vocalizations in a natural setting that would supplement our playback trials.

### Recordings

All vocalizations used for playbacks were recorded using a Sony digital audio tape-recorder (Model TCD-D8) and a Sennheiser directional shotgun microphone (Model ME 66) with a foam windscreen. Vocalizations were recorded during the day with no rain and little wind. Splendid fairy-wren Type I and Type II vocalizations were recorded from a distance of 10 m. Other avian species' vocalizations were recorded within 15 m (for one species, the Australian magpie [*Gymnorhina tibicen*], the recording distance was approximately 30 m).

Vocalizations used for playbacks were chosen based on their clarity. All vocalizations were transferred from digital to analog tapes and played back using a Realistic tape player (Model CTR-76) and Sony amplified speakers (Model SRS-A-60). Because of constraints in the field, we were unable to measure the amplitudes of playbacks prior to trials. All vocalizations were played at a level that sounded comparable to recorded volumes and volume was held constant in both the general playback survey and the playback presentation trials (see below).

### General Playback Survey

Our general playback survey was designed to add information about the context of Type II vocalizations. Trials took place in Nov. and Dec. of 1998.

Vocalizations of 10 avian species were recorded, as explained above. Five species were known predators or potential predators of adult fairy-wrens or their nests, and five were non-predators. The predators were the gray shrike-thrush (*Colluricincla harmonica*), Australian raven (*Corvus coronoides*), Australian magpie, gray currawong (*Strepera versicolor*), and black-faced cuckoo-shrike (*Coracina novaehollandiae*) (Lucas & Dudley Le Souëf 1911; Lea & Gray 1935–36; Tarburton 1991; Porter 1993; Lepschi 1994; Miller & Naisbit 1994; Tremont 1995; Rowley & Russell 1997; Gardner 1998; Major et al. 1999). The non-predators were the galah (*Cacatua roseicapilla*), spiny-cheeked honeyeater (*Acanthagenys rufogularis*), striated pardalote (*Pardalotus striatus*), chestnut-rumped thornbill (*Acanthiza uropygialis*), and Gilbert's whistler (*Pachycephala inornata*) (Lea & Gray 1935–36). Only one exemplar vocalization was used for each test species for the playback trials.

A total of 18 fairy-wren groups was used in this survey and only one male per group was the focal animal in a trial. Primary males were the focus in all but one of the 101 trials. Speakers were set up inconspicuously in the middle of the territory, tilted upwards at an angle of approximately 45° from the ground, and faced away from vegetation which could muffle sound. The time of day of trials and number of different playbacks per group were not controlled. The only criteria were that individual males were not presented with more than one playback on the same day, nor exposed to a playback of the same avian species more than once. Trials (i.e. the playbacks) began when a male came within 5–20 m of the speakers, and we recorded whether or not he responded with a Type II vocalization. As mentioned above, fairy-wrens give the Type II vocalization just once in response to a stimulus (i.e. the vocalization is not repeated).

### **Experiment 1: Gray Butcherbird/Willie Wagtail Playbacks**

This experiment, conducted in Oct. and Nov., was designed to examine the context and potential functions of Type II vocalizations. With a comparative design, we aimed to determine whether fairy-wrens respond differently, in terms of emitting the Type II vocalization, to vocalizations of a gray butcherbird (predator) and a willie wagtail (*Rhipidura leucophrys*) (non-predator). Gray butcherbirds are potential predators on both nests and adults (Lucas & Dudley Le Souëf 1911; Lea & Gray 1935–36; Tarburton 1991; Rowley & Russell 1997; Gardner 1998; Major et al. 1999) and were observed to be the primary species that elicited splendid fairy-wren Type II vocalizations prior to the onset of this study. We chose the insectivorous willie wagtail because it poses no obvious threat to fairy-wrens (Lea & Gray 1935–36). We also wanted to choose a species whose vocalization was comparable in length to the gray butcherbird vocalization. The willie wagtail vocalization lasts about 2 s, and the gray butcherbird vocalization lasts 2–3 s (Fig. 1); both are relatively continuous compared to some other species whose vocalizations consist of a series of short calls (i.e. some parrots). Testing

single male and double male groups allowed us to compare Type II vocalization responses of primary and secondary males.

We used three exemplar recordings from at least two different individual gray butcherbirds and willie wagtails to reduce the possibility of particular recordings having stronger or weaker behavioral effects than others (Kroodsmma 1986). Both gray butcherbirds and willie wagtails have more than one type of vocalization in their vocal repertoire. We chose to use the particular gray butcherbird vocalization commonly heard to elicit Type II vocalizations and the willie wagtail vocalization that was most commonly heard in the field. Each exemplar consisted of a single vocalization that was not repeated during playback trials.

From our study population, we randomly selected 11 groups without secondary males and nine groups with only one secondary male for playback trials. One male did not clearly fit into either the primary or secondary category and subsequently was dropped from all analyses. At the beginning of the season, he was in a group with two males and two females, but within 7 d of the experimental trial, he had formed a definitive social group with the secondary female from his original group. Trials were conducted between 06:30 h and 12:00 h. The time of playback presentation varied among groups, but was held constant within groups to control for potential circadian rhythm effects. Speakers were set up as in the general playback survey.

Each of the 20 groups, consisting of one breeding female and either one or two males, was exposed to one of three gray butcherbird exemplars in one trial and one of three willie wagtail exemplars in the other trial. At least 48 h elapsed between trials for each group. Gray butcherbird or willie wagtail exemplars were chosen for presentation using a stratified random design so that each exemplar was played in approximately seven trials. The order in which a group received the two playbacks was also randomized to control for any order effect. Only groups separated by at least one territory were tested on the same day. In one case, however, two non-contiguous neighboring groups were tested on the same day, but the trials were 4 h apart and playbacks were from different species.

As in the general playback survey, a trial began when the focal male or males came within approximately 5–20 m of the speakers. We recorded whether focal males emitted Type II vocalizations or looked to the speaker, and in groups with a secondary male, we noted which male sang first. Type II vocalizations emitted during playbacks were counted as elicited by the playback (in all cases, a Type II vocalization was made immediately after the start of a playback or not at all). A look to the speaker was counted as a response to the playback only if the male turned his head towards the speaker during the playback (Payne et al. 1988).

We knew the exact or minimum age of the males tested in this experiment through banding records. We also measured the volume of the cloacal protuberance in males, which is correlated with age in fairy-wrens (Mulder & Cockburn 1993; Tuttle et al. 1996) and thus may be indicative of quality (see Kokko 1998 for further discussion). The cloacal protuberance is formed by a pair

of seminal glomera that act as the site of sperm storage in male passerines (Wolfson 1952; Tuttle et al. 1996). Volume was calculated as:  $\text{volume} = \pi L[(D/2)(W/2)]$ , where  $L$  = length,  $D$  = depth and  $W$  = width of the cloacal protuberance (Briskie 1993; Mulder & Cockburn 1993; Tuttle et al. 1996). We collected cloacal protuberance measures from eight of the 20 primary males and seven of the nine secondary males in our experimental groups.

We identified each secondary male's mother by assigning maternity to the breeding female in the territory where he hatched. By this method, we determined the relative genetic relatedness between secondary males and resident females. Brooker et al. (1990), based on allozymes, and Mulder et al. (1994) and Dunn & Cockburn (1999), based on DNA fingerprinting, found no cases where young did not match their putative mothers in splendid fairy-wrens and superb fairy-wrens, respectively. Therefore, there is no evidence at present that our assumptions of relatedness are invalid.

### Experiment 2: Nest Trials

This experiment was designed to test potential functions of Type II vocalization by comparing the responses of females to Type I and Type II vocalizations of their mates. We chose females because they should be the intended receivers of the Type II signal according to certain hypotheses (Langmore & Mulder 1992; see Discussion). Specifically, we chose nesting females because they were easy to locate, and we examined their flushing behavior as a potential response. We defined a flush as the point when a female sitting in her domed nest moved to the opening and immediately flew away. We reasoned that if Type I and Type II vocalizations conferred different information, a female might respond differentially to the two vocalization types. For instance, if a female left the nest in response to the Type I song (the typical territorial song) of her mate to join him in territorial defense against intruding fairy-wrens, but not in response to the Type II vocalization, the data would suggest that she treated Type I and Type II signals differently.

Type I and Type II vocalizations were recorded from the social mates of eight females. In each case, the recorded Type II vocalization was elicited by a gray butcherbird playback to keep the context consistent with that in other experiments. The Type I song was recorded from each male on his territory when only members of his group were present. Type I songs were elicited from playbacks of Type I songs of other splendid fairy-wrens.

Each female was the focal animal in two trials separated by at least 24 h. One trial consisted of a playback of the Type I song of the female's social mate and the other of a playback of his Type II vocalization. The order of playback was randomized, and the speaker was in the same spot, 5–10 m from the nest, for both trials. Each playback consisted of a single vocalization (i.e. the vocalizations were not repeated during the playback). Once the female was in her nest for at least 1 min, the trial began and we recorded whether or not she flushed during the playback.

## Results

### Field Observations

A total of 182 Type II vocalizations was heard during field work and categorized by the stimulus eliciting the call (Table 1). Of these, 102 Type II vocalizations were elicited by identified avian calls, of which 93 (91%) were predator calls. Of these predator calls, 69 (74%) were gray butcherbird calls. Other predators that elicited Type II vocalizations, either through their vocalizations or presence, included the Australian raven, Australian magpie, gray currawong, gray shrike-thrush, and accipiter hawks. In one case, a brown goshawk (*Accipiter fasciatus*) elicited Type II vocalizations from several males in sequence as the hawk flew over multiple territories. In addition to responding to calls of predators, males emitted Type II vocalizations in response to non-predators such as human observers or during interactions with extra-group splendid fairy-wrens. They also emitted Type II vocalizations in response to non-predators flying quickly overhead (e.g. purple-crowned lorikeets, *Glossopsitta porphyrocephala*) and to the calls or presence of avian non-predators, including a group of white-browed babblers (*Pomatostomus superciliosus*), red wattlebirds (*Anthochaera carunculata*), a crested bellbird (*Oreoica gutturalis*), and a spiny-cheeked honeyeater (Table 1). We also heard Type II vocalizations frequently as part of the pre-dawn chorus, but did not attempt to determine whether they were elicited by other species' calls. Interestingly, although fairy-wren responses to gray butcherbirds were common, we never observed a Type II vocalization given in response to a silent, but visually conspicuous gray butcherbird moving through a fairy-wren territory.

### General Playback Survey

Playbacks of only two of the 10 avian species (gray butcherbird playbacks were not included in this survey) elicited Type II vocalizations from males. The gray shrike-thrush elicited Type II vocalizations in two of 10 playback trials, and

Table 1: Field observations of Type II vocalizations

Presumed elicitor	Number of observations
Avian predator call	93
Unknown	36
Intraspecific interactions	13
Human	11
Avian non-predator flying overhead	9
Avian non-predator call	9
Avian predator flying overhead	6
Unknown avian call	3
Avian non-predator in area	2
Total count	182

the Australian magpie elicited a Type II vocalization in one of 10 trials. Playbacks of the other three predator vocalizations did not elicit Type II vocalization responses.

### Experiment 1: Gray Butcherbird/Willie Wagtail Playbacks

Males responded more often with Type II vocalization to gray butcherbird playbacks than to willie wagtail playbacks ( $\chi^2 = 38.11$ ,  $df = 1$ ,  $p < 0.0001$ ). None of the 29 males emitted a Type II vocalization during willie wagtail playbacks, whereas 18 of the 20 (90%) primary males and five of the nine (56%) secondary males emitted a Type II vocalization during gray butcherbird playbacks. Males were also more likely to look to the speaker during a gray butcherbird playback (23 of 24 observed males) than a willie wagtail playback (14 of 25 observed males;  $\chi^2 = 10.51$ ,  $df = 1$ ,  $p = 0.001$ ). All gray butcherbird exemplars elicited a Type II vocalization and none of the willie wagtail exemplars elicited a Type II vocalization.

The social status of males affected their likelihood of responding with a Type II vocalization to gray butcherbird calls. The primary males included in our experimental trials were either in single groups with no secondary males or in double-male groups with only one secondary male. Including the 11 males in single groups as primary males, there was a trend for primary males to respond more often than secondary males (Fisher's Exact test:  $n = 29$ ,  $p = 0.056$ ; Fig. 2). It was also true, however, that primary males were older (mean  $\pm$  SE =  $3.25 \pm 0.3$  years) than secondary males ( $1.22 \pm 0.2$  years; Mann-Whitney U-test:  $U = 17.5$ ,  $n_1 = 20$ ,  $n_2 = 9$ ,  $p = 0.0006$ ). Eighteen of 19 primary males and five of five secondary males looked to the speaker during playbacks of gray butcherbird calls (Fisher's Exact test:  $n = 24$ ,  $p > 0.999$ ), and eight of 17 primary males and six of eight secondary males looked to the speaker during willie wagtail playbacks (Fisher's Exact test:  $n = 25$ ,  $p = 0.234$ ). There was also no difference in looking to the speaker during gray butcherbird playbacks between males that

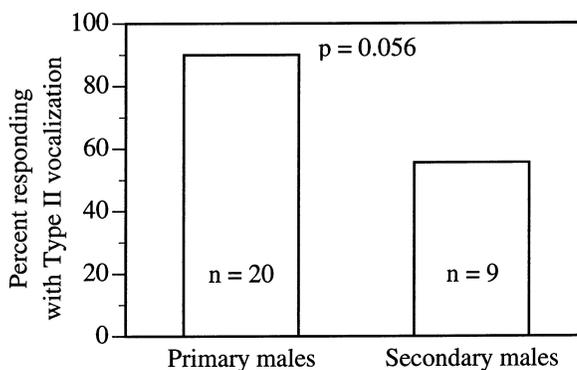


Fig. 2: Percent frequency response of primary and secondary male fairy-wrens to gray butcherbird playbacks

responded with Type II vocalizations (20 of 21 looked to speaker) and those that did not (three of three looked to the speaker; Fisher's Exact test:  $n = 24$ ,  $p > 0.999$ ).

We further evaluated the difference in response between primary and secondary males by re-examining the data using only the nine groups with both a primary and a secondary male, so that primary males were only from groups with a secondary male. Again, primary males were older, with a mean age of  $3.3 \pm 0.4$  yr, whereas secondary males averaged  $1.22 \pm 0.2$  yr (Mann-Whitney U-test:  $U = 4$ ,  $n_1 = 9$ ,  $n_2 = 9$ ,  $p = 0.0013$ ). Primary males (eight of nine) were not more likely than secondary males (five of nine) to respond to gray butcherbird playbacks with Type II vocalization (Fisher's Exact test:  $n = 18$ ,  $p = 0.294$ ). However, in each of the four trials in which both males gave a Type II vocalization, primary males called first.

Genetic relatedness between secondary males and resident females affected the likelihood of responding with a Type II vocalization to gray butcherbird playbacks. Secondary males that were sons of resident females (five of six) were more likely than those that were not sons (zero of three) to respond with a Type II vocalization to gray butcherbird playbacks (Fisher's Exact test:  $n = 9$ ,  $p = 0.048$ ). There was no such relationship between secondary males and resident primary males (three of six putative sons and two of three putative non-sons emitted Type II vocalizations; Fisher's Exact test:  $n = 9$ ,  $p > 0.999$ ).

Of the 15 birds from which we had cloacal protuberance measurements, 11 responded with Type II vocalizations during gray butcherbird playbacks and four did not. Males that responded to gray butcherbird playbacks with a Type II vocalization had significantly larger cloacal protuberance volumes than those that did not (Mann-Whitney  $U = 6.0$ ,  $n_1 = 11$ ,  $n_2 = 4$ ,  $p = 0.037$ ; Fig. 3a). Only one of these males that did not emit a Type II vocalization was a primary male. There was a trend for secondary males that responded to gray butcherbird playbacks with Type II vocalizations to have larger cloacal protuberance volumes than those that did not respond (Mann-Whitney  $U = 1.0$ ,  $n_1 = 4$ ,  $n_2 = 3$ ,  $p = 0.077$ ; Fig. 3b).

Although this experiment was designed to determine male vocal responses to butcherbird and willie wagtail trials, it also afforded us the opportunity to observe female behavioral responses to Type II vocalizations that had been elicited by the butcherbird calls. Females were present within our view (and not on nests) in 17 of 20 butcherbird playback trials (each of which elicited Type II vocalizations from focal males). We didn't observe any females emit a Type II vocalization in any of these trials. Likewise, we didn't observe any fairy-wrens, regardless of their gender, hiding or mobbing in response to either butcherbird or Type II vocalizations.

### Experiment 2: Nest Trials

There was no difference in the flushing behavior of females in response to playbacks of their mates' Type I and Type II vocalizations (Fisher's Exact test:

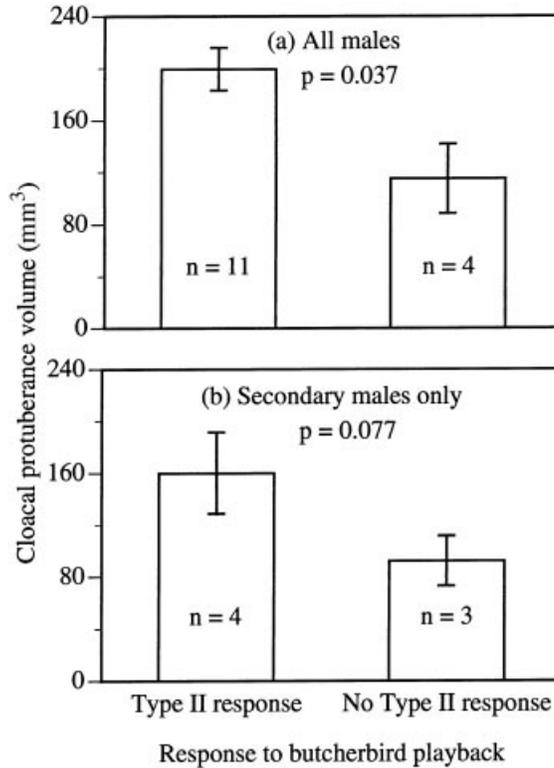


Fig. 3: Mean ( $\pm$ SE) cloacal protuberance volume and Type II vocalization response of fairy-wrens to the gray butcherbird playback. (a) All males. (b) Only secondary males

$p > 0.999$ ,  $n = 8$ ). Females flushed in three of the eight Type I vocalization trials and in three of the eight Type II vocalization trials.

### Discussion

Our study and that of Langmore & Mulder (1992) indicate that the majority of fairy-wren Type II vocalizations are emitted in response to calls of avian predators. Nevertheless, the Type II vocalization is not emitted in response to all predators with equal frequency. In our field observations of the natural occurrence of Type II vocalization, most (74%) were given in response to the calls of the gray butcherbird. This is in contrast to the results of Langmore & Mulder (1992) which showed that several predators regularly elicited Type II vocalizations in superb fairy-wrens. Although Langmore & Mulder (1992) did not perform playback experiments using butcherbird calls, they did elicit Type II vocalizations from superb fairy-wrens using playbacks of other predator and non-predator species. Most of the Type II vocalizations they observed were elicited by

predators including ravens, currawongs, shrike-thrushes, and accipiter hawks. Playbacks of non-predator calls elicited the Type II vocalization less frequently, although that of the magpie lark (*Grallina cyanoleuca*) did so in 39% of 18 trials (Langmore & Mulder 1992). In our general playback survey, however, fairy-wrens either failed to respond or responded only rarely to the calls of other potential predators besides the gray butcherbird. Indeed, we could not detect a significant difference in response to predators vs. non-predators, although our survey did not include gray butcherbird playback trials. In our playback experiment contrasting fairy-wren responses to gray butcherbirds and willie wagtails, however, the results were striking: fairy-wrens consistently emitted the Type II vocalization in response to the gray butcherbird playbacks, yet never did so in response to the willie wagtail playbacks. When all these data are considered together, it is clear that on our study site the Type II vocalization is given primarily in response to gray butcherbird vocalizations. Perhaps just as striking, however, is the fact that we didn't observe any fairy-wrens emit the Type II vocalization in response to nearby non-calling gray butcherbirds, and only rarely in response to other vocalizations of the gray butcherbird.

Within fairy-wren social groups, only males emit Type II vocalizations. Neither we nor Langmore & Mulder (1992) ever observed a female fairy-wren giving a Type II vocalization, although female splendid and superb fairy-wrens frequently sing Type I songs (Cooney & Cockburn 1995). Our data suggest that in splendid fairy-wrens, primary males tend to be more responsive with Type II vocalizations than are secondary males. This difference does not appear to result from differences in attentiveness or vigilance between the two social categories, because primary and secondary males were equally likely to look towards the speaker during a playback trial, regardless of whether they ultimately emitted the Type II vocalization. The difference in responsiveness may be related to age or state of sexual activity, as primary males are generally older and have larger cloacal protuberances than secondary males.

Perhaps the most striking result of our study is that secondary males living with their mothers were more likely to emit a Type II vocalization than were those living with unrelated female breeders. If the Type II vocalization serves as a signal directed at other group members, the pattern of secondary male response seems to indicate that indirect fitness benefits may play a role. Although secondary males rarely achieve mating success either within or outside the social group (Mulder et al. 1994; Dunn & Cockburn 1999), they do gain indirect fitness benefits when their mother is the breeding female on their territory because any offspring she produces will be at least their half-siblings. Thus, secondary males may employ a loud signal when it benefits their genetic interests, but not when the potential benefits are low. This variation in Type II calling between sons and non-sons would fit well within an alarm call framework as described by some authors (e.g. Sherman 1977; Hauber & Sherman 1998; but see below), in which emitting the calls is costly (because doing so alerts predators to one's location) and discretion in choosing when to signal alarm would be favored. That primary males consistently emit the Type II vocalization is also compatible with such an

explanation because the fitness of male fairy-wren breeders is strongly dependent on their holding a territory with a breeding female. Thus, primary males are likely to engage in risky behavior to protect their mates, whereas secondary males would do so only if it was likely to increase their indirect fitness. However, if indeed the Type II vocalization serves as a signal directed towards breeding females, its message remains unclear because incubating females did not differentially respond to Type I and Type II vocalizations.

Although the alarm call explanation is compelling, several features of Type II vocalization are inconsistent with such a hypothesis. First, the stimuli that elicit Type II vocalizations are generally loud and conspicuous. Therefore, the production of a subsequent alarm call seems redundant and ineffective as a signal directed toward conspecifics. Secondly, alarm calls should be given in response to both silent and vocal predators because each poses a potential threat. Although the Type II vocalization is occasionally given in response to stimuli that may not be available to the entire fairy-wren group, as exemplified by our observation that a brown goshawk flying overhead elicited a Type II vocalization, our field observations indicate that loud conspicuous stimuli serve as elicitors far more often than visual stimuli. Indeed, the fact that fairy-wrens do not emit the Type II vocalization in response to a silent yet conspicuous gray butcherbird, supports the contention that the call is not a general indicator of danger. Thirdly, the lack of obvious response to the Type II vocalization by non-calling group members argues against it serving as an alarm signal (Langmore & Mulder 1992; this study). In most birds and social mammals, when alarm calls are given, receivers typically respond either by dashing into vegetation or other safe zones to take cover or by mobbing (e.g. Marler 1955; Payne et al. 1985; Jurisevic & Sanderson 1994; Blumstein & Armitage 1997; Clutton-Brock et al. 1999). Neither we nor Langmore and Mulder observed either of these behaviors by non-calling fairy-wrens in response to a Type II vocalization. Fourthly, Langmore & Mulder (1992) pointed out that the call does not seem to have the structural characteristics of typical avian alarm calls (Marler 1955; Brown 1982; Greene & Meagher 1998), although Jurisevic & Sanderson (1994) showed that vocal alarm responses could take a wide variety of forms. In any case, fairy-wrens emit a different call in other threatening situations, such as when humans or other species disturb their nests (Rowley & Russell 1997).

Langmore & Mulder (1992) concluded that Type II calling in superb fairy-wrens most likely serves as an honest signal of male quality. Under their scenario, female fairy-wrens infer relative quality of neighboring males based on their responses to specific cues, namely, to predator calls. Because the stimulus is loud, both the female and nearby males hear the predator call. Females assess relative male quality by their propensity to respond. Male response is considered to be honest based on the assumption that only those males in good condition should be capable of recognizing the cue and emitting the response, despite potential energetic costs or risk of attracting predators (see Zahavi 1975, 1977). The scenario requires that females remember how accurately various males respond over a long period of time, a contention that is plausible because each male

apparently emits a unique rendition of the vocalization (Langmore & Mulder 1992).

One prediction of this 'male-quality' hypothesis is that variation in male genetic reproductive success (which reflects female choice) should co-vary strongly with variation in Type II response, that is, variation in the propensity to call in response to the correct stimuli. In fairy-wren populations, realized male reproductive success is highly skewed, with only a few primary males siring the majority of the offspring produced in a given season (Brooker et al. 1990; Mulder et al. 1994; Dunn & Cockburn 1999). Analysis of microsatellite loci in our study population reveals the same pattern (Pruett-Jones, unpubl. data). Nevertheless, despite the outcome that there is a high variance in male reproductive success, virtually all primary males that we tested responded to a gray butcherbird call with a Type II vocalization. In other words, we observed little variation among primary males in their likelihood of giving Type II vocalizations, and yet there is extreme variation in mating success. However, in our study, each male was tested only once, and it is possible that an individual male's response might vary over time. The male-quality hypothesis also does not explain the observed patterns of Type II vocalization in son and non-son secondary males. Indeed, secondary males should be more likely to signal their 'quality' to unrelated females than to their mothers. This pattern is based on a small sample size, and we recognize that the male-quality hypothesis is difficult to refute; however, the available data suggest to us that this hypothesis does not fully explain either the occurrence, or variation in, Type II response.

Another hypothesis is that 'alarm' calls may be directed toward the predator to indicate that the caller is unprofitable prey (Reby et al. 1999; Zuberbühler et al. 1999). However, the fact that fairy-wrens do not give the Type II vocalization in response to silent predators argues against this idea. Langmore & Mulder (1992) discussed several other hypotheses that might account for Type II vocalizations. Because they provided refutations for each of them, we need not discuss them further here. We can add, however, that in addition to the reasons for rejecting the various hypotheses outlined by Langmore & Mulder (1992), none of the hypotheses can account for the patterns of son vs. non-son Type II responses that we observed in our study.

Although the function of the Type II vocalization remains difficult to explain, our study reveals certain patterns: (i) the Type II vocalization seems to provide no information about predators that is not readily available to other group members in most cases; (ii) differences in calling response between primary and secondary males, as well as between sons and non-sons, suggest that the Type II vocalization may be a signal directed towards other group members, most likely the breeding female; (iii) the social circumstances under which Type II vocalization is given suggest that indirect fitness benefits may be an important component of the explanation. We suggest that investigation into the social roles of secondary males within the group as a function of their genetic relatedness to group members may further illuminate the information contained in the Type II vocalization.

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