



Acoustic and physical mate guarding have different effects on intruder behaviour in a duetting songbird

Jenelle Dowling ^{a, b, *}, Michael S. Webster ^{a, b}

^a Department of Neurobiology and Behavior, Cornell University, Ithaca, NY, U.S.A.

^b Cornell Lab of Ornithology, Cornell University, Ithaca, NY, U.S.A.



ARTICLE INFO

Article history:

Received 12 April 2017

Initial acceptance 16 June 2017

Final acceptance 4 October 2017

Available online 26 December 2017

MS. number: A17-00322R

Keywords:

acoustic mate guarding

male removal

mate guarding

sexual selection

vocal duet

When males compete for mates, they often defend paternity through mate guarding. In addition to physical guarding, in vocal species, especially duetting birds, individuals may duet with their mates in order to guard them. The acoustic mate-guarding hypothesis posits that duetting deters rivals. We experimentally tested the effectiveness of physical and acoustic mate guarding in a duetting songbird, the red-backed fairy-wren, *Malurus melanocephalus*, using a novel variation of a classic removal experiment. We temporarily removed males, such that females received either no guarding (mate removed), or only acoustic guarding (mate removed, his duet response played from speaker). We found that rival intrusion rates were highest when all guarding was prevented, slightly lower when only acoustic guarding occurred and lowest when pairs were unmanipulated, and both physical and acoustic guarding occurred. This suggests that both guarding techniques deter intruders, but acoustic guarding less so. Intruder display rate during removals was higher than in unmanipulated trials, regardless of acoustic guarding. Results suggest that acoustic guarding may function as a long-range signal that reduces the likelihood of rival intrusion, but physical guarding is necessary to prevent rivals from courting mates. We confirm that physical and acoustic mate guarding serve as important components of intruder deterrence, although they act at different levels. Our study broadens our understanding of multimodal paternity assurance strategies.

© 2017 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

When female mates are limited, males are expected to vary the amount of effort they invest in different mating efforts, depending on which profitably yield fitness returns. In species that form social pair bonds, males can invest in offensively competing for matings with other males' partners, or they can invest in defence, to assure they sire young with their social mate (Tuttle, 2003). For example, males can invest in defensive behaviours like mate guarding, which may take the form of close following, frequent copulation and/or vocal duetting (i.e. acoustic mate guarding, wherein a male duets with his mate to signal her mated status to rivals; Brylawski & Whittingham, 2004; Møller & Birkhead, 1991; Sonnenschein & Reyer, 1983; Stokes, 1968). Physical mate guarding (close following) and frequent copulation are behaviours commonly seen across taxa (Brylawski & Whittingham, 2004), whereas acoustic mate guarding appears to be a more specialized behaviour that occurs only in certain species among those that have coordinated

vocal displays (Hall, 2009). In each case, it is assumed that guarding reduces female rival interactions, thus increasing the chances that the guarding male will sire his mate's young (Møller & Birkhead, 1991).

The question of whether physical mate guarding effectively guards a male's paternity has received both observational and experimental attention (Brylawski & Whittingham, 2004; Marthinsen, Kleven, Brenna, & Lifjeld, 2005). Results of these studies suggest that physical guarding decreases intrusion rates of rival males (Dickinson, 1997) and consequently decreases the prevalence of extrapair young, both during short-term (Brylawski & Whittingham, 2004; Chuang-Dobbs, Webster, & Holmes, 2001) and long-term (Currie, Krupa, Burke, & Thompson, 1999; MacDougall-Shackleton, Robertson, & Boag, 1996) male detention experiments. However, in previous studies, males were removed completely, preventing researchers from separately measuring the effectiveness of the male's physical presence and of acoustic mate guarding.

Vocal duets have been well studied in birds, with territory defence consistently emerging as a primary duet function across species, whereas acoustic mate guarding has seen considerably less

* Correspondence and present address: J. L. Dowling, Division of Biological Sciences, University of Montana, 32 Campus Dr., Missoula, MT 59812, U.S.A.

E-mail address: jenelle.dowling@mso.umt.edu (J. Dowling).

support (Hall, 2009; but see Levin, 1996b; Marshall-Ball & Slater, 2004; Sonnenschein & Reyer, 1983). However, most previous studies of duet function have been conducted in species with either very low (e.g. Douglas & Heath, 2012; Gill, Vonhof, Stutchbury, Morton, & Quinn, 2005; Hall & Magrath, 2000; Hall & Peters, 2008; Hall, Rittenbach, & Vehrencamp, 2015) or unknown (e.g. Bradley & Mennill, 2009; Logue & Gammon, 2004) rates of EPP; it is perhaps unsurprising that few previous studies find direct support for a mate-guarding function of duetting.

Only two previous studies have been conducted on species with high rates of extrapair paternity (Benedict, 2010; Dowling & Webster, 2016). In addition, previous studies that test the acoustic mate-guarding hypothesis conclude that males acoustically guard paternity because they respond more strongly to male than to female song playback (Levin, 1996b; Marshall-Ball & Slater, 2004), or because males initiate duets most often while female mates are fertile (i.e. duets are considered a form of 'vocal supervision', Sonnenschein & Reyer, 1983). To date, no study has experimentally tested the core assumption of the acoustic paternity-guarding hypothesis: that males form duets with females because this vocal display repels rival males (Møller & Birkhead, 1991; Sonnenschein & Reyer, 1983; Stokes, 1968). This hypothesis includes an implicit assumption that if duets evolved at least partially for this function, then vocal duets should decrease rival intrusion rates, independent of physical guarding. Our experimental approach allowed us to directly test the acoustic mate-guarding hypothesis.

We investigated the relative effectiveness of physical and acoustic mate guarding by separating the two mate-guarding behaviours into distinct experimental conditions, a novel variation on the classic removal design that allows us to control the male's mate-guarding effort and determine whether duetting alone effectively deters intruders. We studied the red-backed fairy-wren, *Malurus melanocephalus*, a species that is well suited for this investigation, since they have moderately high rates of cuckoldry (54% of young result from extrapair matings; Webster, Varian, & Karubian, 2008). They also sing frequent polyphonic duets (nonidentical songs overlap in frequency and time; Dowling & Webster, 2013) that have been confirmed to function for acoustic mate guarding, as part of a suite of mate-guarding behaviours that also includes physical guarding (Dowling & Webster, 2017).

We conducted short-term (1 h) male detentions. Males were either removed completely, or removed but females were 'guarded' with their mate's duet response played from a speaker. In unmanipulated conditions, males guarded their mates both physically and acoustically. This yielded three conditions: no guarding, acoustic guarding only and unmanipulated. This experiment tested the hypothesis that males can form vocal duets with their mates to help prevent rival male intrusions and displays, which may prevent usurpation of their paternity or position in the pair bond (i.e. acoustic mate guarding; Hall, 2004). We predicted that if a female were more effectively guarded during a particular condition, then we would see fewer intrusions and displays during that condition, and if she were less effectively guarded, we would see more intrusions and displays.

METHODS

General Field Methods

We conducted fieldwork in the beginning of the breeding season (September–November) in 2013 at Lake Samsonvale (27°16'S, 152°41'E), 30 km northwest of Brisbane, Queensland, Australia. Study subjects were 25 breeding red-backed fairy-wren pairs in an early breeding stage (before onset of incubation, when the female was receptive to mating). Breeding males had red-black plumage

(>66% plumage = red/black, scored on six body regions; Karubian, Sillett, & Webster, 2008) in 17 groups, and brown plumage (<33% plumage = red/black) in eight groups. We also categorized males based on age, with males 2 years or younger considered 'young' and males older than 2 years considered 'old'. All brown males were 1 year old (young), whereas eight red-black males were 1–2 years old (young) and nine were 3 years old or older (old). We chose this age classification because it divided our focal males approximately in half, and because previous research shows marked differences in mate-guarding behaviours in male red-backed fairy-wrens after the age of 2 (Potticary, Dowling, Barron, Baldassarre, & Webster, 2016). All birds in focal groups were captured in mist nets and marked with a unique combination of colour bands, and basic breeding biology data were collected as per our previous studies (see Varian-Ramos, Karubian, Talbott, Tapia, & Webster, 2010; Webster et al., 2008).

Experimental Set-up

We manipulated the breeding male's acoustic and physical mate guarding in one of three conditions: (1) no mate-guard: focal male captured and removed from the territory where he was unable to sing or follow the female (prevents both acoustic and physical mate guarding, $N = 8$ trials); (2) acoustic mate-guard: focal male captured and removed, but recordings of his songs were played with precise timing by observers to replicate a duet with the female (female acoustically but not physically guarded, $N = 10$ trials); and (3) unmanipulated: focal male captured and then immediately released (acoustic and physical mate guarding allowed, $N = 7$ trials). Pairs were assigned to conditions randomly with respect to the male's age/plumage status, and pairs did not have helpers. Females/pairs were allowed a 15 min reacclimation period after male capture, and we waited until the female/pair resumed normal foraging before we began collecting data. We observed each female/pair for 1 h after the male was captured and quantified female/pair behaviour and intrusion and display behaviour of neighbouring males. In all cases where the male was detained, he was kept in the shade in a small birdcage (48 × 36 × 58 cm) covered with a breathable dark cloth and provided with food and water, several territories away. Male detentions were typically 75 min and never exceeded 2 h. Detention length varied because after the male was captured, we began the trial when we located the female, which took a variable amount of time.

Observation Procedure

In all conditions, two observers followed the female/pair within 15–20 m throughout the 60 min observation. Observers continually dictated female/pair distance from where the male was captured, distance between male and female, general behaviour (movements, foraging, flights and who followed), any vocalizations and any intruding conspecifics (description and identity, plumage percentage, distance from female/pair, all behaviours and displays and female/male reaction). Males who were considered 'intruders' on focal territories exhibited specific behaviours that indicated they were on an extraterritorial courtship foray. Red-backed fairy-wrens, like many other fairy-wren species, engage in forays and courtship displays that are directed primarily at extrapair females (Potticary et al., 2016). Displays performed by intruding males included puff-back displays and chases (Potticary et al., 2016). At the end of the observation, we noted the length of the observation, and the male was retrieved and released (if applicable). On capture, we estimated the focal male's plumage percentage and categorized him as either red/black or brown (no males in experiments had intermediate plumage type).

Download English Version:

<https://daneshyari.com/en/article/8488720>

Download Persian Version:

<https://daneshyari.com/article/8488720>

[Daneshyari.com](https://daneshyari.com)