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SHORT COMMUNICATION

Similarities in expression of territorial aggression in breeding pairs of northern cardinals, *Cardinalis cardinalis*

M. Susan DeVries[1,2] · Caitlin P. Winters[1] · Jodie M. Jawor[1,3]

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Abstract

Avian pairs that defend resources year-round may demonstrate similar territorial behavior. We examined male and female responses of northern cardinal pairs to male simulated territorial intrusions. Pair members demonstrated comparable responses towards a male 'intruder', as latency to respond and proximity scores were very similar between pair members in the majority of pairs examined. Similarity in territorial behavior could be important in cardinal pairs for maintaining year-round resources.

Keywords Breeding pairs · Territoriality · Aggression · Birds

Introduction

Similar behavioral expression between pair members is important for species where both sexes participate in territorial defense. By responding to territorial threats together, mated pairs may more efficiently remove intruders, a valuable strategy for species that maintain long-term territories. In birds, territorial behavior of mated pairs is often assessed as song duets between mates, how mates coordinate duets, and what duetting signifies (Colombelli-Négrel 2016; Hall 2004; Ręk 2018). In studies that quantify the level of physical aggression exerted by pair members, strong variation can exist in behavior expressed by pair members, who is being attacked by whom, and the level of aggressive shown by each member. Members of a defending pair may show strong, or exclusive, intrasexual aggressive behavior (Burtka and Grindstaff 2015; Templeton et al. 2016), or they may display intersexual aggression (Bossema and Benus 1985; Schuppe et al. 2016). In some avian species, males 'lead' in response to an intruder, with females demonstrating less aggression overall to intruders (of either sex), (Appleby et al. 1999; Bard et al. 2002; Busch et al. 2004; Butler and Janes-Butler 1982; Mays and Hopper 2004). Alternatively, forms of territorial behavior exhibited or levels of aggression demonstrated might not be sex-specific; a situation relatively common among tropical birds (Bossema and Benus 1985; Fedy and Stutchbury 2005; Greenberg and Gradwohl 1983; Hall and Peters 2008; Koloff and Mennill 2013; Quinard and Cézilly 2012; Schuppe et al. 2016).

Here, we assess aggressive behavior shown by members of northern cardinal (*Cardinalis cardinalis*; 'cardinals') pairs defending territories from male decoy 'intruders' during simulated territorial intrusions (STIs) within the early breeding season. In cardinals, both males and females participate in territory defense and intrasexual and intersexual aggression has been observed with both sexes (Halkin and Linville 1999). Prior studies demonstrate that male cardinals will attack decoys of male cardinals during STIs (DeVries et al. 2012) and incubating female cardinals will aggressively respond to female cardinal decoys placed near the nest (DeVries et al. 2015; Jawor et al. 2004; Winters and Jawor 2017). However, aggressive responses of mated cardinal pairs towards a standardized male territorial 'threat' have not been assessed, and the response of female cardinals to a perceived territorial threat prior to the initiation of nesting is unknown.

Cardinals defend multi-use territories (Halkin and Linville 1999), and in some locations, pairs occupy territories year-round (Gentry 2015). During the breeding season, both

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✉ M. Susan DeVries
devriesm@uww.edu

[1] Department of Biological Sciences, University of Southern Mississippi, Hattiesburg, MS 39406, USA

[2] Biological Sciences, University of Wisconsin-Whitewater, Whitewater, WI 53190, USA

[3] Department of Biology, New Mexico State University, Las Cruces, NM 88003, USA

sexes have been observed intruding on territories; however, male intrusions seem to either be more numerous or more obvious in nature (MSD and JMJ, pers. obs.). Given that both members of cardinal pairs are dependent on the successful defense and maintenance of a territory with adequate resources, we predicted that both pair members would respond to male STIs and that the level of response would be similar between pair members.

Materials and methods

Research was conducted with a banded population of cardinals at the Eubanks/Lake Thoreau property owned by the University of Southern Mississippi in Hattiesburg, Mississippi, USA (31° 20′ 55.821″ N; 89° 25′ 1.228″ W) in the early breeding seasons of 2009–2010. On a year-round basis, cardinals were captured in mist nets or Potter traps between 0600 and 1200 h for banding. All birds in this population received a U.S. Fish and Wildlife steel band plus a unique combination of three plastic color bands for field identification. Following banding, all individuals were released from their original capture point.

Males begin singing in this population in December (Jawor et al. 2014) and territorial behavior (e.g., song and aggressive conflict) is displayed by both sexes as early as January (DeVries et al. 2012). Throughout February and March, we confirmed territories by observing the responses of individuals to short bouts of recorded conspecific song (from non-local populations) and identification of banded individuals at song posts. Boundaries of cardinal territories remain relatively unchanged from year to year (Halkin and Linville 1999).

Simulated territory intrusions (STIs) began in March and consisted of placing a taxidermied male cardinal decoy at the center of a focal pair's territory and playing a recording of cardinal song (as in DeVries et al. 2012). A speaker (Altec Lansing Orbit-MP3 iM207) attached to a portable MP3 player was placed beside the decoy (same decoy in all trials) to allow a recording of male cardinal vocalizations (different from earlier territory assessment) to accompany each intrusion. At the onset of each trial, camouflaged observers retreated 15–20 m away from the decoy and began a randomly selected recording (one of three) of standardized male cardinal vocalizations (85 dB SPL at 1 m) from non-population sources (all solo male territorial song, no counter-singing; Cornell Macaulay Sound Laboratory). Trials lasted 20 min or until a territory owner struck the decoy. Male and female cardinals share monomorphic song and perform other vocalizations in aggressive contexts (e.g. chipping) that cannot be differentiated by ear. Therefore, measures of aggression in this study included: (1) assigning each individual in a pair a proximity score based on approach to decoy, and (2) recording the latency of focal pair members to respond to the STI. Proximity scores were adapted from Kontiainen et al. (2009): 0 = No approach to the decoy, 1 = Aggressive posturing (crest raised, bill wiping) from a distance > 5 m, 2 = Aggressive posturing from distances 2-5 m, 3 = Aggressive posturing within 2 m, 4 = Threat displays (crest depressed, body lowered, wings slightly opened) and/or flights over the decoy within < 2 m, 5 = Physical contact with decoy. Latency to respond (LOR) was defined as time between the beginning of playback and appearance of the focal pair at the site of the STI.

Statistical analyses were performed with R (3.2.5). Mann–Whitney *U* tests determined differences between years in proximity scores and LOR measures. Spearman rank correlations compared behavioral measures between pair members and compared individual behavior to date (time within season which could impact level of aggressive behavior shown). Correlations also determined if proximity scores and response measures varied over the duration of the early breeding season. Chi-square tests were used to assess variation in intrusion attendance by pair members. There were no repeated pairs assessed between 2009 and 2010 and no individuals within pairs (e.g., comprising part of a new pair) were assessed twice.

Results

Yearly variation

A total of 38 intrusions were completed across two breeding seasons (2009 $n = 13$; 2010 $n = 25$). In 33 of 38 intrusions (86.8%), at least one pair member responded to the simulated intruder; in five (5) trials neither pair member responded. For males, there was no difference between 2009 (median = 660.0 s) and 2010 (median = 330.0 s) in LOR (Mann–Whitney *U* test: $U = 95.0$, $Z = -1.290$, $p = 0.197$) or in highest aggression score recorded (2009, median = 3; 2010, median = 4; $U = 155.0$, $Z = -0.240$, $p = 0.811$). For females, there was no difference between 2009 (median = 693.5 s) and 2010 (median = 421.0 s) in the LOR ($U = 49.5$, $Z = -1.202$, $p = 0.229$), nor in the highest aggression score recorded (2009, median = 1; 2010, median = 1; $U = 141.0$, $Z = -0.687$, $p = 0.492$). Because there were no differences between years in variables of interest, we combined years in analyses of male and female aggressive responses.

Seasonal variation

Male and female LOR and highest level of aggression displayed were compared to Julian calendar date. For males there was no correlation between day and LOR (Spearman rank correlation; $r_s = -0.19$, $p = 0.23$, $n = 38$) or highest recorded aggression score ($r_s = 0.15$, $p = 0.36$, $n = 38$). For females, there was no correlation between day and LOR ($r_s = 0.017$, $p = 0.91$, $n = 38$) or highest recorded aggression score ($r_s = 0.019$, $p = 0.90$, $n = 38$). Trial length did not correlate with day when the STI occurred ($r_s = -0.27$, $p = 0.09$, $n = 38$).

Individual and pair response

During simulated intrusions where only one pair member responded, the sole responder was more likely to be male ($\chi^2 = 9$, $p = 0.003$, $df = 1$) and there were no trials where females responded alone. In trials where both pair members responded, not simultaneously, males were more likely to respond before females ($\chi^2 = 5.56$, $p = 0.018$, $df = 1$; Fig. 1).

Both pair members were more likely to respond to the intrusion than lone individuals ($\chi^2 = 6.81$, $p = 0.009$, $df = 1$). In 39.4% of STIs, pair members were detected simultaneously (Fig. 1). In all instances where males struck the decoy ($n = 15$), both pair members arrived simultaneously. There was no observed difference in the likelihood that pair members would respond simultaneously to the intrusion as opposed to pair members arriving asynchronously ($\chi^2 = 1.5$, $p = 0.220$, $df = 1$). When comparing proximity scores, pair members were more likely to have scores within 2 or less categorical differences, than 3 or more categorical differences ($\chi^2 = 16.03$, $p = 0.00006$, $df = 1$; Fig. 2). There was no

Fig. 1 Response order of cardinal pair members to simulated territory intrusions

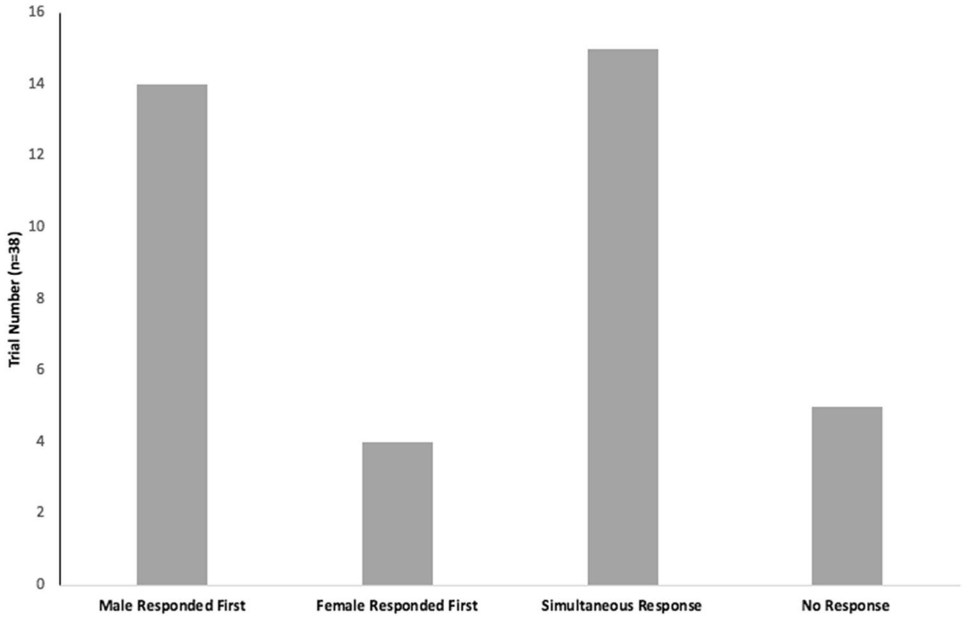
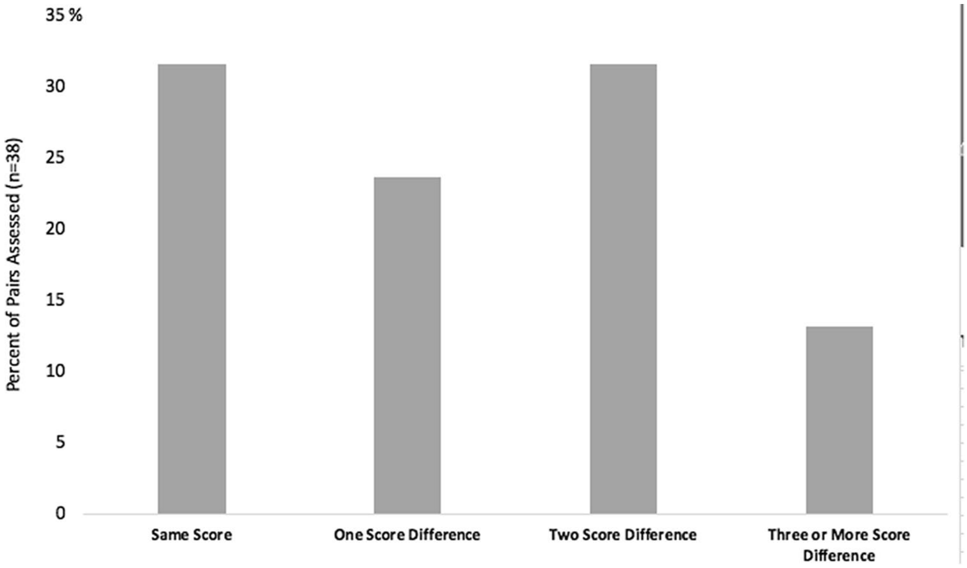


Fig. 2 Percentage of similarity between aggression scores of cardinal pair members responding to simulated territorial intrusions



difference between male LOR among pairs with 2 or less score categorial differences or pairs with 3 or more categorical differences ($U=43.0$, $Z=-1.356$, median = 332, $p=0.190$). All pairs that arrived simultaneously ($n=15$) had proximity scores within 2 or less categorical differences.

Within each sex, LOR and highest aggression score achieved during the intrusion were correlated (males; $r_s=-0.57$, $p=0.0001$, $n=38$; females; $r_s=-0.83$, $p<0.0001$, $n=38$); quicker responders had a higher aggression score. When comparing the behavior of pair members, LOR was correlated ($r_s=0.49$, $p=0.0001$, $n=38$, Fig. 3) as were highest aggression scores achieved ($r_s=0.53$, $p=0.0005$, $n=38$). Male LOR in pairs that arrived simultaneously did not significant differ from male LOR in pairs that arrived asynchronously ($U=44.5$, $Z=-1.314$, median = 532.5, $p=0.194$).

Discussion

Here we demonstrate that pairs of cardinals perform similar behavior when presented with a simulated male territorial 'intruder' and pair members respond at nearly the same time and demonstrate similar levels of aggression. When pair members did not arrive together, males usually responded first. In addition, if pair members did not have identical proximity scores, males typically had the higher score.

Our findings suggest territorial defense within the breeding season is a joint effort for cardinal pairs. This is similar to what has been seen in a number of avian species with long-term territory occupancy and long-term pair bonds (Fedy and Stutchbury 2005; Greenberg and Gradwohl 1983; Hall and Peters 2008; Quinard and Cézilly 2012; Schuppe et al. 2016). Because female cardinals sometimes responded after their mates, or not at all, we cannot rule out a role for sex-specific responses. Yamaguchi (1998) found that male and female cardinals can discriminate between the songs produced by each sex and responded differentially based on the perceived sex of the intruder. However, female cardinals have been observed responding with song to live male intruders and physically attacking naturally occurring male intruders (JMJ, pers. obs.), suggesting that aggressive patterns observed in pairs of cardinals, e.g., males respond first or females not respond, might be less sex-specific responses and potentially linked to other phenomenon. Females who did not respond may have been off of the territory, were not noticed by researchers, or did not perceive the intruder as enough of a threat to warrant a response (as in Schuppe et al. 2016). Tests focusing on female STIs or using song indicating wider variation in potential individual quality may allow for a better definition of how females function during pair territory defense in cardinals, how pairs respond together, and whether pairs adjust activity based on the level of perceived threat.

The patterns observed here could arise in several ways. This could develop through active alteration of behavior where pair members match each other purposefully. In happy wrens (*Pheugopedius felix*), females coordinate songs with mates during territory defense, even if this leads to females being out of match with the songs of simulated intruders (Templeton et al. 2016). Pairs of downy woodpeckers (*Picoides pubescens*) modify their agonistic responses based on partner behavior (Schuppe et al. 2016). This suggests that individuals can modify behavioral responses as needed to defend territories and resources effectively (Ręk 2018). Alternatively, behavioral similarity could arise from assortative mating between individuals. In eastern bluebirds (*Sialia sialis*), pair members show similar levels of aggression while defending nest boxes and appear to mate assortatively by similarities in territorial behavior (Harris

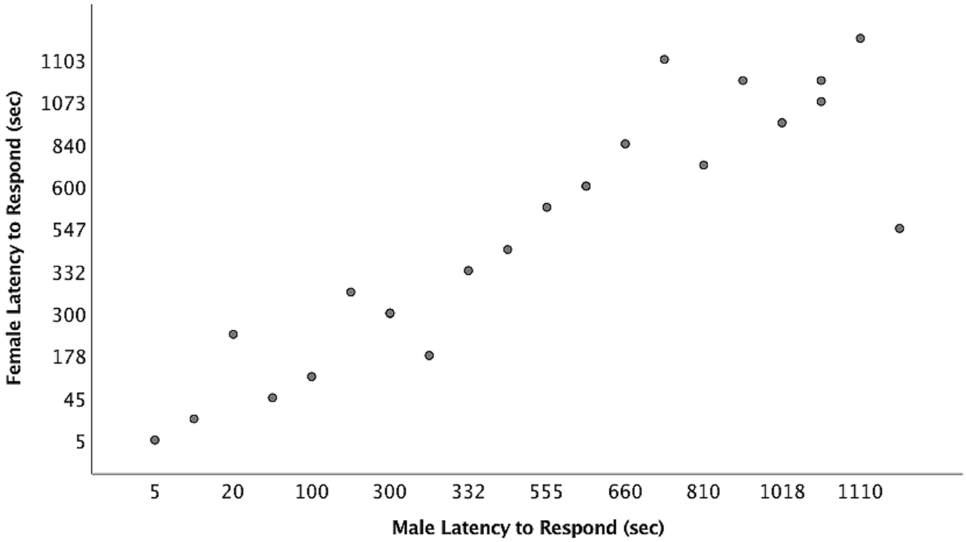


Fig. 3 Latency to respond in cardinal pairs responding to simulated territory intrusions

and Siefferman 2014). Cardinals mate assortatively by ornamentation (Jawor et al. 2003) and pair members are similar in nestling feeding behavior (DeVries and Jawor 2013; Linville et al. 1998). Considering that cardinals must defend territories on a nearly year-round basis, individuals could be mating assortatively for behavioral aggression as pairs showing similar behavior might be more successful in protecting resources over a prolonged period of time. Last, in species like cardinals where pair members can act together or alone during territory defense, there may be influences of both assortative mating and active behavioral matching as individuals with similar behavioral styles coordinate activities to effectively eject territorial intruders.

Future work should assess how cardinal pairs respond to female intruders. While intruding males seem more prevalent, this may be related to the more obvious appearance and singing behaviors displayed by intruding males. When females have been observed intruding on territories, their behavior is more circumspect with less song produced (JMJ, pers. obs.) and females are more cryptic visually. How pairs respond to female intrusions could differ from how they respond to males. Last, pairs of cardinals could intrude on territories together and this could demand a different sort of response from territory owning pairs. Future work should attempt to incorporate a variety of intrusion types given that either single cardinals (of either sex) or pairs can be intruders.

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