

The social context of a territorial dispute differentially influences the way individuals in breeding pairs coordinate their aggressive tactics

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Abstract

In diverse species, individuals coordinate behavior to accomplish shared goals or tasks. Such coordination, however, often occurs selectively, and the contextual information animals use to determine when they coordinate and when they do not is unclear. We investigate this issue in the highly territorial downy woodpecker (*Picoides pubescens*) by exploring how individuals within a social breeding pair differentially modulate coordinated aggressive responses during graded simulated territorial intrusions (STIs). Analyses show that resident pairs mount a more robust aggressive response to STIs that represent a greater threat. Moreover, in this social context, pair members produce contact vocalizations in a way that predicts their partner's aggressive behavior. We also show that, when presented with a low threat, individuals that first respond to intrusions decrease their aggressive output once their partner attends to the stimulus; the partner, in turn, increases their levels of aggressive behavior. This does not occur in high-threat STIs, where both partners maintain high levels of aggression throughout the entire encounter. Together, these results show that individuals within a pair flexibly adjust their aggressive tactics in response to different social competitive contexts, and this includes adjusting the way in which

individuals coordinate certain aspects of their agonistic repertoire. We speculate that this ability reflects an adaptive mechanism that allows individuals to fine-tune territorial tactics to reduce overall costs of aggression.

Significance statement

Although research has demonstrated that individuals often coordinate their behavior to accomplish common tasks, little is known about the factors that determine when such coordination occurs and when it does not. We address this issue for the first time in the highly territorial downy woodpecker by testing how the level of threat associated with a territorial interaction influences the coordination of defensive behavior. We find that, when facing intruders that pose a greater threat, residents adjust levels of aggressive output in response to the number of vocalizations produced by their breeding partner. By contrast, this relationship is not observed when pairs face intruders that pose a relatively lower threat. Our data therefore provide striking evidence that coordination in defensive tactics depends on the residents' appraisal of the social context, such that fiercer competition is associated with greater behavioral coordination.

Keywords Social behavior · Territorial aggression · Cooperation · Monogamy · Downy woodpecker

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Introduction

The way in which social animals work together to accomplish common goals has become an important focus of behavioral ecology (Hall 2004; Schuster and Perelberg 2004; Yip and Rayor 2011; Ioannou et al. 2012). Studies show, for example, that individuals within social partnerships or groups can coordinate their behavior to enhance its efficacy and thereby

augment a particular tactic or strategy (Hall and Magrath 2007; Hall and Peters 2008; Bell et al. 2010; Yip and Rayor 2011; Ioannou et al. 2012; Goodwin and Podos 2014). In these cases, coordination is operationally defined as the organization of behavior among allies in response to a stimulus, followed by the dynamic adjustment of this behavior in response to the actions of one's allies (Werdenich and Huber 2002; Schuster and Perelberg 2004; Wilson and Wilson 2007). However, an important unanswered question within this area of research is how animals determine when they coordinate tactics and when they do not. The fact that coordination occurs selectively suggests that individuals appraise their social environment and consequently determine when integrating behavior with another individual is appropriate. This lack of information regarding flexibility in coordination has created a gap in our understanding of the properties of adaptive social decision-making in animals.

Territorial aggression represents a behavior in which tactical coordination between social partners might be advantageous. For example, studies of avian duetting imply that tight vocal coordination sometimes helps individuals mount a more robust defense of their territory (Hall 2000; Tóth and Duffy 2005; Hall and Peters 2008; Kovach et al. 2014). Duetting behavior, however, may not be the best model to study tactical coordination more generally, given that so few species have evolved this unique mode of communication and that duetting itself is not always exclusively linked to territory defense (Hall 2004; Seddon 2005; Marshall-Ball et al. 2006). To this end, it is possible that territorial animals have evolved ways to coordinate other elements of their aggressive repertoires when protecting their home turf from intruders. For example, pairs may match levels of aggression when fighting off intruders or they may produce signals that modify how their partner behaves during a fight. In the latter case, coordination may be a subtler phenomenon than simply distinguishing correlated aggressive responses between individuals within a reproductive partnership. Nonetheless, virtually nothing is known about behavioral coordination in this regard.

The context of social disputes profoundly affects animal aggression (Hall and Magrath 2007; Fuxjager and Marler 2010; Fuxjager et al. 2010; Desjardins et al. 2012). For example, territory residents readily modify aggressive output to match an intruder's physical condition or quality (Rivera-Gutierrez et al. 2010; Mowles and Ord 2012), which suggests that residents evaluate opponents and fine-tune their behavioral reactions accordingly. This flexibility is thought to allow residents to exert the least amount of effort to fight off an intruder in a way that minimizes the costs of aggression (Fuxjager et al. 2009; Fuxjager and Marler 2010). Under this framework, we expect that coordination of aggressive tactics similarly occurs in a context-dependent manner, particularly if doing so increases the effectiveness of agonistic output and, in turn, permits individuals to better fight off competitors. This

idea has not been explored previously, and thus the goal of this study is to assess whether social breeding pairs that inhabit the same territory differentially adjust the way in which they coordinate defensive tactics in response to high-threat and low-threat territorial intrusions.

To study this issue, we use the highly territorial and socially monogamous downy woodpecker (*Picoides pubescens*). Like other woodpeckers, this species exhibits joint territory defense (Ligon 1970; Husak 2000; Pasinelli et al. 2001), whereby both sexes simultaneously fight off invaders using a large repertoire of aggressive behavior during frequent territorial intrusions (Kilham 1974; Dodenhoff 2002). Foremost among the species' aggressive signals is the drum, which is an atonal sonation produced by repeatedly and rapidly hammering the bill against a tree or snag (Kilham 1974). The acoustic parameters of the drum (i.e., length, cadence, and frequency) are identical between males and females (Stark et al. 1998), and past work indicates that longer drums with more beats are positively associated with an individual's aggressive intent (Short 1974; Wilkins and Ritchison 1999). Thus, given the clear positive predictive relationship between acoustic signal length and male condition and attractiveness (Nelson and Poesel 2011; Mager et al. 2012; Nelson and Poesel 2012), longer drums likely signal a greater threat to residents. Downy woodpeckers also produce a number of vocalizations, including whiny and pik calls. The former is an overt aggressive signal used to ward off opponents (Kilham 1974; Jackson and Ouellet 2002; Dodenhoff 2002), while the latter is generally considered a social contact call (Dodenhoff 2002). Interestingly, piks are also produced during territorial disputes (Jackson and Ouellet 2002; Kellam and Lucas 2014) and are thought to influence intra-pair spacing during competitions (Dodenhoff 2002). In light of this information, we hypothesize that resident downy woodpecker pairs differentially adjust both their aggressive repertoires and these repertoires are coordinated in response to dissimilar levels of threat during territorial intrusions.

To test this hypothesis, we measure the aggressive output of resident pairs in response to simulated territorial intrusions (STIs), in which we broadcast drums that are longer and more threatening (i.e., contain more beats/drum) or drums that are shorter and relatively less threatening (i.e., contain fewer beats/drum). We predict that residents will exhibit a more intense aggressive response toward long drum stimuli, given that this STI represents a greater threat to resident birds (Short 1974; Wilkins and Ritchison 1999). We also predict that residents are more likely to coordinate aggressive responses to long drum stimuli, as this situation likely calls for a more effective means of territorial defense, which behavioral coordination is thought to bring. We assess coordination in two main ways, based on its operational definition described above. First, we test whether partners adjust their behavior in response to each other during the STIs by measuring (i) if

partners produce correlated levels of aggressive output and (ii) if partners produce social contact/spacing calls (piks) in a manner that predicts partner aggression. Second, we test whether partners organize or re-adjust their behavior in response to a stimulus and whether their partner is attending to the stimulus by measuring how individuals alter their aggression during an STI when their partner is on site or away. If any or all of these relationships are detected, then our results will provide evidence of behavioral coordination. If these relationships are, in turn, context-dependent, then our results will provide evidence that coordination is modulated in response to an appraisal of the social environment.

Methods

Animals

We used downy woodpecker breeding pairs that inhabited the woodlands and greenways in Forsyth County, North Carolina, USA. Data were collected during April, as this corresponds to the breeding season in which territorial aggression and defense are strongest (Conner 1980; Jackson and Ouellet 2002; Dodenhoff 2002). The Wake Forest University Institutional Animal Care and Use Committee (IACUC) as well as the U.S. Fish and Wildlife Service and North Carolina Wildlife Resources Commission approved the research herein.

We determined the territory boundaries and location of the nest cavity for each pair included in our study. We did not band birds for individual identification; instead, to avoid inclusion of a single pair more than once, we only used pairs that maintained territories spaced at least 1 km apart (calculated from nest cavity to nest cavity using GPS coordinates). This approach is appropriate in our study species, given that downy woodpecker pairs maintain small non-overlapping breeding territories [$0.05 \pm 0.03 \text{ km}^2$ (mean \pm SD)] from which residents seldom leave during the breeding season (Graber et al. 1977; Schroeder 1983; Jackson and Ouellet 2002). We calculated that a distance of 1 km between territories equates to over 3 standard deviations above the average size of the birds' home range, which provides strong assurance that data were never recorded more than once from the same individuals. Similar approaches have been used previously to distinguish among conspecifics in studies of avian territoriality (Rogers et al. 2004; Koloff and Mennill 2011; Benedict et al. 2012; Kovach et al. 2014; Leedale et al. 2015). During STIs, observers identified males by the highly conspicuous and sexually dimorphic red plumage on the nape.

Experimental design

We used STIs to examine how drum length affects (i) the amount of aggression resident individuals produce to defend

their territory and (ii) the degree to which individuals within a breeding pair coordinate the output of such aggression. We therefore randomly subjected downy woodpecker pairs to one of two STI conditions. In the first condition ($n=9$ pairs), the length of the drum broadcast during the STI was experimentally increased to 19 beats/drum. In the second condition ($n=8$ pairs), the length of the drum broadcast during the STI was experimentally decreased to 11 beats/drum. Both of these drum lengths fall well within the natural distribution of drum lengths produced by downy woodpeckers in this study population. We validated this by collecting recordings of spontaneously produced drums during the breeding season (range of drum length 4–23 beats/drum; mean drum length \pm SD 15.01 ± 2.97 beats/drum; see the electronic supplemental material for methodological details and Table S1).

Stimulus drums were created in Audacity (v. 2.0.6) using recordings from three wild males that drummed on three separate substrates. These recordings had a high signal-to-noise ratio and thus had virtually no ambient background noise. To generate stimulus drums, three recordings were randomly selected and beats within several drums were copied or removed (selection of beats was at random) to either increase the drum's length to 19 beats (long drum condition) or decrease the drum's length to 11 beats (short drum condition). Notably, we created both types of STI stimuli from each pre-recorded drum, and thus short and long drum stimuli were paired (individual identity of the drum stimulus was taken into account statistically, see below). In all stimuli, beats were spaced 0.064 s apart, which corresponds to the average cadence of the downy woodpecker drum (Stark et al. 1998; Dodenhoff et al. 2001, see electronic supplemental material Table S1).

To stage an STI, we placed a speaker (JBL; model FLIP) approximately 1.5 m above the ground and 10 m from a pair's nest cavity. Playback of either the long or short drum (see above) stimulus was then initiated and allowed to run for 10 min. During the playback, drums were produced 8 s apart, which corresponds to the average time between drums broadcast by displaying individuals in the local population (see electronic supplementary material Tables S1 and S2). The volume of the playback was always kept at 80 dB measured 1 m from the speaker.

Behavioral recordings

During each STI, two observers recorded the behavior produced by both the male and female individuals within a social pair. One observer did so in a written notebook, whereas the other observer did so by dictating into a digital Tascam recorder (model no. HD-P2) that simultaneously recorded the acoustic production of the pair's behavior (recorded with a directional microphone; Sennheiser ME66; sampling frequency = 44.1 kHz). Both observers recorded the frequency and timing of the two main aggressive acoustic signals: drum

bouts and whinny calls, which are commonly used by woodpeckers (Kilham 1974; Jackson and Ouellet 2002; Dodenhoff 2002). The observers also recorded the time each individual spent within 5 m of the speaker as well as each individual's latency to respond to the STI (i.e., the time of the first aggressive signal produced or the first time to approach within 5 m of the speaker) (Seddon 2005; Moseley et al. 2013). Finally, the observers recorded the total number of pik calls produced by each individual. These vocalizations are not thought to be overt aggressive signals per se (Dodenhoff 2002), and they do not conform to criteria for aggressive signals outlined by Searcy and Beecher (2009). However, we measured pik calls because studies indicate that individuals within a pair use them to coordinate movements within the territory (Jackson and Ouellet 2002; Kellam and Lucas 2014), and thus pik calls may also be used to help direct partner movements in aggressive contexts.

The observer who dictated into the recorder was blind to treatment group, as the stimuli were virtually impossible to distinguish by ear alone. We found that measures of behavior between this (blind) observer and the other were highly similar (97 % agreement between observers).

Statistical analyses

Statistical analyses were performed using SPSS 22.0 (IBM). Data that were not normally distributed were natural log transformed [$\ln(1+X)$] to achieve normality, as $Q-Q$ plots indicated that these transformations yielded more normally distributed data (Zar 2010). Two-tailed tests ($\alpha=0.05$) were used for all statistical analyses.

In our first analysis, we examined how drum length broadcast during an STI influences aggressive output of male and female territory residents. We reduced measures of resident behavior using a principal component analysis (PCA), which included the four main aggressive variables: latency to respond to the intrusion, time spent within 5 m of the speaker, number of whinny calls, and number of drums (note that we did not include pik calls in this analysis, because evidence suggests that they are not overt aggressive signals; see above). Our PCA yielded two principal components (PCs), with eigenvalues greater than 1.0 and suppressed factors below 0.4 (Tabachnick and Fidell 1996; Budaev 2010). We assessed how drum length influenced PC scores by running a linear mixed model (LMM) for each PC. In both models, we included treatment and sex as the fixed factors as well as pair identity as a random factor to account for non-independence between these two individuals. We also input the identity of the individual used to construct the drum stimuli as a random factor to account for any effect that this variable might have on the residents' behavior.

We next examined how drum length broadcast during an STI influenced the behavioral coordination between resident

individuals. First, we used two mixed-effect regression models (MRMs, one per drum condition) to test whether individuals in a pair produce correlated levels of aggressive behavior during the STI. In both models, the identity of the individual used to construct the stimulus drum was input as a random factor. Second, we used two additional MRMs (one per condition) to test whether total pik calls given by one individual within a pair predict the aggressive behavior (PC score) of the other individual (the partner). In these MRMs, both pair identity and the identity of the individual used to construct the stimulus drum were input as random factors. Additionally, the amount of time each individual responded to the stimulus was used as a covariate.

Finally, we used an LMM with a within-subject factor design to compare the amount of aggression produced by the first individual to respond to the STI, both before and after its partner initiated a response. In this model, the between-subjects factor was treatment while the within-subjects factor was the amount of behavior produced by first responder before and after its partner responded. We considered the partner's first response as either coming within 5 m of the speaker or producing an acoustic signal. Using this information, we calculated the time each first responder spent with and without their partner attending to the STI. The total time the first responder behaved during the intrusion was used as a covariate, and the identity of the individual who provided the stimulus drum was used as a random factor. We also used an LMM to assess whether the production of pik calls changed in response to the partner's arrival. This model was identical to the one described above, but with the amount of pik calls produced before and after their partner responded as the within-subjects factor. Significant effects were followed by simple main effect post hoc analyses, with Bonferroni corrections used to control for inflation of type I error.

Results

Effects of drum length (threat level) on pair aggression

Our PCA reduced aggressive behavior into two PCs, which explained 66 % of the data's variation (Table 1). The first PC (PC1) accounted for 39.39 % of this variation, and it negatively loaded latency to respond and positively loaded time within 5 m of the speaker (Table 1). The second PC (PC2) accounted for 26.48 % of the variation in the data. This PC positively loaded a number of aggressive acoustic signals broadcast (whinny calls and drums) but also negatively loaded approach latency (Table 1). Based on these analyses, high values of PC1 indicate shorter latencies to respond and longer times spent close to the speaker, while high values of PC2 indicate high numbers of whinny calls and drums and shorter latencies to respond.

Table 1 Principal component analysis of response difference following playback of long and short drum stimuli

Behavioral response	PC1	PC2
Latency to respond	<i>-0.770</i>	<i>-0.480</i>
Time within 5 m	<i>0.916</i>	<i>-0.182</i>
Drums	<i>-0.034</i>	<i>0.627</i>
Whinny calls	<i>0.083</i>	<i>0.730</i>
Percent variation explained	39.39	26.48

This analysis yielded two principle components that explained 66 % of the total variation. *Italic values indicate variables that loaded strongly into each PC*

We tested whether long drums elicited a more robust aggressive response from residents. PC1 scores did not differ according to drum condition ($F_{1,31.04}=2.43$, $p=0.13$), sex ($F_{1,27.01}=3.49$, $p=0.09$), or the interaction between these factors ($F_{1,27.39}=1.01$, $p=0.32$). However, PC2 scores were significantly greater in individuals presented with long drums during the STI, compared to short drums (Fig. 1; $F_{1,27.59}=11.41$, $p=0.002$). There was no effect of sex in this model (Fig. 1; $F_{1,27.12}=0.07$, $p=0.80$), nor was there an interaction between drum condition and sex (Fig. 1; $F_{1,27.56}=0.70$, $p=0.41$). These data therefore indicate that both sexes within a pair increase amounts of acoustic signaling and decrease response times when presented with longer drums from an intruder. Accordingly, we used both PC2 and the behavioral variables it encompasses as the main metrics of aggression for subsequent analyses.

Behavioral coordination between individuals within a pair

To investigate intra-pair coordination, we first tested whether resident individuals within a pair produce correlated (i.e., matched) levels of territorial aggression. However, there was no evidence of such a relationship, as PC2 scores from one individual within a pair were not associated with PC2 scores from the partner. This lack of an effect occurred in both the long drum condition ($\beta=0.57$, $F_{1,3.51}=2.81$, $p=0.21$) and the short drum condition ($\beta=-0.30$, $F_{1,4.99}=1.35$, $p=0.30$).

We also tested whether the number of pik calls produced by one individual within a pair influenced their partner's level of aggression. In the long drum condition, pik calls negatively predicted partner's PC2 scores (Fig. 2a; $\beta=-0.41$, $F_{1,7.36}=10.04$, $p=0.015$). There was no evidence of this relationship in the short drum condition (Fig. 2b; $\beta=0.11$, $F_{1,12.55}=1.36$, $p=0.27$). Furthermore, this difference in behavioral coordination was not explained by sex-related ($F_{1,19.47}=1.21$, $p=0.29$) or treatment-related ($F_{1,13.26}=0.21$, $p=0.80$) differences in pik call production (interaction; $F_{1,19.40}=0.60$, $p=0.50$). Additional analyses demonstrated that the number of pik calls an individual produces is not

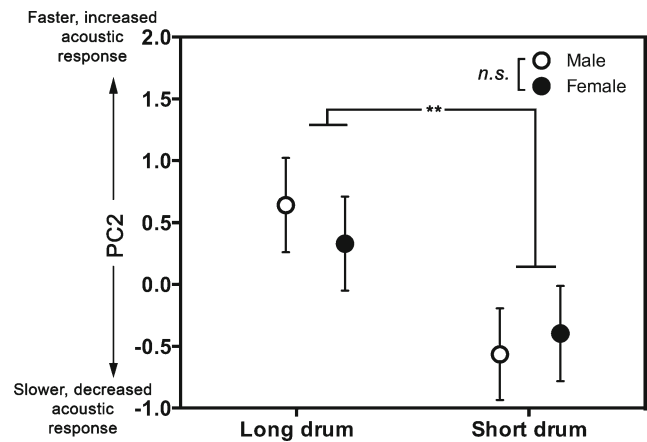


Fig. 1 Changes in PC2 scores in response to long versus short drums broadcast in STIs (mean \pm SEM). Higher values for the aggression score correspond to animals that responded more quickly and produced more aggressive behaviors. $***p < 0.01$, significant differences

correlated with their own PC2 score (long drum: $\beta=-0.58$, $F_{1,14}=0.58$, $p=0.46$; short drum: $\beta=-0.09$, $F_{1,15}=0.89$, $p=0.36$), indicating that piks are not related to one's own aggressive output. These data therefore collectively point to pik calls as a signal that is used largely to influence partner behavior.

We next tested whether an individual's behavior during an STI is affected by the arrival of its partner. In this analysis, we only considered the first individual within a pair to respond to the STI (i.e., the first responder) and we compared the number of aggressive acoustic signals (whinny calls and drums) that this individual produced before and after its mate responded. Overall, first responders produced more acoustic signals in the long drum condition than in the short drum condition (Fig. 3; $F_{1,13}=6.15$, $p=0.03$) and there was no general difference in first responder's acoustic signals produced before versus after its partner responded (Fig. 3; $F_{1,13}=0.22$, $p=0.64$). However, we did find a significant interaction between drum condition and before/after signal production (Fig. 3; $F_{1,13}=4.92$, $p=0.048$), with post hoc tests showing that first responders produced more acoustic signals *after* their mate responded in the long drum condition, compared to the short drum condition (Fig. 3; $p=0.002$). Moreover, in the short drum condition, there was a marginally significant trend for first responders to decrease their signal production once their partner responded (Fig. 3; $p=0.07$). There is no evidence of such a change in signal production in the long drum condition ($p=0.72$).

We also investigated whether the production of pik calls produced by the first responder changed following the partner's arrival. We found neither treatment differences in the number of pik calls produced by the first responder ($F_{1,22.19}=0.18$, $p=0.67$) nor a difference in pik call production by the first responder before or after the partner responded ($F_{1,22.09}=0.02$, $p=0.96$). We also did not detect an interaction between treatment and before/after signal production ($F_{1,$

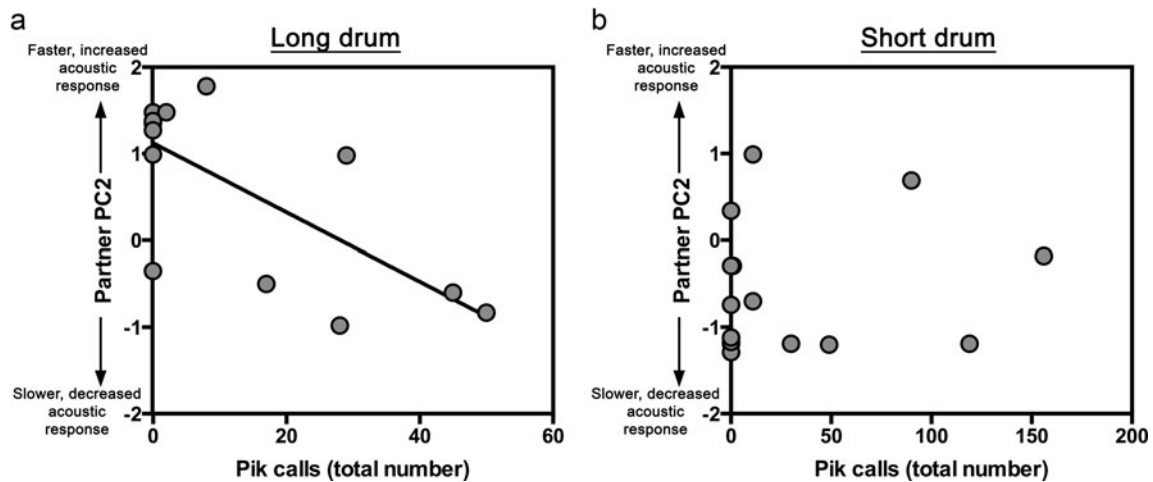


Fig. 2 Relationship between pik calls produced and the PC2 score of an individual's partner. Comparisons were between STIs in which either long (a) or short (b) drums were broadcast. Higher values for the

22.09 = 0.07, $p = 0.80$). Thus, individuals adjust their aggressive signals, but not pik call production, following the response of their partner.

In a final analysis, we found evidence of differences in the behavior of the second responder according to the different treatments. In the short drum condition, the second bird to respond produced significantly more aggressive behavior once they arrived on site, compared to the first responder ($t_7 = -2.85$, $p = 0.025$). This difference was not found in birds from the long drum conditions ($t_5 = 0.11$, $p = 0.92$).

Especially important to all these analyses is the result that males and females were equally likely to first respond to the STI ($X_{2,17} = 0.32$, $p = 0.86$). Thus, we can rule out the

aggression score correspond to animals that responded more quickly and produced more aggressive behaviors. Note the difference in scale on the *horizontal axis*

possibility that the sex of the bird affected any of the results about the first or second responders' behavior.

Discussion

Our data support the hypothesis that breeding pairs of downy woodpeckers coordinate defensive tactics to protect co-inhabited territories, and that such coordination occurs in a context-dependent manner. When pairs were exposed to a long drum from a supposedly high-threat intruder, for example, residents begin to produce pik calls in a way that negatively predicted their partner's aggressive output. This suggests that, in select social situations, residents adjust their behavior in response to their partner's actions. At the same time, when pairs were exposed to short drums from a supposedly low-threat intruder, the first bird to respond to the intrusion altered how many aggressive acoustic signals it produced in a way that depended on its partner's presence. This implies that residents organize their behavioral output differently when their partner is on site versus when it is off site. Taken together, these data suggest that territorial coordination is determined by an appraisal of the threat imposed by a potential intruder, with more threatening intruders eliciting increased aggression and the use of calls to influence a partner's behavior.

Coordination of territorial behavior

Previous work has reported forms of behavioral coordination among conspecifics to accomplish a variety of tasks or goals (Hall and Magrath 2007; Hall and Peters 2008; Bell et al. 2010; Yip and Rayor 2011; Ioannou et al. 2012; Goodwin and Podos 2014). This work, however, does not immediately address how animals might initiate coordination in response to their social environment. We know that such flexibility

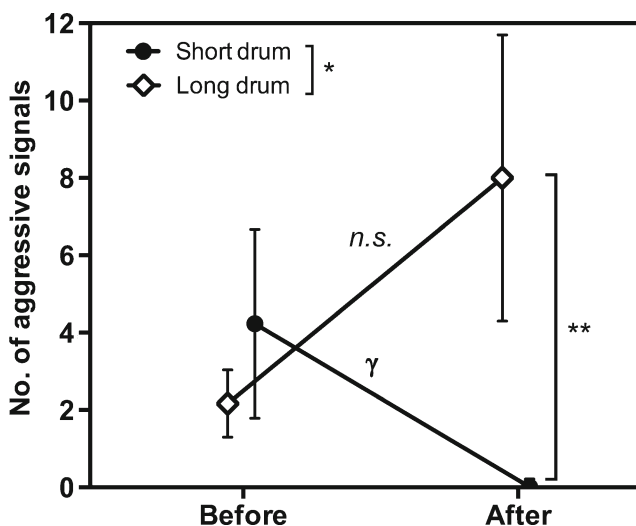


Fig. 3 Changes in aggressive acoustic signals (number of drums and whinny calls) following high- and low-threat STIs. Mean (\pm SEM) difference in the number of aggressive acoustic signals elicited by intruders broadcasting long or short drumming bouts prior to and after the arrival of first responders' mate. * $p < 0.05$; ** $p < 0.01$, significant differences. γ denotes a marginally significant post hoc difference ($p = 0.07$)

occurs, given that animals appear to coordinate behavior in some instances, but not others (McComb et al. 1994; Townsend et al. 2011). Thus, for the first time, our work reveals the conditions under which these determinations are made, by showing that coordination in territorial contexts depends on the nature of the intruder and the threat that this individual likely imposes. Considering that behavioral coordination is thought to enhance the efficacy of a given tactic or strategy (Hall and Magrath 2007; Hall and Peters 2008), we suspect that integrating territorial defense between individuals within a social breeding pair provides a more effective means by which residents can evict unwanted individuals from their home turf.

With this assertion in mind, our results raise the intriguing question of how coordination improves tactical competence and proficiency. Work that examines joint aggression among multiple individuals suggests that such behavior demonstrates a numerical advantage against a lone intruder (Farabaugh et al. 1992; Seddon and Tobias 2003) or may signal greater strength from a group (Hall and Magrath 2007). Joint aggression, however, is not necessarily the same thing as a coordinated behavior, given that the latter depends on the adjustment of behavioral output in response to a social partner. Specifically, with joint aggression, the behavioral output that each resident produces in response to a common stimulus should be unaffected by the presence or the behavior produced by their partner during the intrusion. By contrast, during behavioral coordination, we expect that residents not only pay attention to signals displayed by a social partner, but also adjust their own behavior based on their partner's behavior in response to the intrusion to produce a strategy that allows each individual in the pair to exert the least amount of energy and risk. Accordingly, there is presumably a benefit to the ability to dynamically adjust one's behavior in response to the actions of their social ally, rather than simply increasing the intensity of an agonistic signal by having more than one individual to produce it.

The relationship we uncover between pik calls and partner aggression likely illustrates how coordination may provide more than a numerical advantage during a competitive dispute. The negative association between these two variables is at first counterintuitive; yet, it makes sense in the context of downy woodpecker behavior and ecology. Males and females use piks as contact vocalizations to establish spacing between individuals within a breeding pair (Kilham 1974; Kellam and Lucas 2014), and anecdotal reports suggest that piks produced during aggressive bouts are used to direct one individual in the pair to the nest cavity (Dodenhoff 2002). Additional work suggests that downy woodpeckers use this vocalization to warn their partner imminent threats (Ritchison 1999). Thus, individuals may produce piks during the long drum STIs to strategically spatially partition themselves, such that one bird is left to fight off the intruder, while the other bird is positioned to defend the nest. In this case, we would predict

that the latter individual would produce fewer aggressive signals, given that our STI paradigm does not include any approach to the residents' nest (Townsend et al. 2011). By contrast, such spatial partitioning may not need to occur in the short drum condition, because residents may perceive this intruder as a lower threat that requires less effort to evict.

In line with this thinking, our results are consistent with the idea that the frequency with which pik calls are produced are not used as a recruitment signal to bring in one's partner to the intrusion. If this were the case, then we would expect that the number of pik calls produced by the bird that first responded to the STI would decrease after its partner arrived on site. Yet, we find no difference in the total number of pik calls produced before and after the partner responds to the encounter. Of course, individuals may use other features of pik calls that we do not measure to recruit their partner, including both the temporal patterning and amplitude of pik call production (Ritchison 1999).

Our data also show that individuals alter their behavior in response to their partner's attendance to the STI. This finding may inform our understanding of how aggressive coordination is advantageous. For example, in the short drum STI, we find that the first downy woodpecker to respond decreases its aggressive behavior once its partner arrives to the scene. This change in aggressive output is likely attributed to the first responder taking turns with its partner to defend the territory, such that only one individual at a time attends to a low-threat invader (McComb et al. 1994; Quinard and Cézilly 2012). Indeed, we find that once both birds have responded to the short drum stimulus, the first responder's partner ramps up their aggressive signals. This effect is not seen in the long drum STI, as individuals do not change their behavior once their partner arrives on site and both residents produce levels of aggressive behavior that are statistically indistinguishable. Each bird therefore likely produces the minimal amount of aggression necessary to expel an intruder (Quinard and Cézilly 2012), which is undoubtedly essential in low threat contexts so that individuals can avoid costs associated with aggression (Moseley et al. 2013).

Selectivity in the type of behavioral coordination

Surprisingly, we find that behavior between partners is not ubiquitously coordinated, in which individuals only coordinate certain types of behavior with their partner. For example, our analyses demonstrate that levels of aggressive output are not correlated between members of a social partnership. This result suggests that aggression is not matched between allies in a way that we might otherwise expect from studies of exclusively vocal coordination (e.g., duetting) (Farabaugh et al. 1992; Hall 2004). Yet, considering that we find evidence of vocal-behavioral coordination that is not simply a duet, our findings imply that coordination extends beyond simple

patterns of behavioral matching. Rather, we suspect that behavioral coordination can entail adjusting different components of an individual's behavioral output, with special attention to the state of the immediate social environment.

We, of course, cannot rule out that matching occurs in other contexts that we did not examine. Intruders that produced drums longer than 19 beats, for instance, may actually elicit aggressive matching, if, in fact, it is an even more efficacious defensive tactic. Moreover, we did not measure a more fine-scale coordination between breeding partners, such as physical distance between members of a pair during a fight, which may otherwise provide greater depth to our knowledge on what tactical behavioral coordination looks like (Templeton et al. 2011). Such analyses have been successfully executed in work on avian duets and thus may now be employed in studies like ours.

Within-individual flexibility of territorial aggression

Finally, another important aspect of our paper is that we show that both males and females within a pair adjust their aggressive behavior in response to different territorial threats. Aggressive output from residents, regardless of sex, increases in the STI conditions in which longer drums are broadcast, relative to STIs in which shorter drums are broadcast. This result aligns with our predictions, given that individuals that produce longer acoustic signals with more repetitive notes tend to be higher in quality (Behr 2006; Rivera-Gutierrez et al. 2010; Mager et al. 2012) and superior fighters (Mowles and Ord 2012). Certainly, this is also thought to be true in woodpeckers (Short 1974; Wilkins and Ritchison 1999).

Congruent with our thinking about the adaptive value of coordination, we expect that increasing one's aggressive behavior in response to long drums will enhance one's ability to fight off the potentially high-quality intruder (Mager et al. 2012; Moseley et al. 2013). Given that territorial animals can frequently lose both portions of their territory and mating opportunities from higher-quality territorial invaders, a more robust individual response that ensures adequate protection of resources is suggested to be adaptive (Temeles 1990; Briefer et al. 2008; Moseley et al. 2013). Therefore, the ability for pairs to tailor this response to context and strength of the threat an intruder imposes likely allows individuals to fine-tune aggression, such that the risks associated with fighting are minimized in less important instances without completely eliminating the adaptive benefits of an aggressive disposition. While we do not know the extent to which downy woodpeckers lose territories to high-quality intruders, prior work does indicate that residents typically engage in numerous territorial disputes throughout the breeding season (Kilham 1962, 1974; Kellam et al. 2004). Moreover, downy woodpeckers pairs expend considerable energy to excavate nest

cavities on an established territory (Wiebe et al. 2007), and thus losing a territory (and the nest site) dramatically reduces the chances of reproduction within the year. In this vein, we expect selection to favor mechanisms that promote efficient and powerful territorial vigilance.

Conclusions

We provide some of the first data to show that animals coordinate elements of their aggressive milieu to collaboratively defend a mutual territory. Indeed, we show that in a species that frequently encounters territorial intrusions during the breeding season, residents modify their behavior in response to the presence of their partner and use vocal signals in a way that predicts their partner's agonistic output (Kilham 1962; Lawrence 1967; Kilham 1974). To this end, we find that these effects are context-dependent and thus change in response to the level of threat posed by the supposed territory intruder. Given that behavioral coordination is thought to enhance the efficacy of a given behavioral action, we expect that this ability evolved to help individuals fine-tune territorial defense by enhancing aggression in contexts in which the threat of invasions or exploitation of resources is high.

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Conflict of interest The authors declare that they have no conflict of interest.

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