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Author for correspondence:

Sarah E. Goodwin

e-mail: segoodwi@cns.umass.edu

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Animal behaviour

Team of rivals: alliance formation in territorial songbirds is predicted by vocal signal structure

Sarah E. Goodwin¹ and Jeffrey Podos^{1,2}

¹Graduate Program in Organismic and Evolutionary Biology, and ²Department of Biology, University of Massachusetts Amherst, Amherst, MA, USA

Cooperation and conflict are regarded as diametric extremes of animal social behaviour, yet the two may intersect under rare circumstances. We here report that territorial competitors in a common North American songbird species, the chipping sparrow (*Spizella passerina*), sometimes form temporary coalitions in the presence of simulated territorial intruders. Moreover, analysis of birds' vocal mating signals (songs) reveals that coalitions occur nearly exclusively under specific triadic relationships, in which vocal performances of allies and simulated intruders exceed those of residents. Our results provide the first evidence that animals like chipping sparrows rely on precise assessments of mating signal features, as well as relative comparisons of signal properties among multiple animals in communication networks, when deciding when and with whom to form temporary alliances against a backdrop of competition and rivalry.

1. Introduction

Social behaviour in many animal species features a fine balance between competition and cooperation. For instance, competitive rivals may rescind competition and form temporary alliances when their interests align. Coalitions have been documented in wide-ranging contexts including cooperative hunting, mate attraction and predator deterrence [1]. A fundamental open question about coalitions is how animals decide when and with whom they will cooperate [2]. We expect animals to be highly selective when choosing allies, as too strong an ally could compete for resources, whereas too weak an ally could prove ineffective. One way animals evaluate one another when seeking or competing for mates is by assessing sexual signals, stereotyped displays that provide reliable information about signaller attributes [3]. It follows that animals may likewise assess sexual signals when forming alliances, although this possibility remains unexplored.

In our work investigating territorial dynamics and signalling behaviour in chipping sparrows (*Spizella passerina*), we made the unexpected discovery that neighbouring rival males sometimes form temporary defence coalitions in response to simulated territorial intrusion (see also [4]). More specifically, in trials in which we simulate territorial intrusion via song playback, we have observed neighbours foraging into focal male territories, with the two birds then maintaining close proximity and performing simultaneous, parallel defensive responses directed at the simulated intruder (singing, flying and displaying). Might chipping sparrows forming coalitions use song to guide strategic decisions about when and with whom they will cooperate?

The most prominent feature of chipping sparrow song is its trilled organization, in which notes are repeated in rapid succession (e.g. figure 1*a,b*). Trilled songs are limited in their structure by vocal performance constraints, i.e. biomechanical limits in how birds can activate and coordinate the multiple vocal motor systems involved in song production [5–7]. Males that can best execute challenging motor

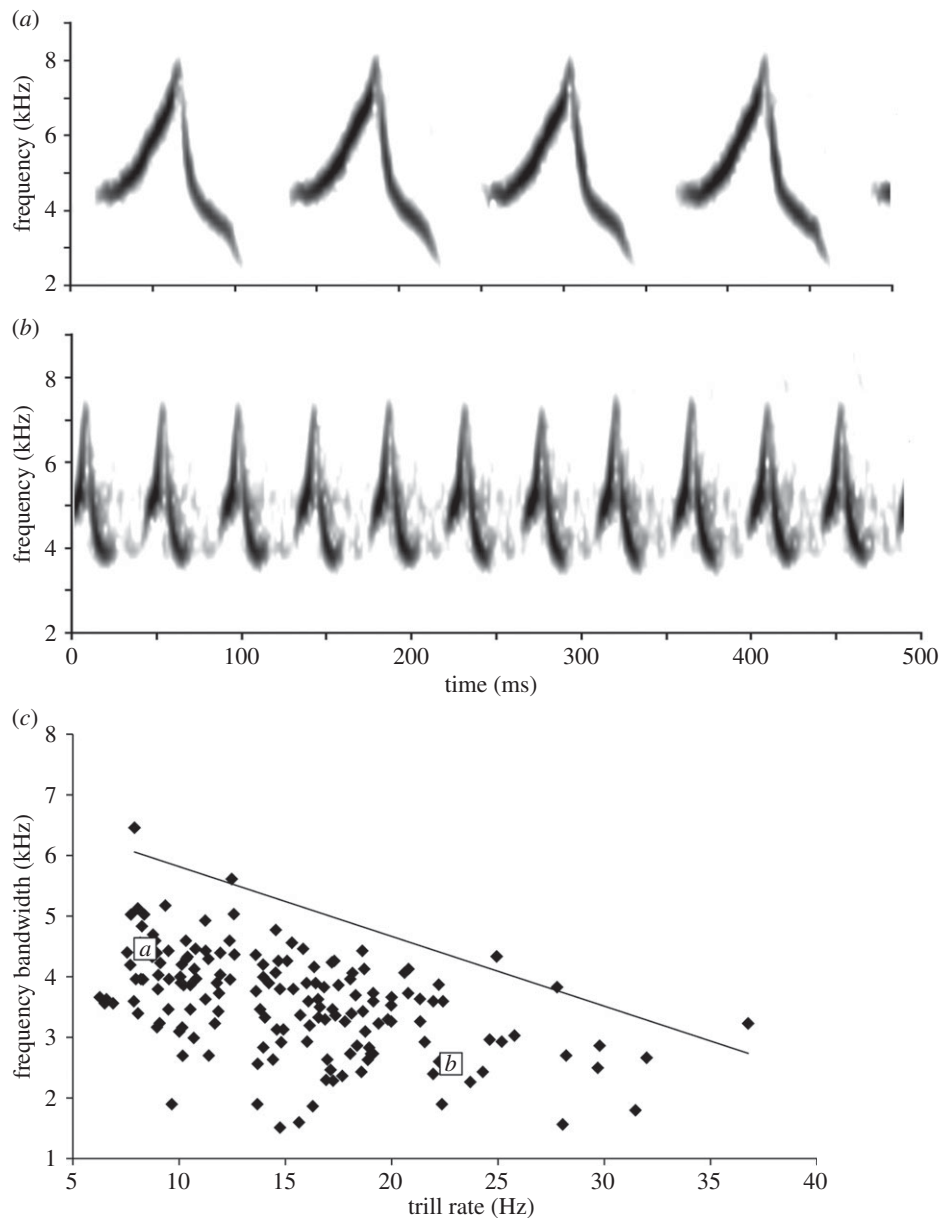


Figure 1. Chipping sparrow songs show evidence of a vocal constraint. (a,b) Chipping sparrow songs (two examples shown), comprised of rapidly repeated notes, show broad population level variation trill rate and frequency bandwidth. (c) Biplot of trill rate and frequency bandwidth ($n = 160$ males) reveals a performance trade-off in vocal production (upper bound regression, $R^2 = 0.89$, $p = 0.002$).

displays tend to be treated as superior rivals [8], and in songbirds accumulating evidence suggests that high-performance trills, e.g. fast trills, are especially threatening [9,10].

Here, we test the hypothesis that males eavesdrop on and assess relative song performance, particularly trill rates, of rivals and would-be allies as a guide to territorial coalition formation. To test this hypothesis, we quantified salient aspects of song variation, tested residents' responses to variation in trill rate using a playback experiment, and examined the circumstances under which coalitions formed.

2. Material and methods

(a) Quantifying song variation and vocal performance

We recorded songs of chipping sparrows in Hampshire and Franklin counties, MA, USA between May 2010 and July 2012 using Sennheiser K6/ME66 shotgun microphones and Marantz PMD660 solid-state recorders, and supplemented field recordings ($n = 70$) with recordings from Cornell University's Macaulay

Library of Natural Sounds ($n = 90$). We used SIGNAL 4.0 to measure trill rate from waveforms and frequency bandwidth from amplitude spectra. We regressed maximum frequency bandwidth from 5 Hz trill rate bins onto trill rate to define the upper bound regression, the putative performance boundary [6].

(b) Playback experiment

We located singing males across western MA, USA between 15 May 2012 and 20 July 2012. We mapped the territories of singing males. Each male ($n = 24$) was presented, between 7 and 10 AM on consecutive days, a fast and a slow trill rate stimulus, simulating territorial intrusion. One stimulus was presented per day, with presentation order alternated across birds. We created stimuli by increasing or decreasing trill rate while ensuring the song was within the observed population range. Playbacks consisted of 4 min of song delivered at $6.5 \text{ songs min}^{-1}$, followed by 2 min of silence, after which a taxidermic mount of a chipping sparrow was revealed to allow residents an opportunity to attack. The playback resumed for another 4 min, followed again by 2 min of silence, totalling 12 min for each playback trial. All behaviours

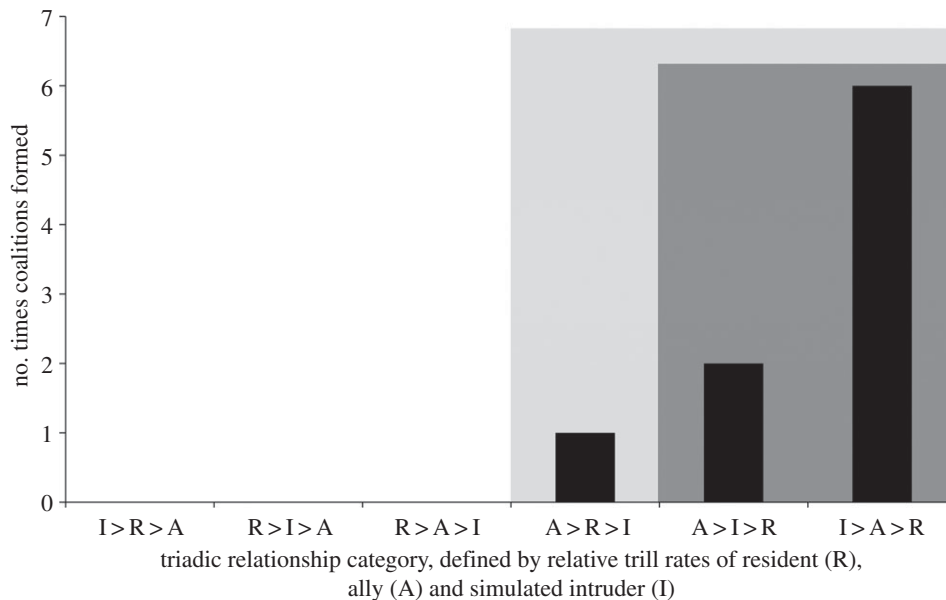


Figure 2. Defence coalitions form under specific triadic relationships. Coalitions ($n = 9$) form only when the ally's trill rate exceeds that of the resident he is assisting (light grey box, binomial exact test, $p = 0.004$). Moreover, given an ally with a faster trill rate, coalitions form most often when trill rates of simulated intruders exceeds both the resident and the ally, or is intermediate to the two (dark grey box). We observed no coalitions in other circumstances, in contrast to what we would expect by chance (multinomial exact test, $p = 0.004$).

were recorded with a Sennheiser K6/ME66 shotgun microphone and Marantz PMD660 solid-state recorder and analysed by an observer blind to treatment type.

We focused first on playbacks in which no coalitions formed. We used a repeated measures design and Wilcoxon signed-ranks tests to compare receiver response to fast versus slow trill rate, for univariate responses as well as combined behavioural responses (principal component analysis (PCA) scores). We also asked whether subjects' responses to playback covaried with the degree to which their own trill rates differed from stimulus trill rates [10]. Finally, for trials in which coalitions formed, we compared trill rates of residents and allies and asked whether particular triadic relationships were more conducive to coalition formation than others.

3. Results

Our analysis of song structure revealed an acoustic signature of constraints on trill production [6]: a triangularly distributed biplot of trill rate by frequency bandwidth, circumscribed by a significantly negatively sloped upper performance boundary (upper bound linear regression, $R^2 = 0.89$, $p = 0.002$, figure 1c). In playback trials in which coalitions did not form, males responded more vigorously to stimuli with fast trill rates. A PCA reduced responses into one principal component that explained 34% of total response variation, with positive loadings for the most aggressive behaviours (e.g. time spent within 2 m of the speaker, number of attacks). PC scores were significantly greater in response to fast trill rates (Wilcoxon signed-ranks test: $p = 0.003$). Similarly, univariate analyses indicate that males responding to faster trill rates approached the speaker more closely (Wilcoxon signed-ranks test: $p = 0.031$), spent more time within 2 m of the speaker ($p = 0.006$) and attacked the mount more often ($p = 0.018$). The aggressive responses of focal males also varied positively and in accordance with the degree to which stimulus trill rates exceeded their own trill rates (linear regression, $R^2 = 0.152$, $p = 0.027$), providing further evidence that trill rates are a salient vocal feature in the assessment of territorial rivals.

In our 48 playback trials, we observed the formation of nine coalitions. In each case, neighbouring males left their territories, trespassed on their neighbours' and directed defensive responses towards the simulated intruder. Analysis of trill rates of resident males, simulated intruders and neighbouring coalition-formers reveals two clear patterns concerning when and with whom neighbours form defence coalitions. First, birds formed coalitions exclusively when their own trill rates exceeded those of the residents they were assisting (nine of nine coalitions observed, binomial test: $p = 0.004$). Second, in eight of nine coalitions observed, trill rates of simulated intruders exceeded resident trill rates ($p = 0.039$). As a further test of the statistical significance of these patterns, we tallied the relative rankings of trill rate of all three parties involved in each coalition (ally, resident and simulated intruder) and tested observed rankings against rankings that would be generated by chance. While there were six possible rankings, coalitions formed only in three triadic relationships: intruder > ally > resident, six cases; ally > intruder > resident, two cases; and ally > resident > intruder, one case (multinomial exact test: $p = 0.004$, figure 2).

4. Conclusion

Chipping sparrow songs show evidence of a vocal performance constraint, consistent with patterns now seen in diverse vocalizing species [11]. Our playback trials revealed that territorial chipping sparrows attend to variation in one prominent performance variable, trill rate. More specifically, birds responded more vigorously when simulated intruders sang the more difficult to produce, faster songs, and also when there was a stronger disparity between intruder trill rates and their own.

More significantly, our results suggest that males eavesdrop on vocal interactions in neighbouring territories, assess relative trill rates of songs involved in these interactions, and initiate coalitions most often when the intruder represents a comparatively elevated threat. This finding aligns with the

hypothesis that cooperative defence coalitions should be initiated only when the benefits of coalition formation outweigh its associated costs [2]. In particular, to the extent that trill rate serves as a reliable indicator of territorial threat [9–11], chipping sparrows with a low trill rate neighbour should benefit by retaining that neighbour as a ‘dear enemy’ [12], in favour of a new neighbour with a higher trill rate. In contrast, chipping sparrows should have little incentive to assist neighbours who themselves have a faster trill rate, and especially not when that neighbour is challenged with an even faster intruder: indeed, we never observed coalitions forming under such circumstances.

Prior studies on cues guiding coalition formation have focused on size disparities and their visual assessment. For example, empirical work on fiddler crabs [13,14] reports coalitions forming most often when territorial allies are larger than intruders, and when intruders in turn are larger than residents. This pattern is predicted because allies should expend less energy evicting an intruder than in re-establishing territory boundaries with a new, larger neighbour. In these species, intruders may even target territory holders that have neighbours too small or weak to assist in their eviction [15]. Both lines of evidence suggest that would-be allies and intruders assess size disparities when deciding to attack or retreat. Our work with chipping sparrows takes the additional step of showing that animals can base decisions about alliance formation, not just on incidental visual size cues, but also on stereotyped communication signals that evolve under pressures of sexual selection.

Acoustic communication networks offer animals opportunities to detect and compare signals of multiple individuals

both rapidly and concurrently. Female songbirds in communication networks sample songs to guide comparative mate choice [16] and may cuckold their mates that are perceived as being on the losing end of song contests [17]. The facility with which male signals in communication networks can be compared by females elevates selective pressures on signal value, structure and strength [18]. Males, likewise, attend to songs within their local neighbourhoods, for example treating established neighbours with reduced aggression at territorial boundaries [12], retaliating against defecting neighbours that intrude [19] or expanding into neighbouring territories when those neighbours fail to vigorously defend their territories against other intruders [20]. Our finding here, that males forming coalitions strategically compare vocal attributes between themselves, neighbours and simulated intruders, further highlights the complexities of the social environment in territorial dynamics, and for the first time demonstrates the use of a stereotyped, specialized signal in establishing brief periods of cooperation among otherwise combative rivals.

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Data accessibility. Vocal performance data: uploaded as electronic supplementary material; playback data: uploaded as electronic supplementary material; trill rate data: uploaded as electronic supplementary material.

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