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Songbird cheaters pay a retaliation cost: evidence for auditory conventional signals

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Conventional signals impose costs on senders through receiver retaliation rather than through investment in signal production. While several visual conventional signals have been described (mainly 'badges of status'), acoustic examples are rare; however, several aspects of repertoire use in songbirds are potential candidates. We performed interactive playback experiments to determine whether song-type matches (responding to a song with the same song type), repertoire matches (responding to a song with a different song type, but one in the repertoires of both singers) and unshared song types serve as conventional signals during male–male territorial interactions in banded wrens, *Thryothorus pleurostictus*. Our results demonstrate that these three signals incite varying levels of receiver aggression: song-type matches induce faster approach than do repertoire matches, and repertoire matches induce faster approach than do unshared song types. Production costs do not differ, while the receiver response does. Because territorial banded wrens approach opponents who signal aggressively, such opponents risk attack. This system will punish and prevent cheaters, as weak males signalling aggression will be subject to escalation by stronger or more-motivated opponents.

Keywords: conventional signals; song-type matching; song sharing; *Thryothorus*

1. INTRODUCTION

Conspicuous colour patches in birds and lizards have been called badges of status when their size or hue varies with the dominance rank or fighting ability of their bearer (Rohwer 1975; Studd & Robertson 1985; Madsen & Masataka 1987; Møller 1987*a*; Thompson & Moore 1991; Olsson 1994; Pärt & Qvarnström 1997). Several investigators have manipulated these patches, thereby producing 'cheaters' who signal a dominant status when they are actually subordinate (or true dominants who signal a subordinate status), in order to verify the function of these signals. Although a few studies have found that individuals with enlarged or enhanced badges at least temporarily increased their status (Fugle *et al.* 1984; Rohwer 1985; Grasso *et al.* 1996; Marchetti 1998), most have found that such individuals were harassed and persecuted by naturally large-badged individuals and paid a high price for their cheating signal (Rohwer 1977; Møller 1987*b*; Qvarnström 1997, 1999). Large-badged individuals whose patches were reduced also paid a cost by having to work harder to maintain their dominance status (Rohwer 1977).

This line of investigation led to the recognition of a distinct class of communication signals, called conventional signals, in which receiver retaliation rather than signal production imposes the costs that maintain signal honesty (Maynard Smith & Harper 1988, 1995; sense two of Guilford & Dawkins 1995; Hurd & Enquist 1998). The cost of actually producing a colour-patch badge of status, often a white patch on a black field or a black patch on a white field, is believed to be trivial. The development of patch size or hue is often under the control of steroid hormones, so the adaptive linkage between dominance and badge size is a reflection of a prior commitment by the individual to an aggressive versus a submissive strategy (Moore *et al.* 1998). A flurry of game-theoretical models demonstrated that such conventional signals could evolve and be stable against cheaters as long as, first, subordinates avoided the costs of aggression by signalling a low status, and second, dominants possessed a 'rule of thumb' for frequently testing the fighting ability of high-status-signalling opponents (Hurd 1997; Enquist *et al.* 1998; Hurd & Enquist 1998). Testing of aggressive-signalling opponents will differentially punish bluffers. Escalated interactions and attacks should be more costly for bluffers than for truly strong or motivated opponents, who will be better able to back up their aggressive signals with aggressive actions.

Little thought has been given to the idea that the auditory signals observed in aggressive contexts might be stabilized by receiver retaliation costs rather than by production costs, and might thereby qualify as conventional signals. Vehrencamp (2001) recently made a case for song-type matching as a conventional threat signal in song sparrows *Melospiza melodia*, and Davies (1981) described a possible vocal conventional signal of territory ownership in pied wagtails *Motacilla alba*. Most studies investigating the factors that maintain the honesty of auditory threat signals have focused on the energetic costs of producing loud and/or rapidly repeated signals or on the physical constraints of body size on the production of low-frequency sounds (Davies & Halliday 1978; Clutton-Brock & Albon 1979). It is well known that songbirds use singing as both a mate-attraction signal and as a territory-defence signal. In approximately 75% of all songbirds, individual males possess repertoires of apparently equivalent song types (Macdougall-Shackleton 1997). Female preference for large repertoire size in the mate-attraction context is ubiquitous and probably the primary selective factor responsible for the evolution of song learning, song mimicry and song complexity in general. However, males in species that possess repertoires of two or more song types often use their song types in structured ways during

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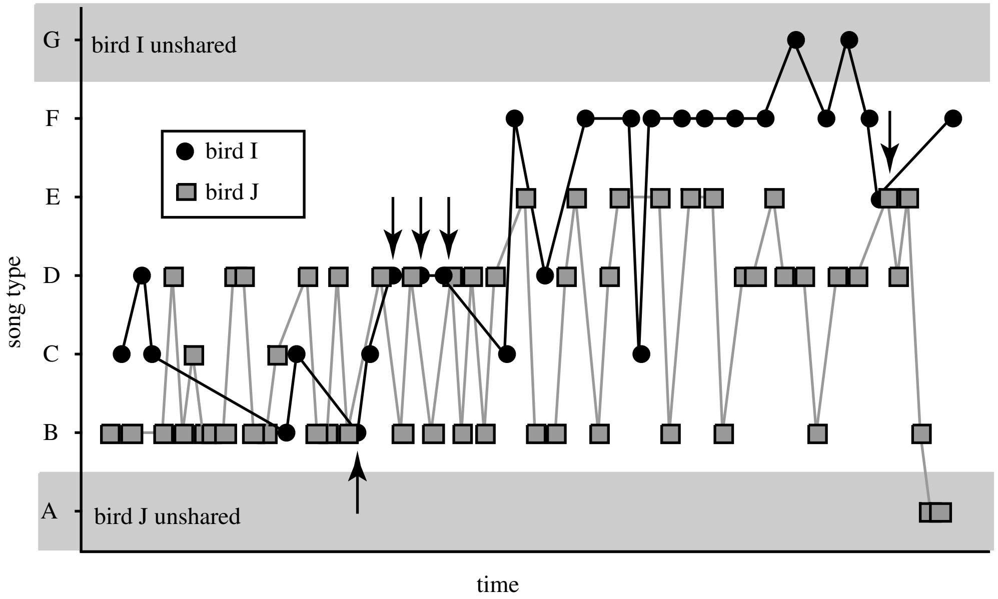

Figure 1. Song-type use during an encounter between two males at their territorial boundary. Out of the seven song types sung during the encounter, song types B–F were shared, although only bird I used shared type F during the interaction. Both males initially alternated between the same three shared song types, occasionally type matching (indicated by arrows). They then introduced other shared song types, and occasionally repeated the same song type several times in a row. Bird I then sang an unshared song type, and shortly afterwards bird J also sang one of his unshared song types. The encounter ended without a fight and both males retreated from the boundary.

territorial and counter-singing interactions with other males. Switching between song types at different rates, using song types that are shared versus not shared with a particular neighbouring male, and song-type matching are three kinds of singing strategies that are known to vary as a function of the level of aggressive engagement between males (Vehrencamp 2000).

The banded wren, *Thryothorus pleurostictus*, is a neotropical songbird that appears to use all three of these strategies in male–male interactions. The birds are permanent residents of the tropical dry deciduous forest, but actively sing and defend their territories mainly during the breeding season in the first half of the rainy season. Males possess repertoires of 20–28 discrete song types, and their short dispersal distances and tendency to copy the songs of local males result in adjacent males sharing between 50% and 90% of their song types. We have shown that males sing with high diversity, usually switching to a new song type after each song, during the dawn chorus and then reduce their diversity during counter-singing interactions later in the morning, sometimes alternating between just two or three song types or, rarely, repeating the same song type many times (Molles & Vehrencamp 1999). We also noticed that males tended to use shared song types during counter-singing interactions, and would occasionally song-type match each other. Unshared song types generally appeared towards the end of an interaction, if at all. Figure 1 shows the song types delivered by two adjacent males during a close encounter at their boundary. This interaction was settled without a physical fight: both males backed away from the boundary after the song exchange.

We hypothesized that singing a shared song was a more aggressive, or interaction-maintaining, signal than singing an unshared song, which seemed to signal the desire to end the encounter. Similarly, song-type matching seemed to be a more aggressive signal than repertoire matching (singing a shared song type without song-type matching; Beecher *et al.* 1996). We tested these ideas in two separate field playback experiments with similar set-ups that simulated a physically retreating invader giving alternative song signals. Two speakers were placed in a focal male's territory, one on the boundary with an active neighbour and another inside the territory on the same side. Using song stimuli from the neighbour, we began the playback trial with the more aggressive signal from the invasive speaker. After a specified time, we switched to the boundary speaker, as if retreating, and either continued to deliver the same signal (the aggression-maintaining treatment) or changed to the less aggressive signal (the de-escalating treatment). The aggression-maintaining treatment not only represents the more aggressive vocal signal but could also be interpreted as a bluffing signal relative to the retreating movement of the intruder, whereas the de-escalating treatment represents an honest signal of submissive intentions. The latency of the bird in approaching the second speaker was our index of his aggressive response. A more rapid approach to the second speaker during the aggression-maintaining treatment not only verifies that the singing strategy is used in the way we hypothesize, but also implies that singers giving a stronger threat signal than their actions indicate are aggressively tested by receivers.

2. METHODS

Playback experiments were performed in 1998 and 1999 during the prime breeding-season months of June to September. Subjects in both years resided in territories near the Santa Rosa biological station in the Guanacaste Conservation Area, Costa

Rica. For details on the habitat, the study area and the methods used to determine repertoire size and song-type matches between neighbouring birds see Molles & Vehrencamp (1999). All subjects were individually colour banded.

Songs for playback were recorded from neighbouring males during dawn singing bouts using a Sennheiser MKH 816 (Sennheiser Electronic GmbH & Co. K. G., Wedemark, Germany) or Audio-Technica AT 4071 (Audio-Technica, Inc., Stow, OH, USA) directional microphone and a Tascam DA-P1 (TASCAM Corporation, Montebello, CA, USA) or Sony TCD-D8 (Sony Electronics, Inc., Park Ridge, New York, USA) digital tape recorder. Suitable songs were digitized using the Canary sound-analysis package (Charif *et al.* 1995) on a Macintosh PowerBook 1400 (Apple Computer, Inc., Cupertino, CA, USA).

We performed playbacks interactively using Singit! software (Bradbury & Vehrencamp 1994) on a laptop computer. An on-screen timer provided a means of keeping playback song intervals consistent. In all trials we maintained a playback rate of one song every 11 s when the focal bird was not singing. When the subject was singing we maintained an identical singing rate if possible, but delayed playback for 1–3 s when necessary to avoid overlapping with the song of the focal bird. Singit! created a log of each trial, including the timing of playback songs and keystrokes indicating focal-bird songs and the estimated distance of the focal bird from the speaker. All playback trials, including the pre- and post-playback periods, were recorded.

For both experiments, each focal male heard both treatments from the same speaker locations, and all the treatments used songs recorded from the neighbour who shared that particular boundary. The alternative treatments for all but one of the males were presented between 1 and 6 days apart (for one male the treatments were 11 days apart). Half of the focal males received one treatment order and the other half received the reverse order. The start times for the trials ranged from 06.55 to 10.30. The three classes of singing behaviour used as playback stimuli (repertoire matches, song-type matches and unshared song types) are illustrated in figure 2. Songs were broadcast through small amplified speakers (Radio Shack 40-168, Radio Shack Corporation, Forth Worth, TX, USA), placed 1–2 m above ground level in vegetation, at sound levels similar to natural songs (90–95 dB at 1 m). The behaviour of the focal bird was monitored for 2 min before and after the playback period. In order to begin playback, the neighbour whose songs were being broadcast had to be silent for at least 1 min and the focal bird's location had to be known. The first half of each playback period was broadcast from an 'invading' speaker placed *ca.* 15 m within the focal bird's territory. The second half of the playback was broadcast from a second 'retreating' speaker placed at the territorial boundary of the neighbour whose songs were used as the playback stimuli. This simulated a retreat by the invading neighbour of *ca.* 15 m, and provided a more natural simulation of an interaction than is possible with a one-speaker design. In all trials, playback did not proceed to this second stage unless the focal bird approached to within 10 m of the first speaker. The key response variable was the latency in approaching the second, 'retreating', speaker, measured as the time between the first song played from the second speaker and a movement of at least 5 m directly towards the speaker by the focal bird.

(a) *Song-sharing experiment*

To compare the responses to shared versus unshared song types, we selected three shared and three unshared song types of similar length from the neighbour of each focal bird. We used unshared song types as shared song types for different focal males when possible. The aggression-maintaining treatment consisted of playing shared song types from both the invading and the retreating speakers (indicated by the shorthand notation shared/shared). During the first half of the playback, three shared song types were played in an alternating (ABABCABABC...) pattern for 2 min from the first speaker. The same singing pattern was maintained during playback from the second speaker. In 1998, the same song types were used in both halves of the playback treatment, but in 1999 three different shared song types were used for the second half of the treatment. The first half of the de-escalating treatment (shared/unshared) consisted of the same playback pattern and song types as the first half of the shared/shared treatment. During the second half, we played three song types from the appropriate neighbour that were not shared with the focal bird.

Six males were tested between 27 August and 1 September 1998 (average repertoire size, mean ± s.e.m. = 21.6 ± 0.52 (range, 18–25) and average repertoire overlap with adjacent neighbours, mean ± s.e.m. = 0.819 ± 0.008 (range, 0.777–0.861)). We tested 13

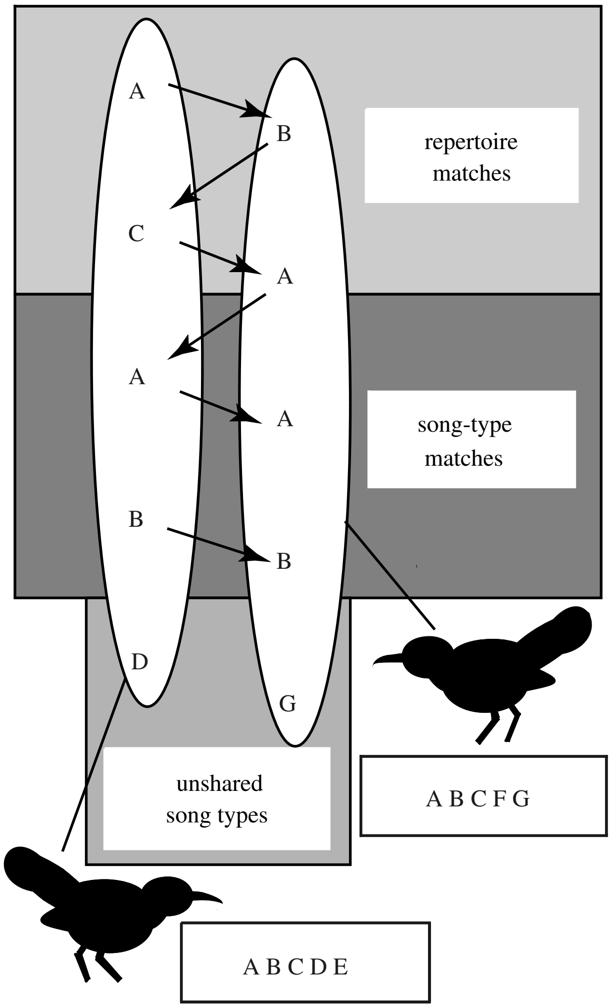

Figure 2. An illustration of the three forms of song matching between two counter-singing neighbours that share some, but not all, of their song types. In a song-type match, a bird responds to its opponent's song with the same song type. In a repertoire match, birds sing song types shared with the opponent without type matching. One or both may sing an unshared song type, which prevents the opponent from type matching.

males between 7 June and 21 June 1999 (average repertoire size, mean ± s.e.m. = 22.5 ± 0.62 (range, 18–28) and average repertoire overlap, mean ± s.e.m. = 0.754 ± 0.014 (range, 0.648–0.955)). Three birds were tested in both years. Two of these three birds heard different neighbours' songs each year.

(b) *Matching experiment*

The aggression-maintaining treatment consisted of matching the focal bird's song types from both the first 'invading' speaker and the second 'retreating' speaker (match/match). For 1 min, we song-type matched the focal male when possible. Because we attempted to maintain a constant playback rate, the focal bird would sometimes sing two songs before we could respond. If the focal bird used two different types, we matched the more recently sung type. If the focal bird did not respond with a song within 12 s, we continued playback by repeating the same song type. During the second half of the playback, we continued to song-type match the focal bird from the 'retreating' speaker. The de-escalating treatment consisted of match/non-match. For the first minute of playback, we type-matched the focal bird from the 'invading' speaker as in the first part of the match/match treatment, and in the second half we played repertoire-matching (shared) song types.

For the matching experiment, it was necessary to precede each trial with a lure playback period to induce the focal bird to approach and sing (so that we could match him). We played three shared song types in an alternating (ABABCABABC...) pattern from the 'invading' speaker. The playback treatment did not begin until the focal bird was within 20 m of the speaker and had begun counter-singing with the lure playback. If the focal bird did not meet these requirements within 180 s, we paused playback for either 1 min or until he approached or sang. This process was repeated until the conditions were met. If a focal bird failed to respond to the lure within 400 s, we abandoned playback and returned at a later date.

Five focal males were tested between 15 and 26 September 1998 (average repertoire size, mean ± s.e.m. = 24.0 ± 0.667 (range, 21–27)). We tested 14 males between 7 and 24 July 1999 (average repertoire size, mean ± s.e.m. = 22.7 ± 0.561 (range, 18–28)). The average length of the lure period was mean ± s.e.m. = 126.81 ± 4.41 s (range, 20–376 s). In 30 out of the 38 trials, focal birds responded within the initial 180 s lure period. Three birds were tested in both years, two with different neighbours.

(c) *Statistical analyses*

Since birds tended either to approach the second speaker quickly or not approach at all, the latency-to-approach response variable was bimodally distributed. We used the PROC MIXED module of SAS (1997; v. 6.12, SAS Institute, Inc.) to quantify the significance of the treatment effects on approach behaviour because of its model design flexibility and its diagnostics for model fit and error distribution. Playback treatment was entered as a fixed effect. The covariates and potential confounding variables that were initially considered included bird-ID, playback set (birds tested twice were considered as independent samples), year, time of day, Julian day, switching rate of playback (matching experiment only) and lure length (matching experiment only). The nominal variables bird-ID, playback set and year were entered as random effects. These variables, and relevant interaction effects, were removed from the model if they had p values of greater than 0.2. We report the final analysis of variance (ANOVA) model that met the conditions of a positive definite estimated G matrix and roughly normally distributed residuals, and gave the best fit (lowest Akaike's information criterion) with the fewest variables.

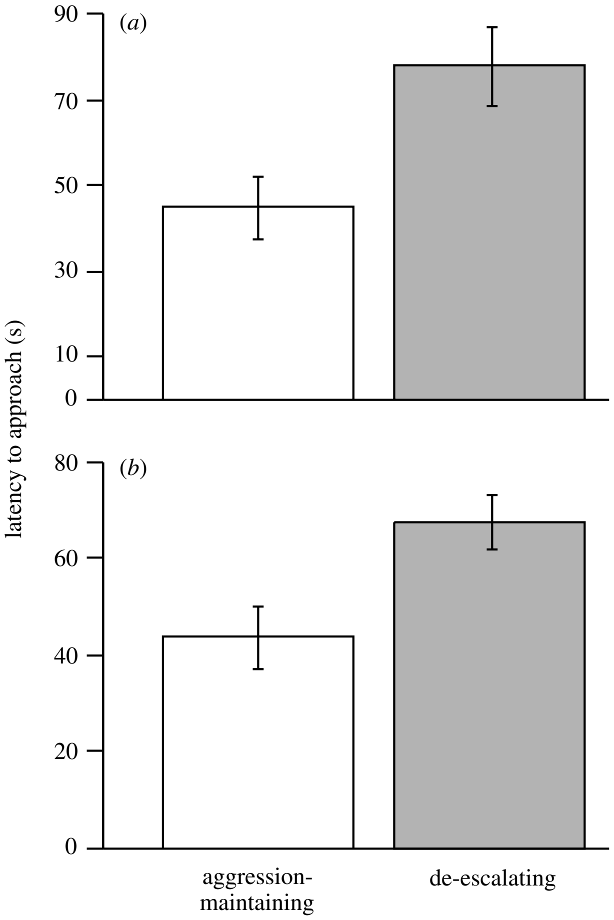

Figure 3. Approach responses (± s.e.m.) to the 'retreating' speaker for cheater (aggression-maintaining) versus honest (de-escalating) playback treatments, (*a*) song-sharing experiment, where the cheater treatment continues to sing shared song types while retreating and the honest treatment switches to unshared song types, and (*b*) matching experiment, where the cheater treatment continues to song-type match while retreating and the honest treatment switches to repertoire matching. Focal birds approached the cheater treatment faster in both experiments.

3. RESULTS

Figure 3*a* shows the approach responses of focal birds in the song-sharing experiment. Birds were much more likely to approach the 'retreating' speaker when it was playing shared song types (aggression-maintaining treatment) than when it was playing unshared song types (de-escalating treatment). The playback treatment effect was very significant ($F_{1,20} = 12.98$, $p = 0.002$). The final model also included playback set ($F_{20,20} = 2.55$, $p = 0.021$), indicating that individual birds differed in the magnitude of their responses and also varied when tested in different years. For bird-ID, year, time of day and Julian day, $p > 0.2$, and they were dropped from the analysis. All the dropped covariates combined accounted for less than 3% of the variation in responses.

Similar results were obtained for the matching experiment (figure 3*b*). Birds were much more likely to approach the 'retreating' speaker when it continued to type match (aggression-maintaining treatment) than when it shifted to non-matching while retreating (de-escalating treatment). The final ANOVA model was similar to the one in the shared experiment, with a significant effect of playback treatment ($F_{1,18} = 12.98$, $p = 0.004$) and a nearly significant effect of playback set ($F_{18,18} = 2.00$, $p = 0.074$). For bird-ID, year, time of day, Julian day, switching rate of playback and lure length, $p > 0.2$, and they were dropped from the analysis. All the dropped covariates combined accounted for less than 4% of the variation in responses.

4. DISCUSSION

The results support our hypotheses that shared song types were considered more aggressive than unshared song types and that matching song types were considered more aggressive than non-matching song types. Furthermore, these signals fit the definition of conventional signals: aggressive and submissive signals are arbitrary in form, there are no differential production costs between the signals, and costs are incurred through receiver retaliation against aggressive signallers, particularly bluffers (Maynard Smith & Harper 1988; Hurd & Enquist 1998).

Generally, all of a male's song types are shared with at least one of his neighbours, although we occasionally found banded wrens with song types not shared by any other study male. Consequently, any song that is used as an unshared song type when interacting with one neighbour can be used as a shared song type when interacting with a different neighbour. This indicates both that there are no differential production costs for alternative signals, and that signal form is arbitrary. In this experiment, we further avoided any effects of production cost by pairing shared and unshared song stimuli by length. It was not possible to control for playback-song length in the matching experiment, because the focal birds' song choices dictated which song types were played back. However, matching song types are always shared, and could be used as non-matching song types with no difference in production cost.

Cheaters could easily exploit acoustic conventional signals, as their production costs are low relative to other aggressive signals (Maynard Smith 1982; Zahavi 1993). Acoustic signals, after all, are ephemeral and can be changed almost instantaneously. However, like most visual conventional signals studied, these acoustic conventional signals do carry differential costs in terms of receiver retaliation: strong signallers are tested, which allows for the detection and punishment of cheaters. In our experiments, focal males quickly approached retreating 'opponents' that continued to signal aggressively. These simulated opponents were, in essence, 'cheating' by sending signals that did not correspond to their actual intentions or actions. In real interactions, a retaliator's approach would put a similarly 'cheating' signaller at increased risk of attack. Even our simulated 'honest' de-escalating signallers were sometimes approached, although focal birds tended to wait longer before approaching them. This may reflect the fact that in natural interactions the losing banded wren often stops singing entirely and retreats to a more central area in his territory before singing again. In contrast, our 'honest' signaller appropriately signalled de-escalation while retreating, but by maintaining the interaction, rather than withdrawing entirely, still risked retaliation by the focal bird.

The experimental method, using a two-speaker design, was critical in determining how banded wrens treat these two kinds of signals, and in demonstrating how receiver behaviour serves to punish bluffing signallers. Playback from within territorial boundaries almost invariably triggers a rapid approach and vigorous attack from territory owners, which hinders the detection of differences in reaction to different playback stimuli (Molles 1999). Playback experiments performed at territorial boundaries may run into the opposite problem: focal birds may not exhibit strong approach responses to such a low-level threat. A series of playbacks similar to the matching experiment discussed here, but conducted entirely from one boundary position, found that changes in playback song alone did not affect males' relatively weak approach responses (Molles 1999). Weak approach responses further limit the opportunity to discern differential responses in habitats where poor visibility makes it impossible to follow bird movements far from the experimenter. In our experiment, we began with a simulated invasion that provoked a strong response and brought the bird within visual range so that we could accurately track his subsequent movements. By then 'retreating' to the boundary, we not only simulated a more natural interaction, in which an invader backs down when challenged, but also set up a situation where the focal bird could show us, through his movements, how insolent he considered his opponent to be. We made the simulation even more relevant to focal birds by using songs only from an appropriate and familiar neighbour; the voice and songs they were responding to were those they would most expect to hear at that location, rather than those of an unfamiliar or displaced bird.

Recognition is a key factor in the sustainability of conventional signalling systems (Van Rhijn & Vodegel 1980; Silk *et al.* 2000). Individual recognition is thought to be standard among territorial songbirds (Stoddard 1996) and has been demonstrated in banded wrens (Molles & Vehrencamp 2001). In this and many other sedentary territorial species, neighbours interact frequently throughout a breeding season, or even throughout several successive breeding seasons. In such situations, cheating may be costly; with frequent testing, cheaters will be quickly detected and punished. The cheater cannot simply move on to new, naive opponents without giving up a very valuable resource: his territory. The recognition and reliability of signals also help neighbours to avoid unnecessary escalation, an important benefit of long-term associations.

However, even long-term associations are not static. Changes in competitor condition, motivation and intention will inevitably occur over time. Frequent testing of signallers allows birds to detect such changes when they occur. For example, banded-wren territory boundaries can shift throughout the year. Males often expand their boundaries when new nest sites lie near territory borders; if the boundary is shared with a neighbour then rates of counter-singing and aggressive encounters increase (P. A. Trillo, J. M. Burt and S. L. Vehrencamp, unpublished data). The neighbour with the expanding boundary should be highly motivated to defend this area, and this should be reflected in his increased willingness to send aggressive signals and to hold his ground when tested by the border-sharing opponent.

Auditory conventional signals are ideal for conveying the short-term information relevant to such interactions. In repeated interactions with known opponents, communication of motivation, intention and immediate condition is crucial. These functions contrast sharply with those of long-lasting conventional signals such as colour badges. Such relatively permanent signals code for more temporally stable 'quality' characters such as strength, body size or a general tendency towards aggression (Vehrencamp 2000) and serve to signal individuals' social status in social groups (Rohwer 1975; Fugle *et al.* 1984). The need to communicate fine and short-term variations in motivation and intention may have shaped the inexpensive but complex auditory conventional signals of banded wrens.

Game theory predicts that conventional signalling will only be sustainable when conflicts arise over relatively low-value resources; when resource value is great, higher-cost signals will be required (Maynard Smith & Harper 1988; Pärt & Qvarnström 1997; Enquist *et al.* 1998; Hurd & Enquist 1998). In any single conflict between neighbouring banded wrens, the resource in question is no more than a few metres of land, a very small portion of a territory. However, the interactions are still critical and subject to escalation. In part, this may indicate costly long-term consequences of ceding territory. Allowing a neighbour to annex territory unchallenged may invite further incursions. An owner may suffer losses on other boundaries if he spends too much time in conflicts with one particular neighbour. Additionally, the value of a small portion of territory can change during a breeding season, for example when nest sites change. Banded wrens' conventional signals appear to remain reliable even when the value of the contested area is high. Whether these conflicts over high-value resources involve more complex signalling, or more frequent escalation to costlier physical tactics, remains to be seen.

Acoustic conventional signalling may be much more common than suspected, particularly among territorial birds with long tenure. In such species, individual recognition and repeated interactions will limit the effectiveness of cheaters and allow low-cost signals to remain reliable and informative. Uncovering their use, as we have found, requires careful experimental design that is mindful of the structure of natural interactions between neighbours. Fortunately, advances in playback equipment and interactive techniques are making such designs both more practical and more sensitive. Armed with these tools, we may discover increasingly complex signalling strategies among birds.

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