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Original Article

Negotiation of territorial boundaries in a songbird

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How do territorial neighbors resolve the location of their boundaries? We addressed this question by testing the predictions of 2 nonexclusive game theoretical models for competitive signaling: the sequential assessment game and the territorial bargaining game. Our study species, the banded wren, is a neotropical nonmigratory songbird living in densely packed territorial neighborhoods. The males possess repertoires of approximately 25 song types that are largely shared between neighbors and sequentially delivered with variable switching rates. Over 3 days, boundary disputes among pairs of neighboring males were synchronously recorded, their perch positions were marked, and their behavioral interactions were noted. For each countersinging interaction between 2 focal males, we quantified approach and retreat order, a variety of song and call patterns, closest approach distance, distance from the territorial center, and female presence. Aggressors produced more rattle-buzz songs during the approaching phase of interactions, whereas defenders overlapped their opponent's songs. During the close phase of the interaction, both males matched frequently, but the key determinant of which one retreated first was song-type diversity—first retreaters sang with a higher diversity. Retreaters also produced more unshared song types during the interaction, and in the retreating phase of the interaction, they overlapped more. A negative correlation between song-type diversity asymmetry and contest duration suggested sequential assessment of motivational asymmetry. The use of this graded signal, which varied with distance from the center and indicated a male's motivation to defend a particular position, supported the bargaining model. The bargaining game could be viewed as a series of sequential assessment contests.

Key words: **countersinging contest, motivation signal, sequential assessment, song-type use, territorial bargaining game, *Thryophilus pleurostictus*.**

INTRODUCTION

There is considerable interest in how territorial birds resolve boundary conflicts. Several decades of playback studies have identified putative threat signals encoded in singing behaviors (reviewed in Searcy and Beecher 2009; Bradbury and Vehrencamp 2011). These signals are believed to convey information about variable levels of aggressive motivation (Waas 1991; Burt et al. 2001; Beecher and Campbell 2005; Ręk et al. 2011). However, there is an inherent problem associated with interpreting relative approach responses by a territorial owner to the playback of 2 alternative stimuli: Is the stimulus most closely approached by the owner the one that is most challenging to it, or is the reverse the case, is it avoiding the other more intimidating challenge (Searcy and Nowicki 2000; Collins 2004)? This has been argued in both ways. One solution is to examine both the owner's response as a receiver and its subsequent signals and behaviors (the so-called receiver and sender perspectives) (Vehrencamp et al. 2007; Searcy and Beecher 2009). Particularly insightful are playback studies that proceed in stages, first challenging a male with a playback stimulus, examining how he sings and responds, and then revealing a taxidermic bird to determine whether the owner attacks and whether any singing behaviors preceded this attack (Searcy et al. 2006; Ballentine et al. 2008; Hof and Hazlett 2010; Akçay et al. 2011). Notable studies of 3 songbird species have developed hypothetical escalation rules and undertaken multistage playback treatments to test this hierarchical view of contest structure (great tit *Parus major*: Langemann et al. 2000; song sparrow *Melospiza melodia*: Akçay et al. 2013; black-throated blue warbler *Setophaga caerulenscens*: Hof and Podos 2013).

Several game theoretical models of conflict resolution have been developed to understand the diversity of fighting styles in animals and the functions of different contest structures and agonistic

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behaviors. These models are based on different assumptions about how the information acquired during a contest induces the loser to give up before it is fatally injured (Arnott and Elwood 2009; Briffa and Elwood 2009). There are 2 general classes of such models. In self-assessment models, there is no exchange of information between the contestants per se; rather, each individual assesses its own resource-holding power and makes the decision to give up when the accumulated costs of persisting cross its individual cost threshold (Mesterton-Gibbons et al. 1996; Payne and Pagel 1996; Payne 1998). In mutual assessment models, both contestants display agonistic behaviors that provide reliable information to the opponent and enable them to assess their relative fighting ability or motivation; the individual perceiving itself to be the weaker or less motivated contestant concedes the resource without incurring the cost of an injurious fight (Briffa and Elwood 2009). Because singing in birds is not energetically costly (Ward et al. 2004; Ward and Slater 2005), and songbirds rarely engage in extended physical fights, none of the self-assessment models provide good fits to observed songbird contests. In contrast, several mutual assessment models do seem applicable to countersinging songbirds.

There are 2 mutual assessment models that, at least theoretically, seem the best fits to avian countersinging. The first, the sequential assessment model, assumes that the contestants know little about the opponent's fighting ability and/or motivation (the latter assumed to be a function of resource valuation) at the beginning of the contest, but acquire increasingly more accurate estimates of this information with the repetitive performance of agonistic signals (Enquist and Leimar 1983, 1987; Leimar and Enquist 1984). Fighting ability and motivation are assumed to be uncorrelated and revealed with different signals, most likely physically constrained index signals linked to fighting ability and variably risky threat signals indicating aggressive intentions, respectively. The model also assumes that assessment of both types of signals is associated with perceptual error. Contests typically proceed in phases, with early phases characterized by less costly or risky signals and then escalating to phases with more costly or risky signals if the cheaper signals cannot resolve the initial uncertainties. This model predicts that contest duration and level of escalation should be negatively correlated with the asymmetry in true fighting ability and motivation between the contestants. Duration and escalation level should also be more variable between more evenly matched contestants, because contestants make more giving-up decision mistakes when the differences in fighting ability and motivation are small relative to assessment error (Enquist and Leimar 1983).

A key assumption in this model is that the states that the 2 opponents are attempting to assess in each other are fixed throughout the contest. For this reason, the model is usually applied to contests in which intrinsic fighting ability, body size, hunger level, or some other static property is the unknown trait which contestants try to assess. Territorial neighbors probably know each other's fighting ability and are fairly evenly matched for this trait. However, there are likely many situations in which general motivation levels may be unknown at the outset but fixed during a contest. For example, a territorial owner whose main nesting site was just depredated might become desperate to acquire a new one by carving out a piece of a neighbor's territory. At least during the ensuing contest with that neighbor, both parties enter and leave the contest with fixed motivations: one to gain a bit of territory and the other to prevent losing it. Where motivations can change over medium time frames but remain fixed during a contest, and fighting abilities are known and similar, the sequential assessment model predicts that motivational asymmetry will be the primary determinant of contest dynamics (Enquist and Leimar 1987).

Whereas the first model treats territorial contests as progressive assessments of fixed quantities, Maynard Smith (1982) proposed an alternative model based on bargaining between neighbors over territorial boundaries. In this model, each owner controls a core area that is the minimum required for breeding. Between the core areas of 2 neighbors is a disputed zone whose acquisition would enhance the fitness of either one. Maynard Smith assumed that the value of a boundary at each location between the centers of the 2 neighbors is high and flat inside the core and then declines linearly with an increasing distance from the core edge (Figure 1). He also assumed that the owners possessed a graded signal of motivation that could reflect their valuation of a boundary location. He then asked what conditions would make honest signaling of motivations evolutionarily stable, and what the negotiated boundary would be. The answer to the first question was that: 1) the valuation lines of the 2 owners must extend into each other's core areas, or else there is not enough to lose by always signaling high motivation; 2) there must be significant escalation (fighting) costs if negotiation with signals breaks down; and 3) the escalation costs must be sufficiently large relative to the difference in fitness from holding the core area and having to leave to breed elsewhere. Bargaining was also only favored when both parties were uncertain about the motivation of the other at various locations in the disputed zone. If the conditions noted above were met, the evolutionarily stable strategy (ESS) was to signal motivation honestly and, to answer the second question, the negotiated boundary was that location at which valuations for the 2 parties were equal (downward arrow on the graph). In Figure 1, the slopes of the lines are equal, so a negotiated boundary would divide the disputed zone equally. However, the slopes need

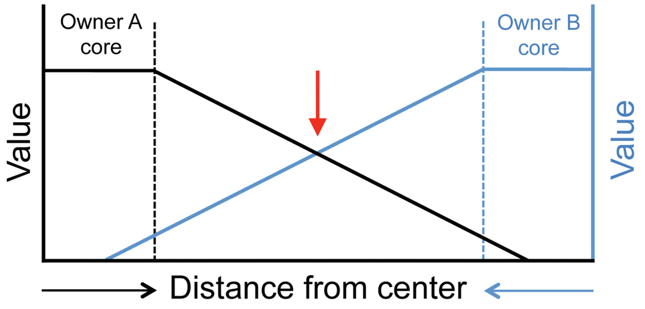

Figure 1
Graphical rendition of the territorial bargaining game as outlined by Maynard Smith (1982). In a 1D habitat, 2 adjacent individuals have territorial centers or nest sites located on the left (black) and right (gray) sides. Each territorial owner requires a core area, denoted by dashed lines, to obtain any fitness. Fitness increases incrementally with increasing distance from the core edge up to a point, beyond which there is no further benefit. The owners can each display a graded signal, indicating their valuation of a boundary location at different distances from the core. An honest signaler displays at the maximum level within its core, and beyond the core displays at a level corresponding to the importance of the place, that is, decreasing in intensity with an increasing distance from the edge of his core area. Two honest strategists compare their display levels at the same position, and if the opponent displays at a lower level, the focal animal advances, whereas if the opponent displays at a higher level, he retreats. The two then agree on a boundary at the point (downward arrow) where their display levels are the same, meaning that their motivations are equal. If the regions of interest do not extend into the opponent's core area, for example, because the territorial centers are farther apart, a mixed ESS of Hawk and Bluffer occurs.

not be the same, in which case the owner with the shallowest slope would obtain the larger share at the ESS. When the honest signaling conditions are not met, for example, if the territorial centers are farther apart so that valuation lines do not extend into the neighbor's core area, the ESS was either 1) a situation in which both parties signaled at maximal levels regardless of the location being contested and escalated to fighting if the opponent did not retreat (all Hawk), or 2) a stable mixture of Hawks and Bluffers, who signaled at maximal intensity but if faced with a Hawk in the contested zone, always retreated. We are not aware of any tests related to this model, although several authors have discussed it (Parker 1985; Adams 2001; Pereira et al. 2003).

Here, we describe the structure of territorial countersinging interactions in freely interacting banded wrens, *Thryophilus pleurostictus*. However, in contrast to the playback studies of songbirds mentioned earlier, our specific goal was to test the applicability of the 2 nonexclusive mutual assessment models outlined above in explaining the dynamics of natural contests between wild territorial owners. To our knowledge, this has not been previously attempted for any songbird. Banded wren males have repertoires of 16–28 song types, an average of 75% song-type sharing between neighbors, and their typical song-type delivery mode is immediate variety singing although they sometimes repeat the same type from 2 to many times (Molles and Vehrencamp 1999). Thus, their countersinging interactions potentially involve several additional strategic signaling options that are not available to repeat mode singers like great tits, song sparrows, and black-throated blue warblers, such as immediate and delayed matching rate, variable song-type switching rate, and variable short-term song-type diversity. Like many other songbird species, banded wrens also signal strategically with song overlapping, use of unshared types, and selection of song types with different key syllable components. Several banded wren countersinging interactions have been illustrated in previous publications (Molles and Vehrencamp 2001; Molles 2006), and playback studies have made some progress in identifying the aggressive function of song-type matching and low switching rate, as well as the likely defensive use of song overlapping (Molles and Vehrencamp 2001; Hall et al. 2006; Molles 2006; Vehrencamp et al. 2007). In addition, certain song types with distinctive acoustic features tend to be preferentially used in different contexts, such as rattle-buzz song types with J-note trills during dawn chorus, longer and broadband song types during boundary interactions, and song types with chevron-shaped trill notes in the presence of female mates (Trillo and Vehrencamp 2005). Some examples of banded wren song types are shown in Supplementary Figure S1.

In pursuit of our goal, we simultaneously followed and recorded pairs of neighboring territorial males and identified interaction events in which one or both birds approached their common boundary while singing. Our study had 3 specific aims: 1) to specify the signaling rules for escalating and de-escalating aggressive encounters, 2) to test the predictions of the sequential assessment model when applied to individual song contests, and 3) to test the predictions of the territorial bargaining model by incorporating locational variables and mixtures of signals as graded indicators of motivation in song contests.

METHODS

Study site and subjects

The banded wren is a sedentary, territorial songbird that inhabits Pacific coast lowland dry forests from central Mexico to northern Costa Rica (Molles and Vehrencamp 1999). This study was conducted in Santa Rosa National Park, a sector of the Area de Conservación Guanacaste in northwestern Costa Rica (10°51′N, 85°38′W). The study site is primarily composed of tropical deciduous forest with areas of regenerating secondary growth (Trillo and Vehrencamp 2005). The breeding season for banded wrens encompasses the first half of the rainy season, approximately April to August, but breeding pairs remain on their all-purpose territories year-round. Males sing more than females and are the primary singers during the dawn chorus and territorial interactions (Molles and Vehrencamp 1999). Because annual survival is high and males rarely move to a different territory, they have at least some of the same neighbors for many years (Hall et al. 2009). Nevertheless, at any point in the breeding season, young males may insert themselves into small unoccupied areas and, subsequently, attempt to expand their boundaries. Males initiate nests and undertake most of the construction. Extrapair paternity is very low in this species (Cramer et al. 2011). Because yearling males do not settle close to their natal territory, their neighbors are unlikely to be kin (unpublished observations).

We recorded a total of 14 adjacent territorial male dyads between 19 May and 26 July 2008. Two birds were recorded twice with different neighbors, thus 26 individual males were observed. Eight of these males were captured and color-banded before this study. Because we needed to act quickly after identifying a dyad of interacting males and did not want to handle and disrupt them before recording, we did not color-band any additional unmarked birds, relying instead on continuous following of males moving around their territories and final verification of male identity using individually distinctive features of their recorded song types. One of the focal males was unpaired, another was courting a visiting female during the recording period, and the rest were paired and in different stages of breeding, including nest building, laying, incubating, and provisioning nestlings or fledglings.

Recording strategy

Although array recording of an entire territorial neighborhood would have been a preferable strategy (see Fitzsimmons et al. 2008; Foote et al. 2008), this method was not feasible in our tropical study area, so we opted for synchronous focal recording of adjacent dyads of male wrens. The field crew consisted of 4 observers who monitored each neighbor in teams of two. We aimed at recording each dyad for 3 consecutive days and approximately 5 h per day from 05:00 h (before dawn chorus) until 10:00 h. There was a 1- or 2-day break in the sequence for 4 dyads due to poor weather. Occasional gaps occurred during recording sessions as a consequence of rainfall, problems with the recording equipment, and brief observer breaks. Two of the focal dyads were recorded for only 2 days due to a dearth of interactions. We monitored the 14 dyads in serial order using the following protocol.

The first day of each dyad cycle was allotted to scouting for new pairs of adjacent territorial neighbors engaged in boundary disputes. Before recording a new dyad, numbered plastic flagging was tied to vegetation to demark the 2 males' territories and preliminary singing perches. Within each focal bird team, one individual was assigned flagging and the other was assigned recording. The 4 team members worked together to keep track of all movements and activities of the 2 focal birds. The focal birds were followed as closely as possible with binoculars, disturbing them as little as possible. The flagger marked the location of each new singing perch with a numbered flag immediately after the bird flew away from it. The bird was considered to be at a previously flagged perch if he was within a 5-m radius of a flag. The flagger also kept written notes of the times of perch changes, as well as the bird's activities, presence of female and young, nest locations, and interactions with neighbors. If the observers lost visual contact with the bird and were not able to precisely localize a song, a record of "near" was noted if the observers were able to identify a flag within 15 m. If they were unable to do so, "no location" was noted for the song and time period.

The recordist recorded all of their focal bird's vocalizations using a Sennheiser ME67 shotgun microphone with a foam windscreen and Marantz PMD690 digital solid-state recorder at a sampling rate of 48 kHz and 16 bits per sample. To facilitate the recognition of their focal bird's songs on the recordings and reduce confusion of bird identification in future analyses, each recordist used a dog-training clicker to audibly mark the termination of their focal bird's songs; one recordist employed a single click, and the other employed a double click. The 2 recordists also carried portable walkie-talkie radios to communicate with each other. At the onset of each morning's session, and each time one team needed to change its recording unit's batteries or memory card and restart recording, the time was announced over the radio into both microphones to synchronize the simultaneous recordings. Periodic radio contact also allowed team members to be aware when one focal bird was near the territorial border with the other.

After completing the recording sessions on a dyad, we measured the GPS coordinates of all perch flag locations with Garmin Etrex GPS Navigators. To minimize errors, 20 waypoints were collected and subsequently averaged for each flag location. Flag coordinates were uploaded to Excel in UTM format using the program G7ToWin© (1997–2013) and integrated with transcribed field notes identifying bird, date, time, flag number, and bird activity using a custom MATLAB® (2009) script. Supplementary Figure S2 shows a map of the study area with flag locations for all focal birds. Territories mapped in this way were roughly circular or elliptical with longest axes averaging 108 m (range: 56–148 m, $n = 28$). Our field methods were approved by Cornell University's animal care and use committee (protocol 98-81-07).

Sound processing

Sound files in WAVE format were analyzed with XBAT-R5©, a MATLAB-based sound visualization and processing application (XBAT 2012). We used the following spectrogram settings: FFT size = 512, window size = 1.0, window type = Hanning, overlap = 75%, giving a frequency resolution of 92.6 Hz and a temporal resolution of 2.6 ms. Two sound files can be simultaneously opened in XBAT and scaled to the same size for simultaneous viewing. We synchronized simultaneous recordings to the nearest 10 ms by expanding the time scales, measuring the time difference of a clear voiced synchronization announcement sound on the 2 recordings, and adjusting the start time of one of the recordings accordingly. Good quality exemplars of each song type in the birds' repertoires were extracted to a separate file for repertoire analysis. We classified song types based on our long-term database of banded wren songs, and labeled them by singer, song-type number, and trill type. We used the spectral cross-correlation-based template detector feature of XBAT to create templates of each song type and ran a detection scan on each sound file using a similarity threshold value of 0.35–0.40 depending on template quality. This routine draws an event box around each detected song labeled by song type. After the scan, 2 or more project members performed a visual check on the recording to correct XBAT detection errors, look for missing or mislabeled songs, and reframe the event boxes to the precise beginning and ending of each song. We integrated data on songs and locations and computed the following variables for each male with regard to his neighbor: type and start/end time of each song, song length, complete or incomplete song, shared or unshared song type, song-type switching rate over the previous 5 songs, song-type diversity over the previous 5 songs, cases of whole and partial immediate matching, delayed matching within 90 s, percentage of neighbor's songs overlapped, and current distance between the males.

We limited the subsequent analyses to those interactions between the 2 focal males in which there was clear countersinging (several alternating songs between 2 males) when noted by the recording teams in the field notes, instances of frequent type matching, and/or one or both birds approached their common boundary. We omitted interactions with very little singing and those with conspicuous interference by a third neighbor. To precisely demarcate interaction events, we generated a continuous plot of distance between the 2 birds throughout each day's recording. The beginning and ending times of a trough on this plot specify the During phase of an interaction. An example of such a plot with several interactions can be viewed in Supplementary Figure S3. We then defined the 5-min intervals before and after the During phase as the Pre and Post phases, respectively. The male that first initiated an approach to the boundary was designated as the instigator (I) and the other male was designated as the responder (R) if he subsequently approached, or the nonapproacher (N) if he never approached. Similarly, the first bird to retreat always terminated the During phase and was designated as the withdrawer (W) and the other male was designated as the persister (P) if he approached and held his position longer, or the nonapproacher (N) if he never approached.

Each interaction was consecutively numbered and designated as a categorical interaction number variable. A final custom MATLAB script computed the following signal variables for each male in the Pre, During, and Post phases of each interaction: song rate, mean song length, presence of unshared song types, switching rate (number of switches/number of songs − 1), song-type diversity (computed as ln types/ln songs to remove dependency on number of songs), percentage of immediate and delayed matches (including partial and trill matches), overlapping (percentage of the focal bird's songs that started before the neighbor's song had ended), percentage of incomplete songs (lacking the trill), and percentage of rattle-buzz songs. Because we could not compute meaningful values for switching rate and song-type diversity unless a bird sang at least 3 songs in a given phase, we scored cases of fewer than 3 songs as missing data for these variables. Although switching rate and song-type diversity are very strongly correlated ($r = 0.605$, $n = 210$, $P < 0.0001$), males can vary them independently to some extent (e.g., a low diversity can be achieved with a high switching rate by alternating between 2 song types), and playback experiments suggested that they could have different functions (Molles 2006), so we retained them as separate variables.

Males also perform a graded series of noisy agitation and aggressive calls which we refer to as "grunting". We scored the complexity of grunting based on the number of different call types (ranked from level 0 [none] to level 5 [highest], see Supplementary Figure S4 for examples). Males grunt at low levels when nest building, when interacting with their mates, and when a human comes too close, but higher levels of grunting are only associated with close male–male interactions.

Contextual variables for each interaction included time of day, presence of the female (visual or auditory detection by the observers within approximately 10 m), mean approach distance between the males in the During phase, and escalation level categorized as countersinging (birds only sang), grunting (one or both birds grunted at level 2 or higher in the During phase), or fighting (typically one or more chases accompanied by scolding calls). The final interaction data set contained 214 valid interaction events (both birds sang a minimum of 3 songs, and there was no third neighbor interference), with a separate row of data for each male (428 total observations).

Quantifying contest structure and escalation/de-escalation rules

For animals that perform discrete agonistic signals and behavioral tactics, the contest structure for dyadic interactions is traditionally assessed using a sequential analysis to compute transition probabilities between behavioral acts (Waas 1991; Egge et al. 2011). When agonistic signals are graded, alternative statistical analyses must be used. We began with a descriptive analysis of the changes in mean signal values for all males across the Pre, During, and Post phases for the 3 categories of escalation using 2-way Anovas. Each signal variable was examined separately as the dependent variable; phase, escalation level, and phase × escalation level interaction terms were included as fixed independent variables; and birdID was included as a random variable to control for multiple measurements on the same males.

To determine which signals were associated with escalation and de-escalation, we used stepwise ordinal logistic regression analyses to identify those song variables most closely associated with being an instigator, responder, or nonapproacher in the Pre and During phases, and with being a withdrawer or persister in the During and Post phases. For these analyses, the bird's status served as the dependent variable, and the set of song variables, grunting level, female presence, time of day, and dyadID were entered as independent variables. We first ran stepwise analyses using forward and backward selection with generous *P*-to-enter and -leave levels (0.25) to narrow down the key variables (dyadID dummy variables were forced into the models before running the stepwise search). We then examined a subset of alternative models involving the key variables. All these models contained the categorical variable dyadID to control for dyad differences, as well as the categorical interaction number nested within dyadID to force a comparison of the relative differences in signal values between the 2 males within each interaction. We selected the model with the lowest AICc score. In a few cases, we chose an alternative model with a slightly higher AICc score if an added variable was significant and made good biological sense, as recommended by Anderson (2008). The final results are summarized in tables that give the significance (likelihood-ratio L-R χ^2) and direction of correlation for each independent variable in the final model.

We noticed that contest instigators were sometimes the first to retreat (withdrawers) and sometimes the second to retreat (persisters). We, therefore, explored the combined effects of approach status and retreat status on signaling behaviors in the During phase using 2-way factorial Anovas. Each song variable served as the dependent variable in separate analyses; approach status, retreat status, and approach × retreat interaction terms were included as fixed independent variables; and dyadID was included as a random variable to control for multiple measurements on the same dyads. This data set included only those interactions in which both birds approached and retreated; individual males that sang fewer than 3 songs were also omitted (final n = 188). We were particularly focused on the signaling behaviors that showed a strong interaction term, which would indicate different signaling tactics for initiators that merely tested the boundary and then retreated compared with initiators that followed through with a more aggressive stance.

In all dyads, both males initiated interactions at least some of the time, but in most dyads, one male was substantially more often the instigator and appeared to be expanding his territory into the area occupied by the neighbor. To explore the general signaling consequences of this general asymmetry in aggressive motivation, we assigned either the aggressor role (A) or the defender role (D) to each male within a dyad. This assignment was based primarily on the percentage of interactions in which the male was the instigator versus responder, and in dyads with more similar instigator rates, we included our knowledge of territory sizes, boundary shifts, and nest site locations to assign these roles. We then conducted a series of stepwise logistic regression analyses with this overall aggressive status as the dependent variable, and the Pre, During, or Post song variables plus dyadID and nested interaction number as independent variables, to identify any vocal behaviors associated with persistent aggressive tendencies.

Based on the significant relationships found in these analyses, we constructed a flow diagram of likely escalation and de-escalation rules for the banded wren following the recommended format of Searcy and Beecher (2009) and Hof and Podos (2013).

Testing predictions of the sequential assessment model

The main predictions of this model are that contest duration and escalation level should be negatively correlated with the asymmetry in motivation, and that the variation in contest duration and escalation level should be greater for contestants with a similar motivation. We do not have an independent measure of relative motivation for each contest, equivalent to relative hunger levels (or relative body size as a measure of relative fighting ability) used by other researchers in testing this model. However, as shown in previous studies (Molles 2006), and confirmed in our analysis of escalation rules here, a key signaling variable, short-term song-type diversity, is high when a contestant's aggressive motivation is low and it is low when motivation is high. For our model tests, we use this variable as a proxy for aggressive motivation. We thus computed the absolute difference between the During song-type diversities of each dyad in each interaction, and called this variable song-type diversity asymmetry. We then examined whether this independent motivational asymmetry variable predicted contest duration, approach distance, or escalation level (controlling for dyadID). We used the mean number of songs sung by the 2 males during the interaction (ln-transformed) as our measure of contest duration, because it more accurately reflected the amount of signaling during the contest; duration in time was deemed less accurate, because contests were sometimes interrupted by brief excursions, bouts of grunting, or chasing. For approach distance, we computed the mean distance between the birds in the During phase and took the reciprocal of this measure, raised to the power of 0.1 to normalize it, so that higher values represented greater proximity. We omitted interactions in which neither bird approached and those in which either bird sang fewer than 2 songs in the During phase. Evidence of a negative correlation between song-type diversity asymmetry and contest duration, proximity, or escalation level, and a greater variation in these contest outcomes when asymmetry is lower, would support the sequential assessment model.

Testing predictions of the bargaining model

The bargaining model predicts that the birds vary a key graded signal as a function of their distance from the center of the territory. As mentioned earlier, the results of our analysis of escalation rules identified a graded signal, song-type diversity, as a plausible measure of the motivation to defend the boundary. To determine whether this signal varies with distance from the territorial center, we constructed a large data set containing all of the songs sung in the Pre, During, and Post phases of all focal dyad interactions for all birds and days (n = 13,517). For each song delivered from a known flag position, we scored song type, start time, song-type diversity over the previous 8 songs, current distance between the birds, and distance of the bird from the center of his territory (the territory center was computed as the mean of all flag GPS locations). We omitted songs sung before 05:30 h (to remove the influence of high-diversity dawn chorusing), and we also omitted songs sung within a core area of 20 m from the center (to remove songs directed toward the female). We ran a standard ANCOVA with song-type diversity as the dependent variable and distance from the center, birdID, and the birdID × distance interaction terms as fixed independent variables. Because low song-type diversity indicates high motivation, a positive correlation between diversity and distance would support the bargaining model.

The bargaining model also predicts some differences in singing behavior between neighbors with overlapping territorial boundaries compared with neighbors with nonoverlapping boundaries. More distant neighbors are predicted to bluff, so the slope of their song-type diversity versus distance relationship should be flatter or negative compared with closer, honest-signaling neighbors. Therefore, we extracted the slopes of distance versus song-type diversity for each bird with each neighbor (beta coefficient estimates of the birdID × distance interaction term in the ANCOVA analysis earlier) and constructed a slope data set (n = 28). This data set also included percent instigator (percent interactions in which the focal bird was the instigator), the focal bird's breeding stage (Ct = courting, including nest building and laying; Inc = incubating; and Prov = provisioning nestlings or fledglings), and categorical territorial overlap between the 2 neighbors (Ov = overlapping flag polygons, Ab = abutting polygons, and Ga = gap of 15 m or more). With a multiple regression analysis, we tested whether percent instigator, breeding stage, and/or territorial overlap predicted the song-type diversity–distance slope.

Finally, if the bargaining model applies, neighbors that have resolved their boundary position should signal with fairly equal motivational intensity when they approach their joint boundary; that is, the asymmetry in song-type diversity during contests should be low, compared with neighbors that are interacting aggressively at different locations within the overlap zone to find the point of equal motivation. To test this prediction, we used the During phase asymmetry in song-type diversity from the sequential assessment analyses described in the previous section, ran a 1-way Anova analysis on diversity asymmetry versus categorical territorial overlap as defined earlier, and included dyadID as a random variable.

All statistical analyses were performed with JMP Pro 10.0.2 (JMP® 2012). We used P = 0.05 as our criterion for significance. Means ± SEM are reported in the text for simple comparisons, and least-squared means ± SE error bars are presented in the graphical results emerging from multivariate analyses.

Table 1

Mean contest During phase duration, approach distance, and percent of interactions in which the instigator (first approacher) was the first to withdraw, for contests of different levels of escalation

Escalation level	n	During duration (s)	Mean approach (m)	% instigator withdrawal
Countersing	116	179.0 ± 14.14	52.6 ± 1.72	0.837
Grunt	86	253.1 ± 16.42	46.8 ± 2.00	0.714
Fight	12	271.9 ± 43.95	15.5 ± 5.35	0.417

RESULTS

General characteristics of males, territories, and interactions

The 26 male subjects recorded during this study possessed a mean song-type repertoire size of 21.5 types (range: 16–28). On average, 44.1% of their song types contained a rattle and/or buzz (range: 33.3–55.6%). From 1 to 13 of their song types were not shared with their dyad partner (mean: 4.4 types), resulting in a mean sharing index of 0.791 (range: 0.634–0.9). Six of our dyads had overlapping territorial polygons, 4 had abutting territories, and 4 had territories separated by a significant gap; all of the escalated interactions with chases occurred between males with overlapping territories. A summary of male characteristics, territories, and interactions is provided in Supplementary Table S1.

We extracted 214 interactions from the 14 dyads (mean 15.3 interactions/dyad; range: 4–26). Table 1 summarizes the mean duration, approach distance, and instigator behavior of the interactions subdivided by escalation level. Approach distance and interaction duration were positively correlated (Pearson r = 0.152, P = 0.026, n = 214, R^2 = 0.023), but with a great deal of scatter. In 14 of the 214 interactions, neither bird approached the boundary; in 72 interactions, only 1 bird approached; and in the remaining 128 interactions, both birds made some movement toward the boundary. In the analyses that follow, we omitted the cases of zero approaching birds when comparing the behaviors of instigators versus responders and nonapproachers, because we could not specify the first approaching bird in these interactions. In analyses comparing withdrawers and persisters, we also omitted cases in which only 1 bird approached to focus on those interactions in which both birds approached and then retreated.

Contest structure and escalation/de-escalation rules

As the first step toward unraveling the escalation rules, we examined the changes in mean singing behaviors for all males across the 3 phases (Pre, During, and Post) for contests of different escalation levels (countersinging, grunting, and fighting) (Figure 2). A few relationships are worth noting. Switching rate and song-type diversity tended to increase across the phases for countersinging interactions, and to decrease across phases for grunting and fighting interactions. Matching rate nearly doubled in the During phase compared with the Pre phase. Delivery of rattle-buzz songs and unshared song types (not illustrated) was very low in the During phase of escalated interactions. Grunting complexity was, by definition, elevated in the During phase of grunting interactions and was especially high during fighting interactions.

Next, we asked whether interaction instigators differed from responders and nonapproachers in any singing behaviors, using

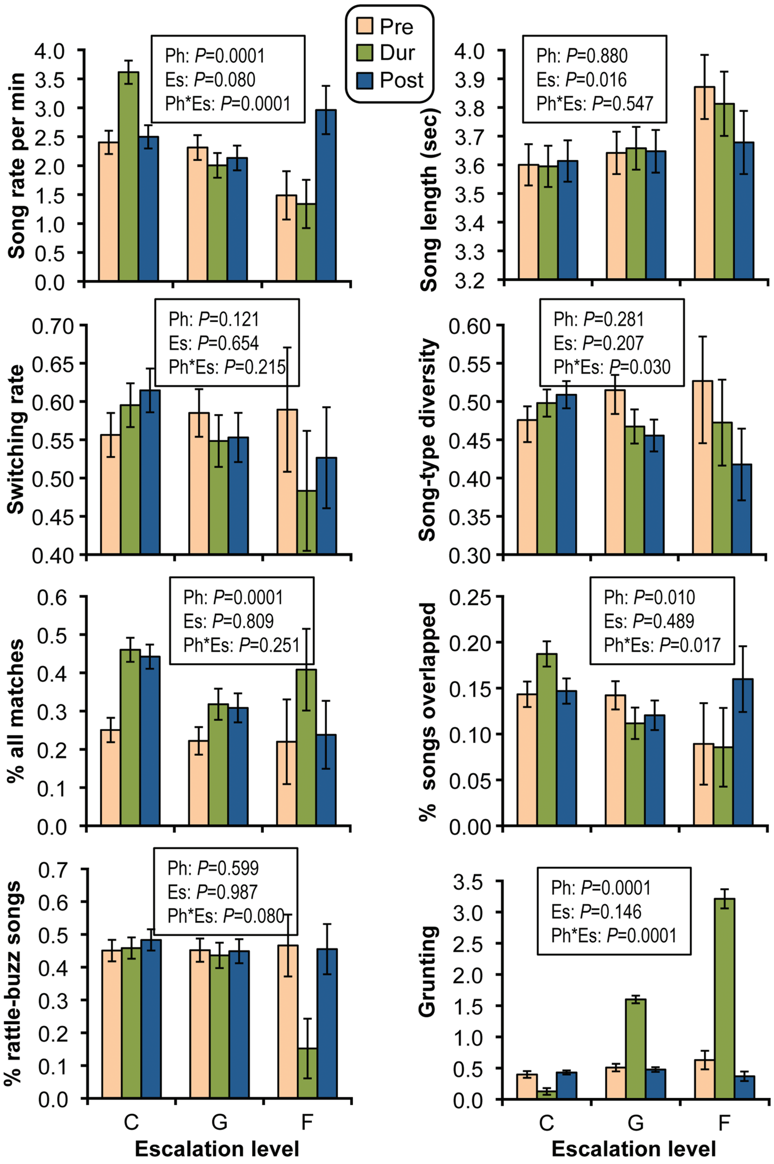

Figure 2

Relationship of singing behaviors to contest phase and escalation levels. Least-squares mean values of song variables for all males in the Pre, During, and Post phases for 3 categories of escalation: C = countersinging, G = grunting, F = fighting. Two-way factorial Anova models controlled for birdID (random). Error bars show ±SE. Observations with fewer than 3 songs for the phase are omitted. Boxes show *P* values for phase (Ph), escalation level (Es), and phase*escalation interaction (Ph*Es) terms.

stepwise analyses to identify song and context variables associated with approach order. For the Pre phase, we found that instigators gave a higher percentage of rattle-buzz types compared with responders and nonapproachers (47.2%, 41.0%, and 41.5%, respectively: Table 2A). Nonapproachers were more likely to have a female present. When the analysis was restricted to cases of both birds approaching, percentage of rattle-buzz songs was still significant and higher for instigators, and overlapping was significantly higher for responders (Table 2B). In the During phase, the percentage of rattle-buzz songs was significantly higher for both instigators and responders compared with nonapproachers (Table 2C). Restricting the analysis to both birds approaching, only the percentage of incomplete songs was significantly related to approach order (Table 2D), with instigators singing more incomplete songs.

We subsequently asked whether withdrawers and persisters differed in singing behavior, again using stepwise analyses to identify song and context variables associated with retreat order. In the During phase, we found that persisters sang with a significantly lower song-type diversity (Table 3A). Withdrawers, on the other hand, gave more unshared song types and more immediate matches. In the Post phase, the withdrawer was more likely to overlap his opponent than was the persister (Table 3B).

The instigator of an interaction was more likely to withdraw (i.e., leave first) than to persist, especially in nonescalated countersinging contests (Table 1). Therefore, we examined whether instigators that withdrew versus persisted sang differently (and likewise whether responders that withdrew versus persisted sang differently) using 2-way Anovas on each song variable. Results are summarized in Figure 3. Instigators that persisted sang with a particularly low

Table 2

Singing patterns associated with approach order (I = instigator, or first to approach; R = responder, or second to approach; N = never approached)

Source	df	L-R χ^2	*P*	Direction
A. Pre interaction singing and context variables that were correlated with approach order (I, R, N: dependent variables), controlling for dyadID and nested interaction number and omitting cases of 0 approaching birds and Pre number of songs < 3, n = 331				
Female present	1	5.249	0.0220	I < R < N
Percent rattle-buzz songs	1	17.707	<0.0001	I > R ≈ N
B. Pre interaction singing and context variables that were correlated with approach order (I, R: dependent variables), controlling for dyadID and nested interaction number and omitting cases of 0 and 1 approaching birds and Pre number of songs < 3, n = 209				
Percent overlapping	1	6.727	0.0095	I < R
Percent rattle-buzz songs	1	8.245	0.0041	I > R
C. During interaction singing and context variables that were correlated with approach order (I, R, N: dependent variables), controlling for dyadID and nested interaction number and omitting cases of 0 approaching birds and during number of songs < 3, n = 299				
Percent rattle-buzz songs	1	4.857	0.0275	I > R > N
D. During interaction singing and context variables that were correlated with approach order (I, R: dependent variables), controlling for dyadID and nested interaction number and omitting cases of 0 and 1 approaching birds and during number of songs < 3, n = 188				
Percent incomplete songs	1	6.747	0.0094	I > R

Table 3

Singing patterns associated with retreat order (W = withdrawer, or first to retreat; P = persister, or second to retreat)

Source	df	*L-R* χ^2	*P*	Direction
A. During interaction singing and context variables that were correlated with retreat order (W, P: dependent variable), controlling for dyadID and nested interaction number and omitting cases of 0 and 1 approaching birds and during number of songs < 3, n = 188				
Song-type diversity	1	14.819	0.0001	W > P
Percent immediate matches	1	5.289	0.0215	W > P
Unshared song types	1	4.247	0.0393	W > P
B. Postinteraction singing and context variables that were correlated with retreat order (W, P: dependent variable), controlling for dyadID and nested interaction number and omitting cases of 0 and 1 approaching birds and Post number of songs < 3, n = 212				
Percent overlapping	1	4.744	0.0294	W > P

Table 4

Singing patterns associated with aggressive status (A = aggressor, D = Defender)

Source	df	*L-R* χ^2	*P*	Direction
A. Pre interaction singing and context variables that were correlated with aggressive status (A, D: dependent variables), controlling for dyadID and nested interaction number and omitting cases of 0 and 1 approaching birds and Pre number of songs < 3, n = 209				
Song rate	1	12.355	0.0004	A > D
B. During interaction singing and context variables that were correlated with aggressive status (A, D: dependent variable), controlling for dyadID and nested interaction number and omitting cases of 0 and 1 approaching birds and Pre number of songs < 3, n = 188				
Percent rattle-buzz songs	1	9.104	0.0026	A > D
Grunting complexity	1	4.619	0.0316	A > D
C. Postinteraction singing and context variables that were correlated with aggressive status (A, D: dependent variable), controlling for dyadID and nested interaction number and omitting cases of 0 approaching birds and During number of songs < 3, n = 212				
Switching rate	1	12.360	0.0004	A > D
Unshared songs	1	8.583	0.0034	A < D
Percent rattle-buzz songs	1	10.824	0.0010	A < D

song-type diversity and switching rate, and gave few unshared song types, compared with other participant categories (Figure 3A–C). Matching rate and grunting complexity showed a strong interaction effect, being high for instigators that persisted and responders that withdrew, a likely consequence of intense mutual matching and mutual grunting in more highly escalated contests won by the instigator (Figure 3D,E). Percentage of rattle-buzz songs showed the opposite pattern, being highest for interactions in which instigators withdrew and responders persisted (Figure 3F). This pattern suggests that males engaging in nonescalated countersinging interactions tended to match each other's use of rattle-buzz song types. Two real-time examples of interactions with a withdrawing and a persisting instigator are illustrated in Figure 4.

The previous analyses compared male singing behaviors as a function of their approach and retreat status on a contest-by-contest basis, whereas our final set of analyses compared singing behaviors on the basis of the males' general aggressive status (aggressor versus defender) over the 3 days of recording. The results are largely consistent with the previous analyses of approach order, with some notable exceptions. Aggressors sang more than defenders in the Pre phase (Table 4A). Aggressors sang more rattle-buzz songs than defenders in the During phase, as previously found (Table 4B). Aggressors also grunted more intensely during escalated interactions, confirming that grunting intensity reflects aggressive motivation. In the Post phase, defenders sang more unshared songs, consistent with our earlier results for withdrawers (Table 4C). Interestingly, defenders also sang more rattle-buzz songs and with a lower switching rate, often highly repetitively, in the Post phase. Defenders thus sang very aggressively after the birds had interacted and moved apart, sometimes in contrast to their behavior during the contest.

Combining all of the earlier results, we can construct the likely escalation rules for banded wren countersinging contests (Figure 5). The instigator first approaches the boundary singing shared, rattle-buzz song types with a high diversity. The neighbor can either opt not to approach but to countersing from a distance while matching and singing with high diversity (nonapproacher), or he can approach (responder) while overlapping and matching. The initiator can then either de-escalate by keeping his diversity high but singing unshared song types and retreat (withdraw), or he can escalate further by reducing his song-type diversity. The responder can also either keep his diversity high, sing unshared song types, and retreat (withdraw), or he can escalate by reducing his song-type diversity and increasing his matching and use of rattle-buzz songs. The primary predictor of which bird will persist longer is based on how low he reduces his song-type diversity and switching rate during the contest. If both birds sing with low diversity, they will escalate to grunting. The more aggressively motivated bird grunts more intensely, which may resolve the contest without a fight. However, if grunting intensity is high for both birds, they will likely escalate to a chase or fight. After the contest, the birds back off to varying distances and continue to sing; the aggressor sings with higher diversity and the defender repetitively sings more unshared and rattle-buzz song types.

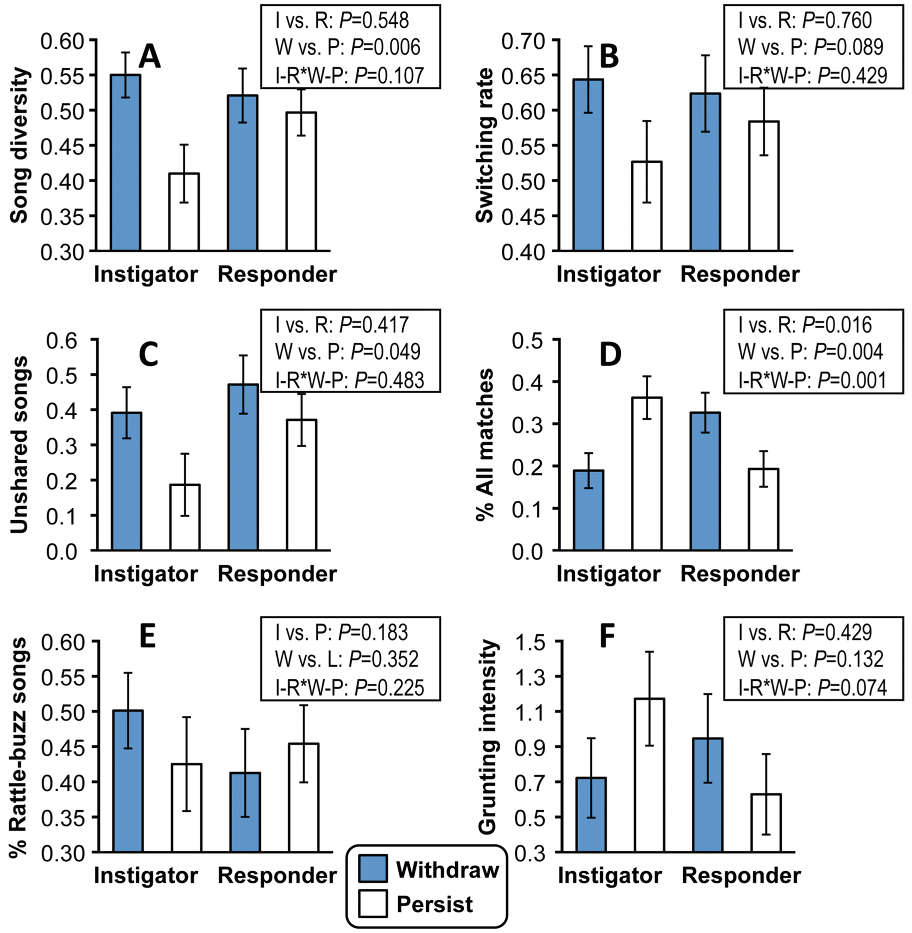

Figure 3

Relationship of singing behaviors to approach and retreat status. Least-squares mean values for song variables analyzed in a 2-way factorial Anova, including main effects of approach order (instigator vs. responder) and retreat order (withdrawer vs. persister), and the interaction between approach and retreat order, controlling for dyadID (random). Error bars show ±SE. Instigators are shown on the left, responders on the right, withdrawers in gray, and persisters in white.

Tests of the sequential assessment model

As outlined in the Methods, we used the absolute difference in song-type diversity between 2 rivals during a countersinging interaction as a proxy for their motivational asymmetry. The sequential assessment model predicts a negative correlation between this motivational asymmetry and contest duration, proximity of approach, and/or level of escalation. Figure 6 illustrates our graphical tests of these predictions. Contest duration (Figure 6A) fits the expectation well, with more similarly motivated contestants having interactions that are both longer and more variable in duration ($F_{1,146} = 14.81$, $P = 0.0002$, $r = -0.312$, $n = 148$). Proximity of approach did not fit expectations and, in fact, showed the opposite relationship, a positive correlation between motivational asymmetry and proximity ($F_{1,140.4} = 11.04$, $P = 0.0011$, $r = 0.239$, $n = 148$; Figure 6B). This effect was driven primarily by fighting interactions, which often exhibited a strong asymmetry in song-type diversity. The test with escalation level as the dependent variable confirmed this finding (L-R $\chi^2 = 3.318$, $P = 0.0685$, $r = 0.212$, $n = 148$; Figure 6C).

Tests of the territorial bargaining game

Using song-type diversity again as the key graded signal of motivation, we tested the main prediction of the bargaining model, namely that song-type diversity should increase with distance from the territorial center. Instead, we found a significant negative correlation between song-type diversity and distance from the center (Table 5); there was also a highly significant difference among the individual birds and a significant interaction term. Some males decreased their song-type diversity when they were farther from their central core, others increased diversity with distance, and some birds showed a flat relationship (see graph of interaction effects in Supplementary Figure S5). This result partially supports one assumption of the bargaining model, that is, the occurrence of a conspicuous graded signal that varies with distance from the center. However, the main effect goes in the opposite direction from the predicted one. If song diversity is indeed a graded measure of aggressive motivation, these results suggest that motivation in these birds does not always decline with distance from the core as assumed by Maynard Smith.

We subsequently tested the second prediction of the bargaining model, namely that the slope of the song-type diversity versus distance-from-center relationship is associated with the extent of territorial overlap between the 2 neighbors, or with characteristics of the bird such as general aggressiveness and stage of breeding. Table 6 summarizes the analysis with the diversity–distance slope as the dependent variable, and territorial overlap, percent instigator, and breeding stage as independent variables. The relationship between the diversity–distance slope and percent instigator was

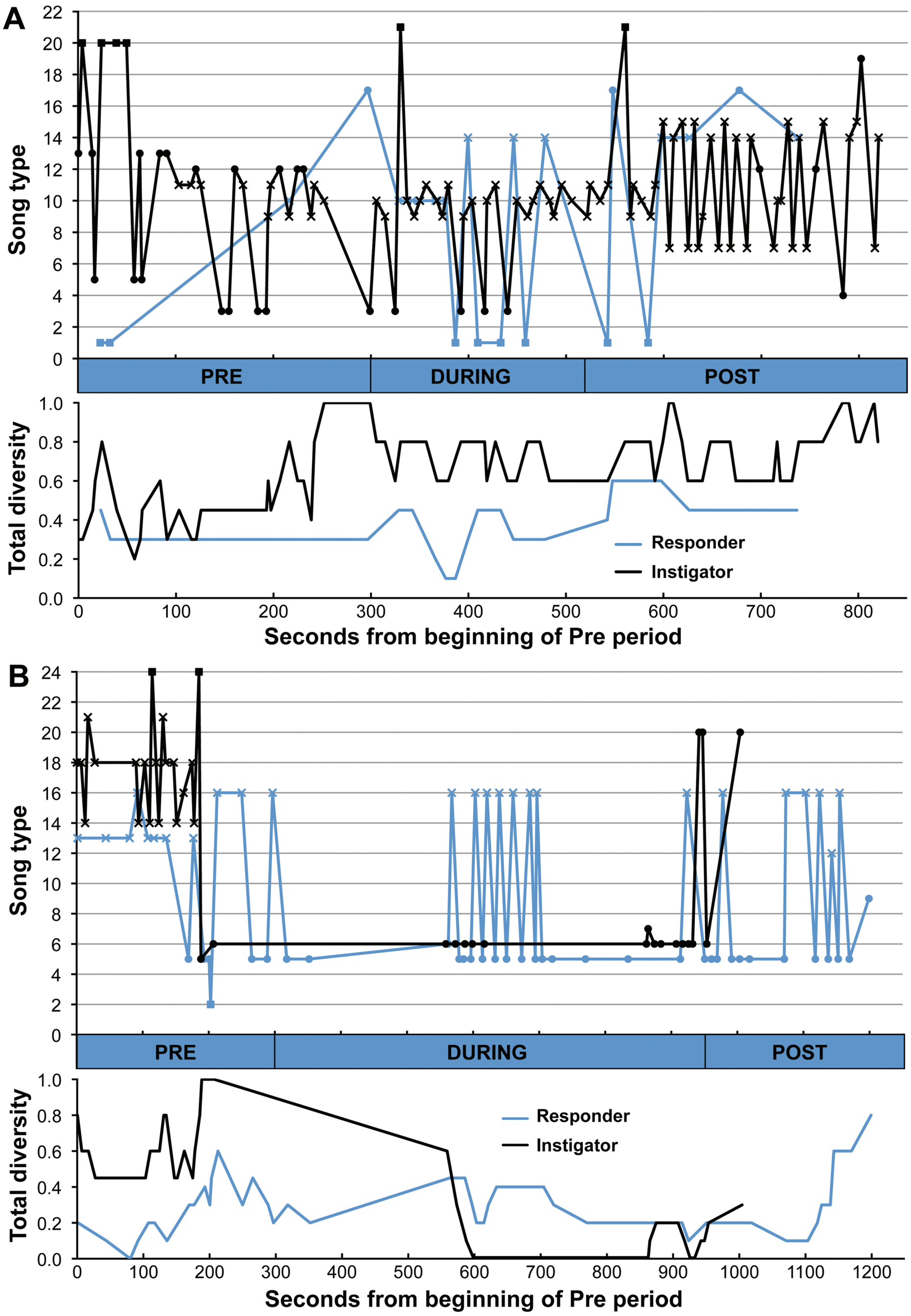

Figure 4

Examples of 2 interactions. The upper graph in each case shows song types (arbitrarily coded with numbers) versus time, and the lower graph shows the 5-song running total diversity (switching rate × song-type diversity) versus time. Unshared song types are indicated by square markers at the top and bottom of the graphs, all others are shared between both birds; rattle-buzz song types are indicated by "X" markers. The instigator (first approacher) is shown in black and the responder (second approacher) is shown in gray. (A) In this interaction, the instigator was the first to retreat. He sang with a higher diversity throughout the interaction and sang many unshared songs. (B) In this interaction, the instigator was the persister. Both birds grunted at level 3 during the interaction between 300 and 500 s, and the relative song diversities of the birds changed afterward, with the instigator singing more repetitively.

significant and positive (Figure 7A), meaning that birds that were more often the instigator in interactions increased their song-type diversity when they were farther from their core area, whereas defenders decreased their song-type diversity when they were farther from their core area, Territorial overlap was marginally significant, with abutting territories having mostly positive slopes and territories separated by a gap having mostly negative slopes. Neighbors with overlapping territories exhibited a broad range of slopes, with aggressors having mostly positive slopes and defenders having mostly negative slopes (Figure 7B). This result is consistent with the bargaining model, where aggressors encroaching into the defender's territory should have a lower motivation (and sing with a higher diversity) because they are farther from their core, compared with a highly motivated defender who is closer to his core area and singing with a lower diversity.

The third prediction we tested examined the relationship between song-type diversity asymmetry during the interaction and territorial overlap. We found that neighbors with gap-separated territories exhibited lower asymmetry in song-type diversity compared with neighbors with overlapping territories, and neighbors with abutting territories were intermediate ($F_{2,8.4} = 6.634$, $P = 0.0187$, $n = 148$; Figure 7C). These results are generally consistent with the bargaining model.

DISCUSSION

Contest protocols in the banded wren

Unlike the discrete escalation stages in sparrows and warblers involving shifts in broad song categories, the escalation rules in banded wrens primarily involve gradual changes in graded signals. Several other songbirds, in particular some New World warblers, deliver song types with immediate variety and may have a similar communication system (MacNally and Lemon 1985; Spector 1991, 1992; Beebee 2004).

This study of freely interacting neighboring banded wren males has confirmed the function of some singing patterns we discovered in earlier observational and playback studies, and has also clarified the function of patterns we did not fully understand. Rattle-buzz song types sound more aggressive, because they contain notes which resemble aggressive grunting calls. We previously found that they were preferentially used during the dawn chorus, a male-directed activity in this species (Burt and Vehrencamp 2005; Trillo and Vehrencamp 2005). In this study, we confirmed that rattle-buzz songs are used by instigators of boundary interactions in the Pre and During phases. Song-type matching was associated with a strong approach to playback speakers in several experiments (Molles and Vehrencamp 2001; Vehrencamp et al. 2007; de Kort et al. 2009). Here, we found that both neighbors increased their matching rates during all types of interactions. Unshared song types, the antithesis of song type and repertoire matching, was found to signal retreat in song sparrows (Burt et al. 2001; Beecher and Campbell 2005). We suspected that it played the same role in the banded wren, and verified in this study that it does indeed precede retreat by both instigators and responders. Song overlapping, believed to be an aggressive threat signal in many songbirds (Todt and Naguib 2000; Naguib and Kipper 2006; Searcy and Beecher 2009; Naguib and Mennill 2010), was shown to repel banded wren male receivers during overlapping playback treatments (Hall et al. 2006), and predicted retreat by the signaler in another study (Vehrencamp et al. 2007). We discovered a more subtle function for this signaling strategy here. Overlapping is used by the responder (second approacher) as he approaches, and by the male that retreats first during the Post interaction phase; it is clearly a defensive signal in this species.

The functions of song-type diversity and its close correlate, switching rate, remained unclear after a previous playback experiment which presented territorial wrens with 3 song-type delivery treatments: repetitive with low eventual diversity, high switching with low diversity, and high switching with high diversity (Molles 2006). In that study, receivers aggressively approached the repetitive treatment but not the 2 switching treatments. The low and high diversity switching treatments elicited parallel low and high diversity singing by the subject, along with frequent delayed matching. Although switching and diversity are often correlated, this study clarifies the fact that they provide different messages. Song-type diversity is a graded signal of motivation when negotiating a boundary location, and the extreme level of no switching seems to indicate the end of negotiation and no further retreat, a strong threat if performed close to the boundary. High-diversity singing is initially employed by aggressors to challenge the neighbor to a countersinging contest. As the birds approach each other more closely,

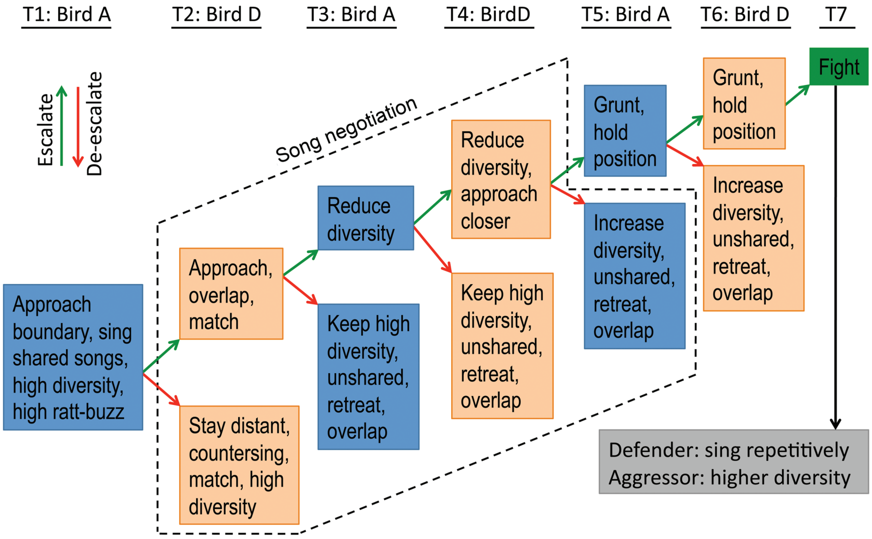

Figure 5

A schematic flow diagram of the banded wren escalation rules. In each time step (T1–T7), the 2 birds, A (aggressor, assumed to be the instigator: blue boxes) and D (defender, assumed to be the responder: orange boxes), alternate making decisions to escalate or de-escalate their singing strategies depending on the opponent's previous singing strategy decision. If both approach to some degree, they engage in a negotiation or haggling exchange using higher or lower song-type diversity. Potential withdrawers may not only display higher diversity singing, but also use unshared song types, and then overlap the opponent's songs while retreating. If singing strategies do not diverge between the birds, they escalate to grunting, which may further escalate to a fight. The aggressor and defender may continue to sing after the fight, with the defender singing more repetitively.

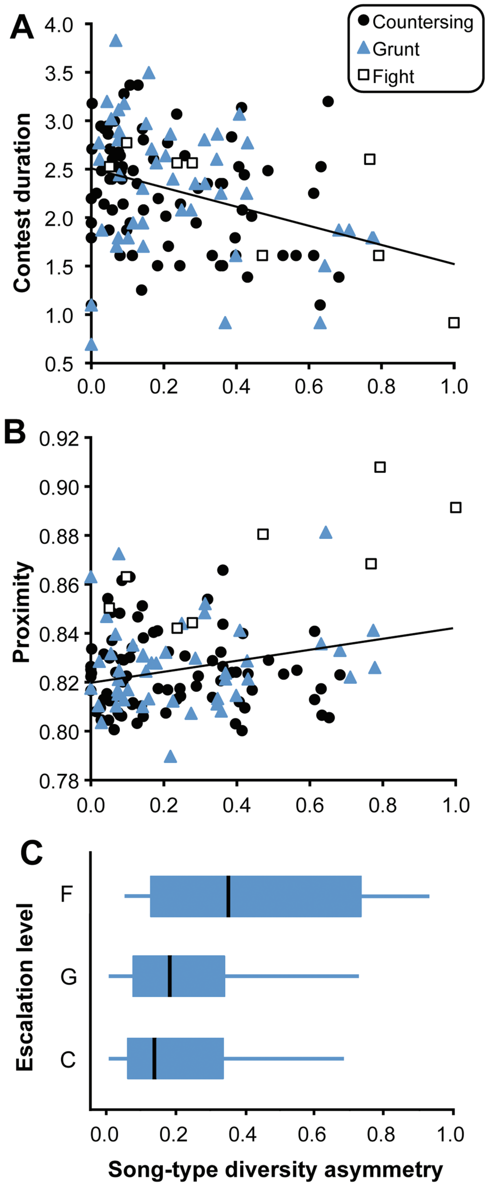

Figure 6

Three tests of the sequential assessment model predictions: contest duration, proximity of approach, and escalation level as a function of the asymmetry in motivation signaling. (A) Contest duration, measured as mean songs sung per bird during the interaction (ln transformed), is longer and more variable when contestants sing with more similarity in song-type diversity during the interaction, in support of the model. Symbols show contests with different escalation levels (countersinging, grunting, or fighting interaction). Trendline shows least-squares regression fit to all points combined. (B) Proximity of the 2 birds in the During phase (reciprocal of mean distance during the interaction, transformed with a power function) is positively correlated with greater asymmetry in song-type diversity between the birds, which contradicts the model. Symbols and trendline as in (A). (C) Escalation level is positively correlated with asymmetry in song-type diversity. Box and whiskers plot show median (black bar), quartile range (gray box), and 95% quantiles (gray horizontal lines).

they reduce their diversity to a level corresponding to their motivation to defend a particular position. If the rivals reach a similar diversity level at an acceptable position, the boundary location can be resolved by countersinging without escalation and both males withdraw. A common pattern is for both birds to switch between 2 song types. If a bird starts singing repetitively, it is more likely to hold its position and escalate if the other continues to advance. The higher-diversity singer usually retreats in this case. If both birds sing repetitively, it indicates they are no longer willing to negotiate. If neither one retreats, they may then stop singing and escalate to grunting. Thus, grunting seems to serve the same aggressive escalation function in banded wrens that soft song and wing waving do in sparrows and warblers (Searcy et al. 2006; Anderson et al. 2007; Ballentine et al. 2008; Hof and Hazlett 2010; Akçay et al. 2011). Grunting intensity is another graded signal associated with motivation, and if the aggressor grunts with a higher intensity the defender often retreats. When both birds grunt at a high intensity, a chase or fight is likely to ensue. After an escalated encounter, both birds may continue to sing, with the defender singing repetitively and the aggressor singing with a higher switching rate and diversity. This postinteraction singing seems to solidify the resolution to the current contest.

Table 5

Song-type diversity (dependent variable) as a function of distance of the male from his territorial center, birdID, and distance × birdID interaction, omitting songs given before 05:30 h and distance < 20 m, *n* = 7104

Source	df	*F*	*P*	Direction
Distance from center	1	14.69	<0.0001	−
BirdID	27	45.21	<0.0001	
Distance × birdID	27	10.92	<0.0001	+ and −

Table 6

Slope of song-type diversity versus distance (dependent variable) as a function of male aggressiveness, breeding stage (Ct = courtship, Inc = incubation, Prov = provisioning nestlings or fledglings), and territorial overlap (Ov = overlap, Ab = abut, Ga = gap), *n* = 28

Source	df	*F*	*P*	Direction[a]
Percent instigator	1	5.500	0.029	+
Breeding stage	2	2.116	0.144	Prov > Inc > Ct
Territory overlap	2	3.631	0.043	Ov < Ab > Ga

[a] A positive slope or higher value means that diversity increases with distance and, thus, motivation decreases with distance.

Fit to the sequential assessment model

These countersinging interactions fit some predictions of the sequential assessment game. Contests with more symmetric song-type diversity between the birds were longer and more variable in duration, consistent with the idea that when the contestants are similar, more signaling is required to assess and resolve the difference, and assessment errors are sometimes made. However, this result did not extend to the analyses of approach proximity and escalation level, which actually showed the opposite pattern with regard to asymmetry in song-type diversity. This inconsistency occurred because nonescalated countersinging contests between neighbors with resolved boundaries tended to be long and characterized by relatively symmetric singing behavior, whereas more escalated contests were quite variable in duration and characterized by greater asymmetry in song-type diversity. This asymmetry arises because the rivals continue to sing while close after escalated grunting and chasing bouts, and often diverge in their song-type diversity to reflect their aggressor or defender status going into the Post contest phase.

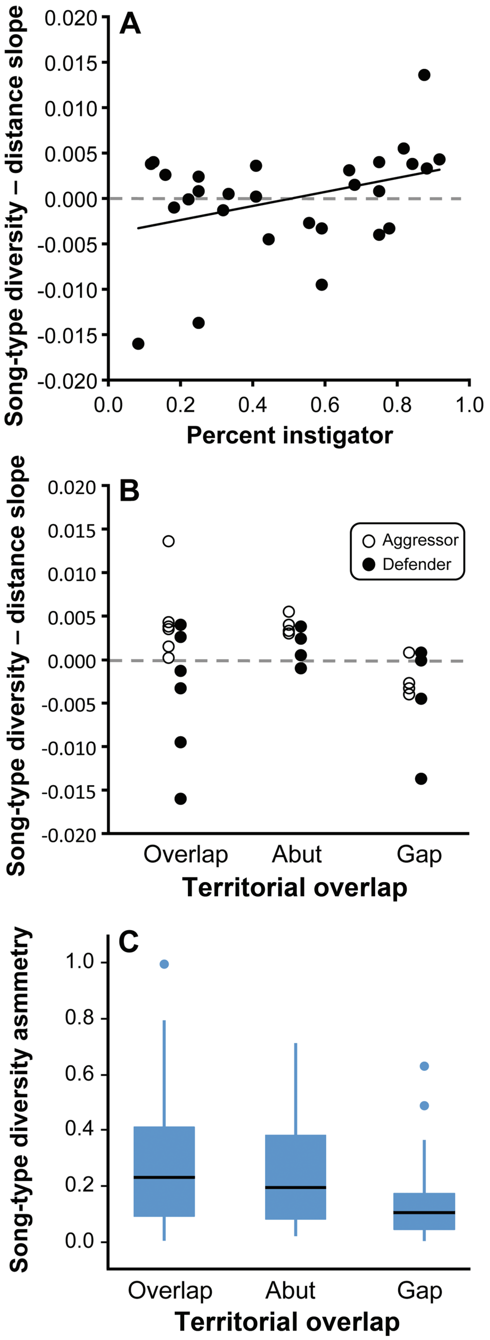

Figure 7

Three tests of the bargaining model. (A) Value of the song-type diversity versus distance slope for individual males derived from the ANCOVA analysis as a function of the percentage of interactions in which the male was the instigator. A positive slope means that diversity increases with distance and motivation decreases with distance. (B) Value of the song-type diversity versus distance slope as a function of the amount of territorial overlap between the neighbor dyads. Persistent aggressive status of individual males indicated by open (aggressor) and closed (defender) circles. Aggressors tended to have positive slopes, and defenders tended to have negative slopes. (C) Asymmetry of song-type diversity as a function of the amount of territorial overlap between the neighbor dyads. Box and whiskers plots show median (black bar), quartile range (gray box), 95% quantiles (gray vertical lines), and outliers.

Fit to the territorial bargaining model

Our results fit the predictions of the bargaining model quite well. The wrens possess at least one conspicuously graded signal, short-term song-type diversity, which varies as a function of distance from the territorial center in ways which are consistent with the graphical model (Figure 1). In the following discussion, we should keep in mind that a lower diversity indicates higher motivation. First, we should consider a neighbor dyad with abutting territories. As the symmetric illustration suggests, their boundary lies at the compromise point (red arrow) where their valuation curves are equal. We found that such dyads exhibit positive diversity–distance slopes, as predicted for honest signalers. Now let us consider an aggressive wren, for example, owner A on the left side of the figure, which needs to expand its territory to accommodate a new nest site. Owner A would invade its neighbor's territory, owner B, by moving to the right side of the arrow. In this position, A would signal with lower motivation (higher diversity) than owner B, who is strongly motivated to defend his core with lower diversity singing. We found that dyads with overlapping territories showed a strong difference in their diversity–distance slopes, with aggressors having more positive slopes and defenders having more negative slopes, in support of the model. For the same reason, the asymmetry in song diversity is greater for dyads with overlapping territories that engage in more frequent escalated encounters because of the strong asymmetry in motivation at invasive locations, compared with dyads with nonoverlapping territories. Dyads with gap-separated territories exhibited mostly negative diversity–distance slopes, meaning that they signal very aggressively from the edge of their territories. This observation also fits the model's predictions—with more separated territorial centers, the owners should not signal their motivation honestly, but show a mixture of Hawk and Bluffer. Finally, song-type diversity varies within contests in ways expected of bargainers. When the birds approach each other during interactions, they appear to compare their relative song-type diversities, and the one singing with higher diversity retreats, as predicted by the bargaining model.

Rather than pose these 2 models as alternatives, we think they may be complementary models. The bargaining model posits multiple mini-contests in which one party tests the other by crossing the current boundary, eliciting an exchange of graded signals that may or may not result in a new equilibrium. Each mini-contest might best be settled by sequential assessment processes. The bargaining game could be treated as a series of sequential assessment contests with the outcome of each contest dependent on its location relative to the participants' core zones. Although the sequential assessment game originally focused on successive recruitment of increasingly costly discrete signals, there is no reason why the cumulative mix of discrete signals might not act as a graded signal. That is, in fact, what we think happens in the case of banded wrens.

Ultimate selective forces

The final remaining question is why the banded wren has evolved such a complex bargaining system. The answer seems to be that populations are fairly dense and boundaries are very dynamic in this species. For one of our subjects which was recorded early in the season and again 6 weeks later, his territory shifted northward by 30 m due to encroachment by his southern neighbor (see male

OOO, Supplementary Figure S2 and Table S1). In 5 of our dyads with overlapping territories, one of the birds was building a nest very close to the contested boundary, and this bird was a frequent aggressor attempting to move his boundary so that the nest would be more centrally located. In 2 of our dyads with overlapping territories, one of the birds seemed to be a young male with a small territory attempting to enlarge it. The dyad with a young expanding male and a male initiating a nest close to the boundary engaged in particularly frequent and intense interactions.

The preferred nesting sites for this species are ant acacias of the genus *Vachellia*, which not only provide predator protection via the ants but also often host wasp nests (Joyce 1993; Haemig 2001). These trees are patchily distributed, so good nesting sites are often limited. The more dynamic nature of boundaries close to nest sites was noted in an earlier study (Trillo and Vehrencamp 2005). Although other neotropical avian species, in particular wrens, also nest in ant acacias, they may not experience the same densities and level of competition for territories as observed in banded wrens. We propose that this competition for patchy nest sites and the resulting rapid shifts in boundaries may be the ultimate factor which selected for a graded signal of motivation in this species.

Songbird species with song-type repertoires fall into 2 broad categories with regard to singing mode: eventual variety (songs types are delivered repetitively in bouts, e.g., AAAAABBBBBCCC…) and immediate variety (song types are delivered nonrepetitively with a high diversity, e.g., ABCDEFACBDFA…). Previous attempts to understand the selective forces driving the evolution of these 2 modes of singing have focused primarily on sexual selection via female preferences (Kroodsma 1977; Read and Weary 1992; Price 2013). All the closest relatives of the banded wren are eventual variety singers as well as duetters (Mann et al. 2009). Our study strongly suggests that the banded wren has evolved immediate variety singing and lost the duetting due to selection for a graded signal of aggressive motivation used to negotiate boundary disputes with neighboring males, that is, via intersexual selection. Eventual variety singers can still employ their repertoires to manage boundary disputes, but they escalate in discrete stages using shifts in song categories (Akçay et al. 2013; Hof and Podos 2013). Repetitive singing may enable interacting birds to better assess the performance capabilities of their rivals, for example, by comparing trill performance, song consistency, song duration, and other structural song features related to fighting ability (Logue and Forstmeier 2008; Podos et al. 2009; Sakata and Vehrencamp 2012; Moseley et al. 2013; Price 2013). We suggest that researchers studying songbird song systems more often consider combinations of graded and discrete singing patterns in their study species, and the possible kinds of information these patterns might provide for assessing motivational and fighting ability asymmetries in male rivals (Vehrencamp 2000).

We dedicate this article to the memory of J. Maynard Smith, who would have been very pleased to see these results largely corroborating his territorial bargaining game.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at http://www.beheco.oxfordjournals.org/

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