Countersinging as a signal of aggression in a territorial songbird

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Neighbouring territorial songbirds often interact through countersinging, where birds sing in response to the singing of neighbours such that their song bouts are temporally related. Complex forms of countersinging such as song type matching or song overlapping appear to be correlated with aggressiveness and readiness to escalate confrontations. Less attention has been paid to the importance of simpler forms of countersinging, where matched song types are not used and where individual songs do not temporally overlap. I examined countersinging behaviour in male Carolina wrens, *Thryothorus ludovicianus*, which countersing regularly. Why they countersing and how countersinging is perceived by neighbours is unknown. By comparing singing behaviour before and after simulated intrusions, I determined that subjects countersing with their neighbours more readily when highly aroused. Comparing responses to countersinging and noncountersinging playbacks showed that countersinging elicited more aggressive responses than did noncountersinging. Carolina wrens appear to exchange aggressive signals regularly through countersinging.

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Animals using acoustic signals can interact dynamically with each other by changing signal type (e.g. by song type matching) or by changing signal timing (e.g. by overlapping or alternating signals). In many anurans and orthopterans, males interact by attempting to produce the leading signal rather than the following signal, and females preferentially orient towards the leading signal (Greenfield 1994). Male songbirds interact vocally with one another through countersinging, such that the song bouts of two birds are temporally related. Countersinging interactions can simply involve one bird singing in response to another, but may also include singing matched song types (matched countersinging; Lemon 1968) and singing so as to overlap individual songs (Dabelsteen et al. 1997). In contrast to the anuran and orthopteran examples, where males attempt to produce leading signals preferred by females, in songbirds, males actively try to produce following or overlapping signals. Several studies have documented that matched countersinging and overlapping are correlated with aggressiveness and readiness to escalate confrontations (McGregor et al. 1992b; Dabelsteen et al. 1997), suggesting that matching and overlapping are honest signals of aggressive intent. Furthermore, those individuals producing overlapping signals are perceived as more serious rivals (Naguib et al. 1999) and seem to be preferred by females as extrapair mates (Otter et al. 1999).

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This contrast between anurans/orthopterans and songbirds raises questions about the function of countersinging in songbirds and why receivers perceive following or overlapping signals as more salient. There is an unanswered question of how these sorts of vocal interactions could provide honest signals of quality, because the potential difference in the cost of using overlapped versus nonoverlapped, or song-type-matching versus non-song-type-matching signals is unclear. Recent studies examining matched countersinging have proposed that song type matching is a conventional signal, in that there is no difference in the cost of producing matched or unmatched song types (Vehrencamp 2000, 2001; Molles & Vehrencamp 2001).

Studies have examined the functional significance of complex forms of countersinging including singing matched song types (e.g. Lemon 1968) or singing so as to overlap individual songs (e.g. Dabelsteen et al. 1997). Song type matching or song overlapping occurs most often during escalated territorial boundary disputes (Todt & Naguib 2000). Less attention has been paid to the importance of simpler forms of countersinging, where there is no escalated boundary dispute, matched song types are not used, and where individual songs may or may not temporally overlap. Studies examining song type matching or song overlapping have not addressed the issue of why the song bouts of males are initially temporally related to one another. To defend a territory with song, males obviously must sing at some point during the day, but it is less clear why territorial signals

should show any temporal relation between males. Regardless of the function of song type matching or overlapping, the question remains whether there is a signalling function to the simple act of singing in response to another singer. Examining the significance of simple countersinging, requiring only that the singing bouts of two individuals be related temporally, may provide evidence for the potential costs of such vocal interaction. In addition, examining the significance of simple countersinging might provide insight into the importance of more complex forms and help explain how matching, overlapping or simple countersinging can be an honest signal of aggressive intent.

Carolina wrens, *Thryothorus ludovicianus*, are good subjects for studying countersinging. Male Carolina wrens countersing regularly, most at some distance from one another and without matching song types. Song type matching occurs more rarely during escalated border disputes (Haggerty & Morton 1995). Most commonly, in a silent neighbourhood, one male begins to sing, neighbours respond with song (countersinging), and soon many nearby males are singing simultaneously. The bouts of neighbouring birds overlap temporally, but individual songs may or may not overlap.

In playback experiments, Carolina wrens show neighbour/stranger discrimination and reduced aggression towards neighbours (Shy & Morton 1986; Hyman 2001) and forgive their neighbours quickly after simulated intrusions (Hyman 2002). However, there appears to be regular exchange of aggressive signals between neighbouring birds through countersinging. I hypothesized that birds in an aggressive state are more likely to countersing with their neighbours. By comparing the timing of song bouts before and after a simulated intrusion, I was able to determine whether subjects answered their neighbours differently when in an aggressive state. If countersinging with neighbours is an aggressive signal, I hypothesized that birds should respond with high aggression to countersinging songs and with lower aggression to other signals. By comparing responses to playbacks that answer a singing subject and those that do not, I was able to determine whether countersinging elicited more aggressive responses than other singing behaviour.

METHODS

I conducted this study at the Mason Farm Biological Reserve in Orange County, North Carolina, U.S.A. (35°N, 79°W), in oak–hickory and riparian forest in June and July 1999. All subjects included in this study had been holding their territories for at least 6 months, as had all of their neighbours. Neighbours were birds whose territories directly adjoined the territory of the subject. Strangers had territories over five territories away from the subject. I estimated territory boundaries by extensive mapping of birds' locations while singing, a task facilitated by a 25-m grid of stakes throughout most of the study area.

I recorded song with a Marantz PMD221 recorder and a Sennheiser K3U/ME88 ultradirectional microphone. I used songs recorded from males in 1998 and 1999 to construct playback tapes. Clear examples of songs were chosen after examining them with a Uniscan II real-time spectrum analyzer. I digitized the songs at 16-kHz and 16-bit accuracy on a 68030 Macintosh computer using Audiomedia hardware and software (Digidesign, Palo Alto, California, U.S.A.). All songs were adjusted to the same maximal amplitude and re-recorded on a Marantz PMD221 recorder. Playback tapes were played from a Marantz PMD221 recorder connected to an Amplivox amplifier and a Realistic horn speaker (frequency response 1.5–2.5 kHz ± 3.0 dB, 2.5–8.0 kHz ± 2.5 dB). Each tape was approximately 45 s long and consisted of seven repetitions of a song type, delivered at a rate of approximately 10 songs/min. Males naturally sing at a rate of 5–15 songs/min, and repeat the same song type up to 250 times before switching (Haggerty & Morton 1995).

Experiment 1

Experiment 1 was designed to examine the countersinging rates of subjects and their neighbours before and after a simulated territorial intrusion. Territorial males were used as subjects. During the preplayback period, I recorded the timing of the beginning and ending of all song bouts by the subject and its neighbours. Following Naguib (1995), I defined a song bout as a sequence of songs with no silences lasting longer than 1 min. Using a stopwatch, I recorded when the subjects' and neighbours' song bouts began and the number of songs sung by the subject. I defined countersinging as any temporal overlap in the song bouts of neighbouring birds. I defined noncountersinging as any time a neighbour's bout began and ended without the subject beginning a bout. This definition of countersinging is more limited than a definition that requires only that neighbours' song bouts be temporally related. After a 15-min preplayback period, I presented the subject with a playback of stranger's songs from a speaker placed in the centre of the subject's territory and clamped to a sapling, 1.5–2 m above ground. I then recorded the singing behaviour of the subject and its neighbours for 15 min after the simulated intrusion. All playbacks were conducted from 0700–0900 hours Eastern Standard Time. I used 12 territorial males as subjects, and used song exemplars from 12 different strangers for playback, such that each subject was presented with songs from a different stranger to avoid pseudoreplication (McGregor et al. 1992a).

Experiment 2

The second experiment tested whether subjects responded differently to countersinging and noncountersinging playbacks. Subjects each received two playback treatments: (1) playback of a neighbour's song beginning when all birds were silent (noncountersinging trial), and (2) playback of a neighbour's song beginning while the subject was singing (countersinging trial), a treatment simulating a neighbour countersinging with the subject. I presented each subject with a playback from a speaker

placed at a location approximating the boundary between the subject and the neighbour's territory and clamped to a sapling 1.5–2 m above ground. As in the first experiment, I avoided pseudoreplication by using 12 subjects, using song exemplars from 12 different neighbours for playback, and presenting each subject with songs from a different neighbour. For each subject, the same exemplar was used in both the noncountersinging and countersinging trials.

In the noncountersinging trials, subjects were at an unknown location at the beginning of the trial. In the countersinging trials, the singing subjects were at least 25 m away from the speaker location. Subjects' responses were recorded for 15 min from the start of the playback tape. Response variables recorded were latency to approach, closest approach, latency to resume singing, number of songs, longest song bout and highest singing rate. Highest singing rate was defined as the highest number of songs occurring in any 1 min. I recorded latency to resume singing because almost all males stopped singing when the playback began.

The response measures that I used are likely to be correlated, so I used principal component analysis (PCA) to calculate a composite score. I used the first principal components in a Wilcoxon matched-pairs signed-ranks test to compare treatments. However, because the countersinging trial began with the subjects in a known location, and the noncountersinging trials did not, consideration was given to the possibility that some subjects in the silent trial may have been farther away or off their territory altogether. For this reason, I analysed approach responses both separately and as part of the larger principal components analysis. Treatments were separated by 4–5 days. All playbacks were conducted between 1800 and 2000 hours Eastern Standard Time.

In both experiments, no effort was made to determine whether the songs used for playback were in the repertoire of the subject. Song sharing between neighbouring Carolina wrens can be very high (Simpson 1982; Haggerty & Morton 1995). Song type matching is often associated with aggression (Lemon 1968), but repertoire matching, or the differential use of shared and unshared song types, is thought to be associated with different levels of aggression as well (Beecher et al. 1996). Specifically, song type matching appears to occur in more aggressive contexts than does repertoire matching (Beecher et al. 2000).

It is possible that the exemplars used in this study include examples of both repertoire matching and non-repertoire matching. However, the failure to control for this possibility is conservative in that it should only add noise to my results. In experiment 1, examining countersinging before and after a simulated intrusion, the relevant comparison was between the preintrusion period and the postintrusion period. If some subjects heard playbacks of shared song types and others heard playbacks of unshared song types, this difference might add overall variation to the subjects' responses, but should not obscure a difference between preintrusion and postintrusion behaviour. In the second experiment, examining responses to countersinging and noncountersinging
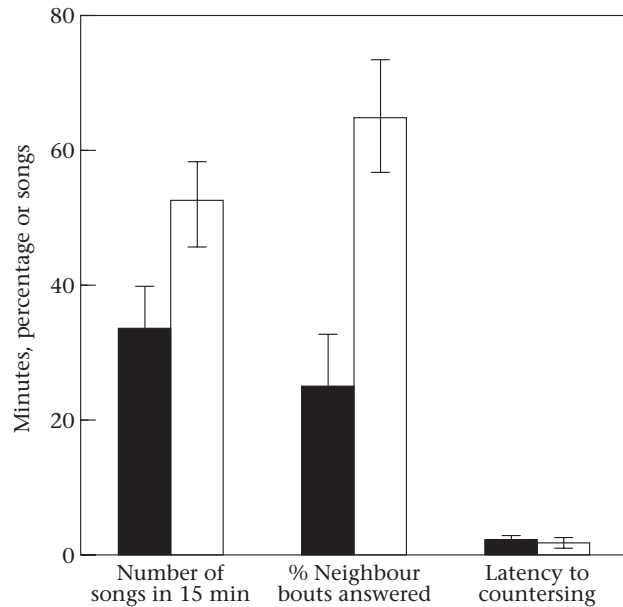
Figure 1. Mean±SE countersinging responses by subjects before (■) and after (□) playback simulating an intrusion on each subject's territory.

playback, the same song type was used in both treatments for each subject. The relevant comparison is the difference in response for each subject. Once again, using shared song types for some subjects and unshared song types for other subjects could add overall variation to the subjects' responses, but should not obscure a difference between the two treatments.

RESULTS

Countersinging Before and After an Intrusion

The singing behaviour of both subjects and neighbours differed before and after the simulated intrusion. Neighbours sang fewer song bouts after the intrusion ($\overline{X} \pm SE = 2.833 \pm 0.271$) than before the intrusion (3.917 ± 0.452, $N=12$; Wilcoxon matched-pairs signed-ranks test: $T=10$, $N=12$, $P<0.05$). Countersinging with neighbours was relatively common in all circumstances. In the preplayback period, subjects countersang, on average, during 25% of their neighbour's bouts. After the simulated intrusion, subjects countersang during a significantly higher percentage of their neighbours' bouts ($T=1$, $N=12$, $P<0.01$; Fig. 1) and initiated countersinging with neighbours' bouts more quickly ($T=1$, $N=12$, $P<0.05$). Subjects also sang more total songs ($T=10$, $N=12$, $P<0.02$). The response variables for the subjects were combined into a composite score using principal components analysis (Table 1). The first principal component explained 55.3% of the total variance in the response measures (eigenvalue 1.658). A pairwise comparison of the first principal component scores showed that subjects' countersinging was greater after the simulated intrusions (0.591 ± 0.125) than before the intrusion (-0.787 ± 0.337; $T=0$, $N=12$, $P<0.01$).

Table 1. Loadings of the different response measures on the first principal component for countersinging responses before and after simulated intrusions

Response measures	Loadings
Number of songs	0.715
Percentage of neighbour's bouts answered	0.783
Latency to countersing	−0.730
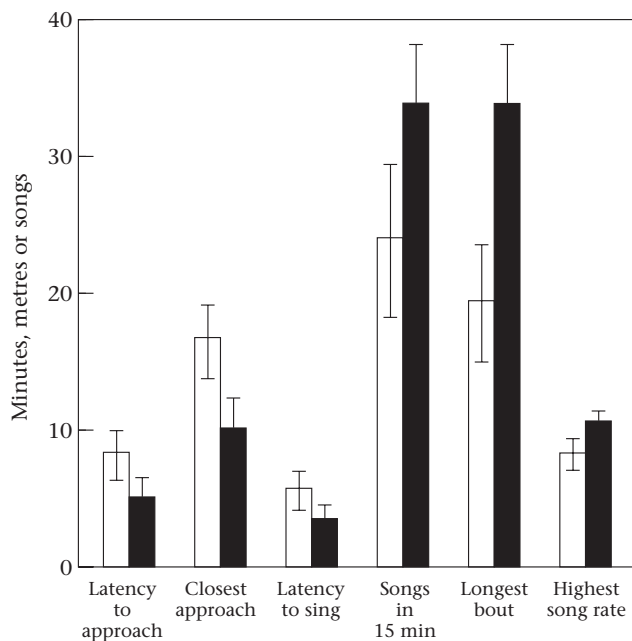
Figure 2. Means±SE responses of subjects to countersinging (■) and noncountersinging (□) playbacks. Response variables included latency to approach, closest approach, latency to sing, number of songs, longest song bout and highest song rate.

Countersinging and Noncountersinging Playbacks

There was no difference in the subjects' latency to approach countersinging and noncountersinging playbacks (*T*=6, *N*=12, NS), and no difference in their response distance (closest approach) to countersinging and noncountersinging playbacks (*T*=11.5, *N*=12, NS; Fig. 2). These response variables were combined into a composite score using principal components analysis (Table 2). The first principal component for the approach scores explained 93.4% of the variance in the response measures (eigenvalue 1.869). A pairwise comparison of the first principal component scores for the approach variables indicates that the subjects' approach responses did not differ in response to the two treatments (*T*=16, *N*=12, NS). Whether the playback began in silence or while the subject was singing had no significant effect on the subject's approach.

In response to noncountersinging and countersinging playbacks, the subjects did not differ in their latency to begin singing (*T*=14, *N*=12, NS). In response to the countersinging playback, the subjects sang more songs

Table 2. Loadings of the different response measures on the first and second principal components for overall response to countersinging and noncountersinging playbacks

Response measures	Loadings	
	PC1	PC2
Overall		
Latency to approach	0.568	0.782
Closest approach	0.561	0.752
Latency to sing	0.656	0.113
Number of songs	−0.837	0.434
Longest song bout	−0.785	0.542
Highest song rate	−0.777	0.195
Approach		
Latency to approach	0.967	
Closest approach	0.967	
Vocal		
Latency to sing	−0.594	
Number of songs	0.930	
Longest song bout	0.923	
Highest song rate	0.795	

In separate analyses of approach response and vocal response, only the first principal component had an eigenvalue greater than 1.

(*T*=5, *N*=12, *P*<0.01), sang longer bouts (*T*=3, *N*=12, *P*<0.01), and sang at faster rates (*T*=13, *N*=12, *P*<0.05). The first principal component for the vocal scores explained 67.5% of the variance in the response measures (eigenvalue 2.701). A pairwise comparison of the first principal component scores for the variables involving singing indicated that subjects' vocal responses were much stronger to the countersinging trials than to the noncountersinging trials (*T*=3, *N*=12, *P*<0.01). The first principal component for vocal and approach variables combined explained 49.8% of the total variance in the response measures (eigenvalue 2.989), and the second principal component explained a further 28.5% (eigenvalue 1.711). Only scores on the first principal component were used for this analysis. A comparison of the scores on the first principal component for vocal and approach variables combined similarly showed that subjects responded much more strongly to the countersinging trials (0.494 ± 0.313) than to the noncountersinging trials (−0.494 ± 0.622; *T*=5, *N*=12, *P*<0.01).

In 11 of 12 countersinging trials, the subject male stopped singing after the first song on the playback tape. For this reason, it was not possible to classify countersinging trials as representing overlapped or alternated song. Thus, it is not possible determine whether there was a difference in the subjects' responses to overlapped and alternated songs.

DISCUSSION

Countersinging Before and After an Intrusion

The likelihood of countersinging and the speed with which birds responded to neighbours increased following

intrusions. During the preplayback period, subjects countersang in response to about 25% of all neighbours' bouts, but birds aroused by the presence of an intruder countersang with a significantly higher percentage (>60%) of their neighbours' bouts. These results suggest that increased levels of countersinging in Carolina wrens are associated with increased arousal and aggressiveness. I did not control for whether the song type used in playback was in the repertoire of the subject. However, these song exemplars were from strangers. The exemplars might or might not have simulated repertoire matches, but repertoire matching is thought to be a way in which signals are graded in communication between neighbours. Presumably, any song from a strange bird should elicit a high amount of aggression, and whether it is a repertoire match or not would be a chance event, dependent only on the population level of song type sharing.

The finding that neighbouring males sang less after intrusions suggests that individuals might eavesdrop on the interactions of others. Perhaps the neighbours are listening for further evidence that a stranger is in their midst. Red-capped cardinals, *Paroaria gularis*, apparently eavesdrop on interactions of neighbours with strangers as an 'early warning system' (Eason & Stamps 1993). Intruders were expelled more readily if they had already been detected and expelled from a neighbouring territory. Neighbours might also be interested in how the territory owner deals with the intrusion. Birds who respond weakly to intruders might be susceptible to losing part of their territory to a neighbour trying to expand his territory. Birds that expel intruders quickly might be stronger opponents. Naguib et al. (1999) demonstrated that nightingales, *Luscinia megarhynchos*, responded more strongly to leaders of simulated singing interactions. They concluded that nightingales respond more strongly to birds that they perceive as more serious rivals.

Countersinging and Noncountersinging Playbacks

Carolina wrens responded more strongly to countersinging than to noncountersinging playbacks, suggesting that the countersinging bout is a more aggressive signal and necessitates a more aggressive response. The subjects' vocal responses were much stronger in response to countersinging than to noncountersinging playback, suggesting that countersinging is indeed perceived as an aggressive signal by male Carolina wrens. Other studies have shown overlapping song to be a more aggressive signal than alternating song (Dabelsteen et al. 1996, 1997). In this study, however, the comparison was not between overlapping and alternating songs, but between countersinging and noncountersinging bouts. As in experiment 1, I did not control for whether the song type used in playback was in the repertoire of the subject. There is potential noise introduced by the fact that some songs may have been repertoire matches; none the less, I found a significant difference in responses to countersinging and noncountersinging playbacks.

What Makes Countersinging an Aggressive Act?

Countersinging by Carolina wrens appears to be associated with high levels of aggression and may be perceived as an aggressive or escalated signal. These findings raise the question of what makes countersinging an aggressive act, or how countersinging can function as an honest signal of aggressive intent. One common hypothesis to explain the function of countersinging is that countersingers direct a signal to a given opponent. Starting a song bout at the same time as another male might alert the first singing male that he is being challenged (McGregor & Dabelsteen 1996). A male might sing a noncountersinging bout in response to his own physiological or behavioural state. Countersinging bouts are sung in response to a competitor's signal. For this reason alone, countersinging would seem to be more aggressive than noncountersinging. The proximate basis for the stronger response to the countersinging bout might be that the countersinging bout is more detectable and easier to range. A singing subject is generally on a higher perch, better for both broadcasting and receiving signals, and a singing subject might not be preoccupied by activities such as foraging, preening or interacting with his mate that could decrease the likelihood of detecting a signal. However, there was no significant difference in the subjects' latency to approach or closest approach to countersinging and noncountersinging playbacks. Although the mean latencies suggest that subjects might respond faster to countersinging playbacks, there was considerable variation and no consistent trend. Thus, there is little support for the argument that countersinging playbacks were simply more detectable than noncountersinging playbacks.

Another common hypothesis suggested to explain the aggressive function of countersinging is that the countersinging male is 'jamming' the first male's signal (Todt & Naguib 2000). By producing a competing signal at the same time as a rival male, the rival male's signal becomes less detectable in the noise. However, it is unclear what advantage could be gained by jamming a rival's signal. One possibility is that overlappers can compensate by producing more songs at another time when they are not overlapped. If overlappers can, in this way, mask competitors' signals, while also producing additional nonmasked signals of their own, then perhaps acoustic signal interference could be a stable strategy as well.

Naguib & Todt (1997) suggested that in many European thrushes, more potential information is found at the end of the song. Thus, the signal of the overlapped bird is diminished, but the end of the overlapping bird's signal remains clear. However, the distance between singing male Carolina wrens, and the fact that countersinging does not often seem to occur with exact synchrony, suggests that a signal-jamming function is unlikely.

Finally, countersinging could function as an honest signal if there are measurable production or opportunity costs associated with more singing, although evidence for production costs of bird song has been mixed (Eberhardt 1994, 1996; Gaunt et al. 1996; Oberweger & Goller 2001).

In experiment 1, after an intrusion, subjects increased their countersinging rate, answered neighbours' bouts more quickly, and sang more total songs. In experiment 2, males responding to countersinging bouts sang more songs, longer bouts and sang at higher rates. These results suggest that countersinging involves a greater investment of time into singing than other behaviours.

Who Are the Important Receivers, Males or Females?

Studies have shown that third parties might attend to the interactions of two males. The songs of territorial male songbirds are long-distance signals, capable of being heard by nearby conspecifics. Territorial birds interact in communication networks (Dabelsteen 1992; McGregor 1993), within which individuals can gain information about their neighbours in multiple ways. Individual birds can listen to the songs of a single neighbour, interact vocally with neighbours, and listen to the vocal interactions of others. Several studies have demonstrated potential cases of eavesdropping in which other males assess the competitive strength of two neighbours (Naguib et al. 1999) or females compare potential extrapair mates (Otter et al. 1999).

Who is the intended receiver of the males' signals? In anurans and orthopterans, the key receiver is the female. Males produce signals to attract mates. As mentioned previously, the apparent synchrony of vocalizations arises as males displaying in aggregations attempt to precede another male's vocalization in a situation where females prefer the preceding signal. But who is the intended receiver in many songbird examples? In many migratory birds, males arrive on the breeding grounds before females, and male song presumably functions initially to defend territories against other males and subsequently to attract females. Male Carolina wrens sing, defend territories and maintain pair bonds year-round. Most of their singing clearly does not serve to attract a mate, nor do they appear to display extrapair behaviour (Haggerty et al. 2001). In other species, however, male singing interactions appears to serve as a signal to potential extrapair mates, as has been shown in great tits, *Parus major* (Otter et al. 1999), and black-capped chickadees, *Poecile atricapillus* (Mennill et al. 2002).

In summary, countersinging in Carolina wrens increased when the birds were provoked by simulated intrusions. Carolina wrens also responded more strongly to playbacks simulating countersinging than to playbacks beginning when the subject was silent. In Carolina wrens, increased countersinging is associated with increased levels of aggression, and countersinging signals are perceived as more aggressive. Studies have shown associations of matching and overlapping with increasing aggression. In the present study, countersinging itself was associated with increased aggression. Countersinging could function as an honest signal if song output involves significant production or opportunity costs, or alternatively, countersinging might be a conventional signal, stabilized by receiver-dependent costs. Even in situations that are not obviously aggressive, the interactions of territorial animals are still characterized by the regular exchange of aggressive signals.

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