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Tit for tat among neighboring hooded warblers

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Summary. The "dear-enemy" relationship of territorial songbirds could be mutually beneficial to neighbors, as males who recognize neighbors and reduce their responses to these neighbors would require less time and energy for territorial defense. In order for this relationship to be evolutionarily stable, this reduction in response to a neighbor must be conditional on reciprocal restraint by that neighbor. This study examined the possibility of such conditional responses in hooded warblers (*Wilsonia citrina*). Responses of territorial hooded warblers to playbacks of neighbors' songs from shared boundaries were measured before and after playbacks that simulated intrusions of those same neighbors (NNNN treatment) or strange birds (NSSN treatment) into the subjects' territories. Each male received both treatments separated by at least 8 days. Males increased their responses to playbacks of a neighbor's songs at the boundary after simulated intrusions of that same neighbor (NNNN) but did not increase their responses to such playbacks after simulated intrusions of strangers (NSSN). This increased response to a "defecting" neighbor suggests that the relationship between neighboring territorial hooded warblers is based on a conditional strategy like tit-for-tat.

Introduction

Established territorial residents often respond less aggressively to neighbors than to strangers, a phenomenon known as the "dear-enemy" effect (Fisher 1954; Ydenberg et al. 1988; Qualls and Jaeger 1991; Fox and Baird 1992). In territorial songbirds, this effect is exemplified particularly clearly by the lower responses of residents to neighbors' songs played at an appropriate boundary than to songs of strangers (reviews by Falls 1982; Ydenberg et al. 1988). Reduced aggression toward neighbors, once boundaries are established, would have advantages as a territorial resident could reduce its expenditure of time and energy and its risk of injury in frequent escalated encounters. Thus male songbirds might benefit by recognizing and reducing their interactions with neighbors.

Explanations for the evolution of this behavior have invoked reciprocal altruism based on a strategy of tit-for-tat (TFT) in an iterated Prisoner's Dilemma (Trivers 1971; Axelrod and Hamilton 1981; Trivers 1985; Getty 1987). This explanation raises two related questions: (1) do territorial relationships fit the conditions for reciprocal altruism as defined by the Prisoner's Dilemma? and (2) do territorial animals' capabilities include conditional strategies like tit-for-tat?

It is uncertain that reciprocal altruism actually occurs in situations involving mutual restraint, such as between "dear enemies", because it is difficult to confirm that restraint incurs a cost (Koenig 1988; Rothstein and Pierotti 1988; Wilkinson 1988; Lombardo 1990). Nevertheless, it seems plausible that mutual restraint in territorial relationships could often fit the conditions for reciprocal altruism in the Prisoner's Dilemma. Escalated fighting by new territorial neighbors suggests that mutual acceptance of a boundary involves relinquishing some potential gain from a larger territory (some possibilities might include a larger catchment for obtaining mates, a larger reserve of food, or greater spacing out for protection from predators). If so, the net advantage for an unchallenged defector would exceed that for mutual cooperators ($T > R$). In addition, the net advantage for a cooperator with a defecting neighbor would fall short of that for mutual defectors that continually contested their boundary ($P > S$) as a cooperator interacting with defectors could potentially lose its mate or territory. Mutual cooperators would presumably do better than mutual defectors ($R > P$), whenever escalated interactions incurred some expense or risk. Under these conditions, then, territorial interactions would meet the conditions for the Prisoner's Dilemma ($T > R > P > S$).

Although the crucial inequality, $T > R$, has yet to be confirmed quantitatively for any territorial animal, it

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nevertheless seems plausible. If neighbors could not realize any gain from unilaterally expanding their territories, then territorial birds would gain nothing from challenging their neighbors nor from returning apparent challenges from neighbors. Only strangers should evoke aggression. On the other hand, if neighbors relinquished some advantage in return for mutual restraint in interactions, a known neighbor that failed to respect the shared boundary should be challenged.

Such retaliation could constitute part of a TFT strategy (Axelrod and Hamilton 1981) or similar, more robust strategies (Nowack and Sigmund 1992). Evolutionary stability of TFT requires (1) an indeterminate number of interactions between individuals and (2) recognition of individual opponents. These conditions are met by territorial songbirds. Interactions between neighbors continue for a prolonged and indeterminate period, and several studies have now demonstrated that territorial songbirds can recognize the songs of individual neighbors (Falls and Brooks 1975; Wiley and Wiley 1977; McGregor and Avery 1986; Brindley 1991; Godard 1991; Stoddard et al. 1991). In addition, TFT requires (3) conditional retaliation against opponents that fail to cooperate. Conditional retaliation has been documented in the dominance relationships of nonhuman primates (Cheney and Seyfarth 1990) and in breeder-nonbreeder relationships of swallows (Lombardo 1985), but has yet to be demonstrated in any territorial relationship.

In this study, I investiagated the possibility of conditional retaliation against noncooperating neighbors in territorial hooded warblers, *Wilsonia citrina*. Playbacks of a neighbor's or stranger's songs well within a subject's territory served to simulate an intrusion. To evaluate the possibility of retaliation, I measured the subject's responses to the neighbor's songs from a shared boundary before and after each simulated intrusion. If territorial hooded warblers retaliate against defecting neighbors, their responses to a neighbors' songs at a shared boundary should increase specifically after a simulated intrusion by that neighbor and not after a simulated intrusion by a stranger.

Methods

This study was carried out at the Mason Farm Biological Reserve in Chapel Hill, NC, from early April to early June in 1990, in a hickory-oak forest with a dense understory primarily of *Viburnum* species. Hooded warblers arrived in the first part of April. During April and early May, In mapped territories of 19 males and recorded their songs with a Sony TC-D5M recorder and Sennheiser K3U/ME88 ultradirectional microphone. Hooded warblers, like other parulines (Spector 1992), sing in two modes, repeat-mode and mixed or serial-mode. The repeated singing of one song type (repeat-mode) occurs throughout the breeding season but predominates when males first arrive on their territories. I used repeat-mode songs from 15 of these males to construct playback tapes. Each tape consisted of one song often used in repeat-mode at approximately 6 songs/min for 3 min (the usual singing rate for repeat-mode). Eight similar tapes of repeat-mode song from males present in the study area in 1989 but not in 1990 were used as additional tapes for the stranger playbacks. As hooded warblers remember their neighbors from year to year (Godard 1991), I did not use these tapes with subjects that had been in the study area in 1989.

In this study, 12 subjects that had at least two neighbors received two different treatments, each consisting of four playbacks. One treatment measured the responses of a male to a neighbor before and after the simulated intrusion of that neighbor into the subject's territory. The other treatment measured the responses of the subject to a neighbor before and after the simulated intrusion of a non-neighboring (stranger) bird. Each subject received both treatments separated by 8–10 days.

Both treatments began with a playback of a neighbor's songs approximately 10 m inside the subject's boundary shared with that neighbor (methods are similar to those reported for playback of neighbors' songs by Godard 1991). The speaker was placed 2–2.5 m above the ground in a tall shrub or small sapling and connected to an Amplivox amplifier driven by a Sony TC-D5M recorder. All playbacks were standarized to 90 dB at 1.0 m in an anechoic environment (a large field with dense weeds). To standardize the subject's behavior and to insure that he was within hearing distance, I began the first playback after the subject had sung for 1 min, 25–60 m from the speaker. As neighbors' songs were used to simulate this intrusion, I also stipulated that the neighbor whose songs were to be used in the playback had to be quiet before playback could begin. Once these conditions were met, playback began and subjects' responses were recorded for the 3 min during the playback and for 9 min afterwards. During this 12-min period, the number of songs, singing mode, number of flights, time to approach the speaker, time spent within 10 m of the speaker, and the closest approach were recorded.

After 20–25 min I presented a second playback at least 50 m inside the same subject's territory. Typical hooded warbler territories in this study area had a diameter of 100–150 m. A flip of a coin determined whether I played the same neighbors' songs or a stranger's songs at this location, subject to a condition that six subjects received neighbors' songs and six received strangers' songs. Because I wanted to ensure that the subject responded to this stimulus, I continued to play songs until the subject approached within 10 m of the speaker (in most cases, songs were played for less than 3 min). Once the male had approached, playback of song was immediately terminated and responses of the subject were recorded for 9 min.

After another 20–25 min I presented a third playback with the same songs as those used in the second playback. The playback speaker was relocated at least 35 m from the second location but still at least 50 m from the boundary. Again, songs were broadcast only until the subject approached within 10 m of the speaker; responses were recorded for 9 min afterwards.

At least 45 min after the third playback ended, I presented a fourth and final playback using the neighbor's songs that were used in the first playback. I placed the speaker 10 m inside the same territorial boundary used in the first playback and did not begin until the subject had sung for at least 1 min, 25–60 m from the speaker and the neighbor whose songs were used was quiet. As before, responses of the subject were recorded for 3 min during the playback and for 9 min afterwards.

Thus six males received four playbacks of the same neighbor: playback of the neighbor at the boundary, followed by two playbacks simulating intrusions of the same neighbor, and then once again the same neighbor at the boundary (NNNN treatment). The other 6 males received two playbacks of the neighbor and two playbacks of a stranger: a neighbor playback at the boundary, followed by two playbacks simulating intrusions of a strange bird, and then the same neighbor again at the boundary (NSSN treatment).

Eight to ten days after the first treatment, each subject received the other treatment using a different neighbor from the one used in the earlier treatment. Thus each male received both the NNNN and the NSSN treatments.

To evaluate the effects of simulated intrusions by neighbors and strangers on subjects' responses to their neighbors, I calculated the difference between each of the measured responses to the neighbors at the boundary before and after simulated intrusions. As many of the behavioral responses were not independent, I used principal component analysis to generate a composite score for each male to each of the playbacks near the boundary. I then calculated the difference between composite scores before and after simulated intrusions to each treatment (NNNN and NSSN) and used these differences in an analysis of variance to examine the effects of the particular treatment (NNNN or NSSN) on the change in the responses a neighbors' songs at the boundary before and after simulated intrusions.

Of the 12 males 2 were not used in the final analysis. One male did not respond to the first neighbor playback inside the territory after broadcasting songs for 20 min. Thus he was eliminated from the study. The other male did not respond to the second boundary playback in the NNNN treatment (the playback after the simulated intrusion). Prior to the playback the male sang quiet songs 25 m from the speaker; 15 before the playback, he flew out of sight and was no longer heard. As he had responded vigorously to the earlier playback in the NNNN treatment and all the playbacks in the NSSN treatment 8 days earlier, it is likely that this male was not within earshot of the playback.

Results

All seven behavior measures indicated that males responded more aggressively to playbacks of neighbors' songs at the boundary after the simulated intrusions of those neighbors (NNNN treatment) than before (Fig. 1 A). For example, males came closer to and approached the speaker more quickly after simulated intrusions of neighbors than before the intrusions. They also spent more time in the vicinity of the playback speaker after the simulated intrusions of the neighbor and the number of flights increased.

On the other hand, only three of the behavioral measures (closest approach, time after, and latency to approach) indicated an increased response to neighbors' songs at the boundary after the simulated intrusions of strangers (Fig. 1 B, NSSN treatment). The magnitudes of these differences before and after intrusions were much less when a stranger as opposed to the neighbor was used as the intruder (Fig. 2). The other four measures in the NSSN treatment indicated no difference in response before and after simulated intrusion of a stranger or actually showed decreased responses after the intrusion. Therefore, territorial males appeared to increase their response to neighbors at the boundary after simulated intrusions of those neighbors but not after simulated intrusions of strangers.

These conclusions were supported by statistical analysis of the difference in principal component scores before and after the simulated intrusions. The type of treatment a male received (NNNN or NSSN) had a significant effect on the difference in the principal component before and after simulated intrusions (Fig. 3; $F_{1,18}=16.9$, $P<0.001$). Simulated intrusions of neighbors evoked a much greater behavioral change in subjects' responses to playbacks of neighbors songs at the boundary than did the simulated intrusions of strangers (Fig. 3).

The order of the treatments (day 1 vs. day 8) also had a significant effect on the scores before and after simulated intrusions (two-way ANOVA $F_{1,18}=6.7$, $P<0.02$). Because there was no significant interaction between treatment and order of presentation (two-way ANOVA $F_{1,18}=0.312$, $P>0.57$) I concluded that both treatments showed similar increases in the scores before and after simulated intrusions between day 1 and day 8.

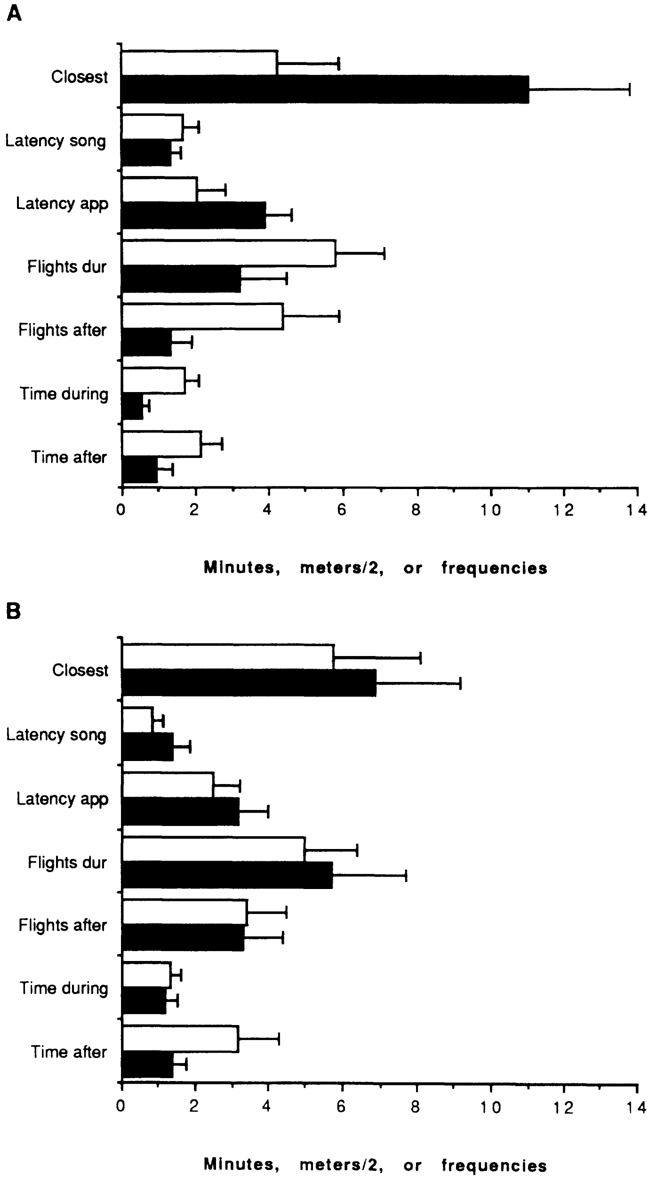

Fig. 1 A. Mean response (±SE) to the first (*black bars*) and second neighbor playbacks (*white bars*) at the boundary in the NNNN treatment. Responses include, *from top to bottom*: the closest approach (m/2), latency (min) to resume singing, latency (min) to approach within 10 m of the speaker, number of flights > 2 m during and after playback, and the time (min) within 10 m of the speaker during and after playback. An aggressive response consists of small values of closest approach and latency to approach and large values of other five behavioral measures. **B** Mean response (±SE) to the first (*black bars*) and second (*open bars*) neighbor playbacks at the boundary in the NSSN treatment. $n=10$ for all samples

Subjects responding to playbacks inside the territory did not react more to neighbors' songs than to strangers'

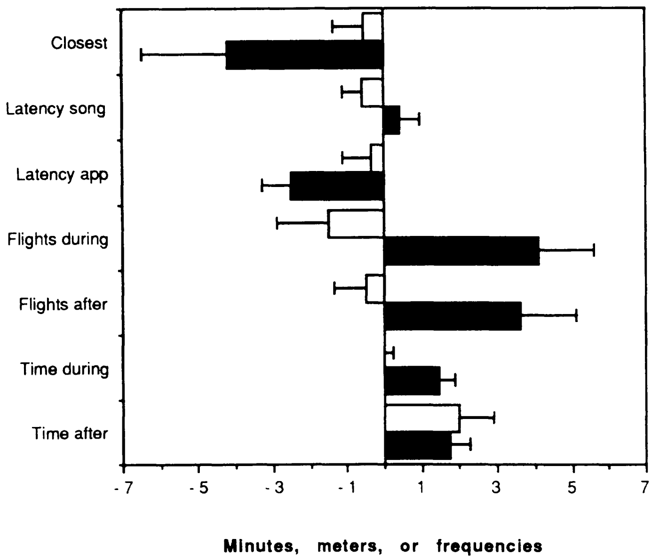

Fig. 2. Mean difference (±SE) in responses between the second and the first neighbor playbacks at the boundary (after and before intrusion) for each treatment. *Black bars*, NNNN treatment; *white bars*, NSSN treatment. *Response values* are the same as in Fig. 1, except closest approach (m/4). *Negative values* of the closest approach and the latency to approach within 10 m indicate a greater response to the second neighbor playback. Positive values to the latency to resume singing, number of flights during and after playback and the time within 10 m of the playback speaker also indicate a greater response to the second neighbor playback

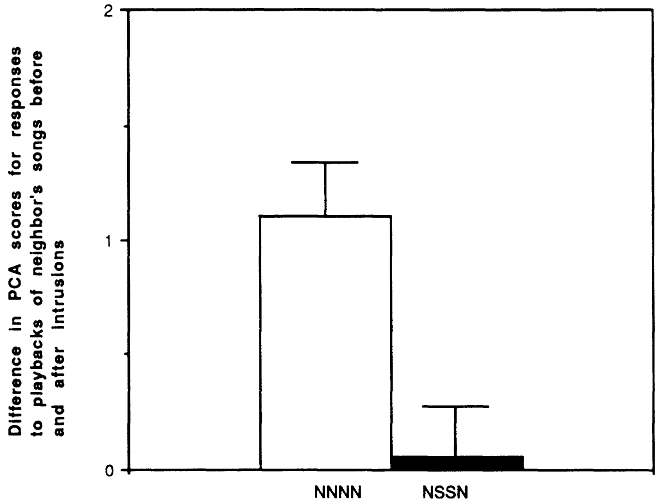

Fig. 3. Mean difference (±SE) in principal component scores between the first and second neighbor playbacks at the boundary for *NNNN* (*open bars*) and *NSSN* (*black bars*) treatments. A large value indicates that the responses to the second neighbor playback were more intense than the first. $n = 10$ for both treatments

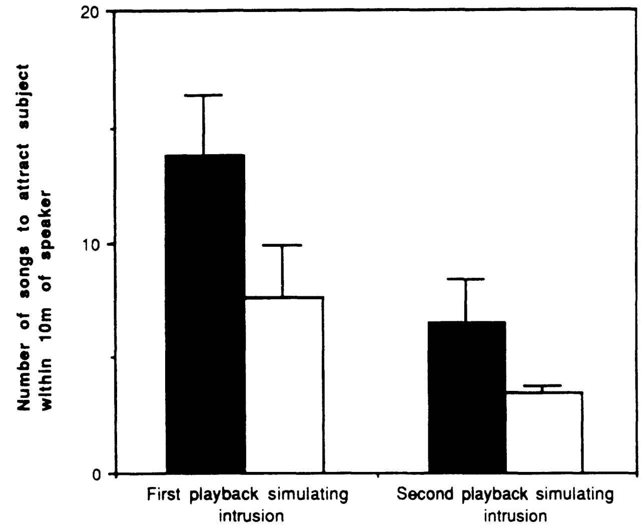

Fig. 4. Mean (±SE) number of songs played inside the territory required to bring subjects within 10 m of the speaker. *Black bars*, NNNN treatment; *open bars*, NSSN treatment. $n = 10$ for all samples

songs. After approaching the speaker, subjects did not respond differently to the first simulated intrusions of a neighbor or a stranger inside the territory (one-way ANOVA, $F_{1,18} = 2.3$, $P > 0.14$). Subjects also responded similarly to the second simulated intrusions of a neighbor and stranger inside the territory (one-way ANOVA $F_{1,18} = 0.006$, $P > 0.93$). Nevertheless, subjects might have been more reactive to strangers' songs as it took fewer songs of strangers to attract males to the speaker in playbacks simulating intrusions than songs of neighbors. This difference, however, only approached significane (Kruskal-Wallis one-way ANOVA, $P < 0.07$) (Fig. 4). The number of songs required to attract a subject during the first simulated intrusion was significantly less than during the second (Kruskal-Wallis one-way ANOVA, $P < 0.01$).

Discussion

Retaliation as a conditional response

This study examined the responses of territorial hooded warblers to neighbors that were simulated to no longer respect mutual boundaries. As is typical of other territorial songbirds (Falls 1982), hooded warblers did not respond much to neighbors singing near a shared boundary (the first playbacks of neighbors' songs in this study; see also Godard 1991). However, after responding to neigbor's songs played inside the subject's territory, hooded warblers increased their responses to playbacks of that neighbor's songs near their shared boundary. This increase in response was not due to general arousal as there was no significant increase in males' responses to a neighbor's songs at the boundary after a simulated intrusion by a stranger. In other words, males increased their responses to a neighbor near a mutual boundary specifically after simulated intrusions by that neighbor.

Responses to the first playback of neighbors' songs at the boundary decreased from day 1 to day 8. This effect of order could result, in part, from the longer period of time that neighbors had been in contact with one another. Perhaps by the time of the later presentations, relationships were more clearly established and thus males were less likely to respond to the first playbacks of neighbors' songs near a boundary. The increased responses to neighbors after either treatment on day 8 has no obvious explanation. However, the absence of a significant interaction between order of presentation and treatments indicated that the effects of the treatments could be accepted with confidence. Thus we can conclude that male hooded warblers retaliate against defecting neighbors. The behavior of territorial hooded warblers appears to fit a conditional strategy like tit-for-tat. Neighboring males do not respond much to one another, even when a neighbor is singing very close to a shared boundary. However, once a neighbor intrudes upon a male's territory, the latter becomes much more aggressive to that neighbor. These behavioral responses resemble the first two rules for the tit-for-tat strategy: (1) cooperate if your partner cooperates and (2) defect if your partner defects. The third rule, forgive your partner immediately, was not directly tested in this study. However, I did not notice heightened interactions between neighbors on days following the NNNN treatment.

Prisoner's Dilemma of asymmetric war of attrition?

Does the Prisoner's Dilemma apply to the relationships among territorial hooded warblers? If two territorial neighbors (N1 and N2) both cooperated, the reward (R) to each results from less energy and time devoted to vigilance and defense without the risk of intrusions by a neighbor. A defector with a cooperating neighbor, however, would do better than two cooperators, as it would spend less time in territorial defense but would still take advantage of access to his neighbor's territory without challenge (T). Though bigamy is rare in hooded warblers, I have found males with two mates; these males typically have very large territories. Thus T could be greater than R if a male could attain an extra mate by enlarging his territory without challenge. Two defectors, however, do less well than two cooperators as each would be subject to intrusions by a neighbor and therefore would have to remain vigilant in territorial defense (P). The cooperator with a defecting neighbor would do least well as its territory would be subject to frequent intrusions (S). As T (could be) $> R > P > S$, mutual restraint at boundaries (the dear-enemy effect) based on a conditional TFT-like strategy could be an example of reciprocal altruism. On the other hand T could be $< R$ if the original boundary was determined by spatial economic considerations such that at boundaries the benefit to cost ratio was reversed. The results from this study do show that neighboring hooded warblers could reduce interactions with one another based on a conditional TFT-like strategy. Whether or not this reciprocal behavior is an example of reciprocal altruism requires estimates of costs and benefits of specific territorial behavior that this study did not measure.

Ydenberg et al. (1988) have suggested that the dear-enemy effect can best be explained by an asymmetric war of attrition rather than by reciprocal altruism. In this game players attempt to assess each other's fighting ability and motivation, and then they "bid" a certain amount of energy and time (essentially cost) to invest in the interaction (Parker 1984). The player with the highest benefit-to-cost ratio should be the winner by drawing from the high-bid distribution. They suggest that neighbors interact less with one another than with strangers because neighbors are familiar competitors. Familiar competitors are less likely to draw bids from the same winner's distribution and as such escalated encounters are unlikely. On the other hand, neighbors and strangers have frequent escalated encounters because unfamiliar competitors are more likely to make role mistakes which results in (1) both players drawing bids from the winner's role and (2) indirectly altering the bid distribution.

They then use this model to explain the increase in response to neighbor's songs by territorial residents when those songs are played from a boundary opposite to the one shared with that neighbor (see Falls and Brooks 1975; Wiley and Wiley 1978; Godard 1991; Stoddard et al. 1991 for examples). A neighbor that appears to have changed territories is likely to gain increased benefits from a territorial dispute. Thus the increased response by the resident results from a reassessment of the neighbor's motivation which then directs the resident to draw a higher bid. If this model is accepted as relevant in explaining territorial relationships, the data from this experiment can be interpreted in the same manner as the data from studies investigating individual recognition. After repeated intrusions, residents reassess their neighbors' motivation and as a result draw a higher bid, resulting in increased responses to neighbors at the boundary after the simulated intrusions of those same neighbors (NNNN treatment). However, a war of attrition model has some restrictive assumptions and thus might not provide the best model for analyzing information exchanged in repeated contests such as neighbors interacting at a boundary (Getty 1989; but see Ydenberg et al. 1989).

These two models are not mutually exclusive. A male's change in aggression toward a neighbor might result from a reassessment of the opponent's motivation but the consequences of this reassessment could result in reciprocal altruism. At any rate the dear-enemy relationship in hooded warblers involves conditional responses of neighbors towards one another. Neighbors reduce interactions at shared boundaries unless one intrudes into the other's territory. If a neighbor invades his territory, a male responds by increasing aggression toward that neighbor.

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