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Conditional strategies in territorial defense: do Carolina wrens play tit-for-tat?

Jeremy Hyman
University of North Carolina at Chapel Hill, Chapel Hill, NC 27599, USA

Neighboring territorial animals are viewed primarily as intense rivals, but there are also opportunities for cooperation among competitors. Many animals respond less aggressively toward neighbors than to strangers. This phenomenon, termed the ‘‘dear enemy’’ effect, should be stable only when the reduced aggression is reciprocal. Territory owners should use conditional strategies in territorial defense, showing reduced aggression toward neighbors who cooperate by respecting territorial boundaries but increasing aggression toward invading neighbors. In this study I examined the response of territory owners to playbacks of neighbors at shared boundaries before and after intrusions by that neighbor or by strangers. Results showed that territory owners did not increase their aggression toward defecting neighbors but did increase their aggression toward neighbors after a simulated intrusion by a stranger. This surprising result might reflect the long-term relationship between neighboring Carolina wrens and the threat posed by rare intruding strangers. *Key words:* communication, cooperation, territoriality, tit-for-tat, *Thryothorus ludovicianus,* wrens. *[Behav Ecol 13:664–669 (2002)]*

Neighboring territorial animals are often viewed primarily as rivals competing for mates and space. Competitive interactions, such as displays and physical contests, may indeed be common, but not all interactions between neighbors are so clearly antagonistic. Indeed, in many cases, animals respond less aggressively toward neighbors than they do to strangers, a phenomenon termed the ‘‘dear enemy’’ effect (Fisher, 1954). Reduced aggression toward familiar competitors could be beneficial to a territorial animal if it decreases the likelihood of escalated contests whose outcome should be predictable. Reduced aggression could be beneficial for both parties by allowing neighbors to spend less time and energy defending shared territorial boundaries (Eason and Hannon, 1994; Logan and Wingfield, 1990).

But reduced aggression could be costly. A lowered response to a neighbor might be inappropriate if that individual continues to contest territorial boundaries and attempts to expand his or her territory. Many territorial animals increase their territory size when neighboring competitors are removed (Adams and Tschinkel, 2001; Both and Visser, 2000; Koskela et al., 1999). Though larger territories are not necessarily beneficial, expansion in the absence of neighbors suggests that competition from neighbors limits territory size. Stable boundaries resulting from reduced aggression toward neighbors come at the cost of relinquishing the possible benefits of territorial expansion. Thus, there is a cost to reducing aggression toward neighbors, and the benefit of reduced aggression can only be realized if the cost is paid by both territorial combatants. In this way, the territorial dear enemy effect resembles cooperation.

Cooperation requires an individual to act in a manner potentially costly to itself for the benefit of another. The evolution of stable cooperation requires either that cooperators receive some future benefit or that the apparently cooperative act actually carries no cost (‘‘by-product mutualism’’; Dugatkin, 1997). There is a potential cost to reduced aggression, however, if it leads to invasions by neighbors or if it means that a territory cannot be expanded, suggesting that the dear enemy effect is not by-product mutualism. When cooperation involves a cost, a possible mechanism for achieving stable cooperation is reciprocal altruism, where pairs of individuals trade bouts of cooperative behavior with one another (Dugatkin, 1997; Trivers, 1971).

Both Getty (1987) and Godard (1993) have suggested that the interaction between territorial neighbors may be modeled as a Prisoner’s Dilemma game, in which two individuals have a chance to cooperate or defect in interactions with each other, and mutual cooperators fare better than mutual defectors (Dugatkin, 1997). Defectors paired with cooperating individuals fare best, whereas a cooperator paired with a defector gets the lowest payoff. In the context of the dear enemy effect, cooperation could mean showing low aggression toward neighbors and respecting territorial boundaries, whereas defecting could mean showing high aggression or even attempting to expand a territory. Dear enemy cooperation could be explained by reciprocal altruism if territorial neighbors use conditional strategies such as tit-for-tat (Axelrod and Hamilton, 1981; Getty, 1987; Godard, 1993; Trivers, 1971). In the tit-for-tat strategy, a subject will cooperate when its partner cooperates and defect when the partner defects. If territorial neighbors use conditional strategies in contesting territory boundaries, we would expect an increase in aggression toward defecting individuals. Godard (1993) found such a conditional response in hooded warblers (*Wilsonia citrina*), which increase their aggression toward neighbors who appear to cross territorial boundaries.

In this study I attempted to replicate the study of Godard (1993) in a species with year-round territoriality, the Carolina wren (*Thryothorus ludovicianus*). Carolina wrens show neighbor/stranger discrimination (Shy and Morton, 1986) and the dear enemy effect (Hyman, 2001), reacting more aggressively toward strangers than toward neighbors. Carolina wrens often expand their territories to encompass areas formerly held by neighbors that have disappeared (Morton and Shalter, 1977), and territory size is density dependent (Haggerty and Morton, 1995; Simpson, 1982). These observations suggest that mutual acceptance of territorial boundaries in Carolina wrens requires birds to forgo the possible benefits of larger territories.

The stability of Carolina wren territories and the long-term

Address correspondence to J. Hyman, who is now at the Department of Biology, Duke University, Box 90338, Durham, NC 27708, USA. E-mail: jhyman@duke.edu.

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relationships between neighbors contrast with the short-term territories of hooded warblers, defended only during the breeding season. The strategies that territory owners might use in response to neighbors and strangers could vary greatly depending on their population demographics. To examine the generality of Godard's (1993) study, I used playback experiments to examine the response of territorial male Carolina wrens to invasions by neighbors and strangers. Following the methods of Godard (1993), I presented territorial males with intrusions of either strangers or familiar neighbors. Playbacks of a neighbor presented well within the subject's territory simulated an intrusion, or defection, by that neighbor, but playbacks of a stranger simulated an intrusion by an unknown individual. Measuring the responses of subjects to playbacks of neighbors at shared territorial boundaries before and after intrusions allowed me to test if territory owners increase their aggression toward defecting neighbors. A simulated intrusion by a stranger served to determine whether higher aggression toward neighbors results from a specific response to a defecting neighbor or from high level of aggression in general. If the subjects increase their aggression specifically toward defectors, I expected to see an increase in aggression only after the simulated intrusion of a neighbor. If subjects increase their aggression after an intrusion as a result of general stimulation, I expected increased aggression toward neighbors after either type of intrusion.

METHODS

I conducted this study at the Mason Farm Biological Reserve in Chapel Hill, North Carolina, USA. I performed experiments in April and May 1999, during the breeding season of Carolina wrens. All territorial birds included in this study as subjects or neighbors were members of mated pairs and had been present on their territory for several months. I estimated territory boundaries by extensive mapping of the locations of singing birds.

I recorded song with a Sennheiser K3U/ME88 ultradirectional microphone and a Marantz PMD221 recorder. 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 and digitized at 16 kHz and 16-bit accuracy on a 68030 Macintosh computer using Audiomedia hardware and software (Digidesign, Palo Alto, California). All songs were adjusted to the same maximal amplitude and rerecorded 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 ± 3dB, 2.5–8 kHz ± 2.5 dB). All playbacks were conducted from 0700–0900 h Eastern Standard Time.

Playback tapes were 45 s long and consisted of 7 repetitions of the same song type, delivered at a rate of approximately 10 songs/min. These tapes simulated natural singing behavior, as males typically repeat the same song type 5–250 times and at a rate of 5–15 songs per minute (Haggerty and Morton, 1995). Neighbors' territories directly adjoined the territory of the subject. Stranger's songs were recorded from birds with territories $>$ 5 territory diameters distant.

Song exemplars used as neighbor or stranger song were not matched with respect to song type. I did not determine the song repertoires of subjects and neighbors; therefore, I do not know if stranger song types were present in the repertoires of neighbors. Song-type sharing between neighboring male Carolina wrens can be high (66%; Haggerty and Morton, 1995), and song-type sharing is also likely to be $>$ 50% over the short distance between subjects and strangers in this experiment (Morton, 1987). Therefore, it is likely that stranger song types could have been in the repertoires of neighbors.

Thirteen subjects each received two playback treatments. One treatment measured the response of the subject to a neighbor before and after a simulated territorial intrusion by that neighbor (NNN trials); the other treatment measured the response of the subject to a neighbor before and after a simulated intrusion by a stranger (NSN trials). I randomized the order of presentation such that half of the subjects received the NNN trial first and half received the NSN trial first. For each subject, the NNN trial and the NSN trial were separated by 7–10 days. Both treatments followed a protocol with three playbacks and three observation periods. The first playback simulated the presence of a neighbor at a boundary shared with the subject. The speaker was placed at a position 5 m beyond the last mapped singing post for the subject and clamped to a sapling 1.5–2 m off the ground. I chose a point beyond the last mapped singing post to assure that the location designated for a playback at the boundary did not simulate a neighbor invading the subjects' territory. Playbacks began when both the subject and neighbors were silent. I used song exemplars from 13 different neighbors for playback, such that each subject was presented with songs from a different neighbor to avoid pseudoreplication. Subjects' responses were recorded for 15 min from the start of the playback.

After 25 min, I presented a second playback near the center of the subject's territory, simulating a deep intrusion. In the simulated neighbor invasions, each male heard the same playback tape that had been used in the first boundary playback. I simulated stranger invasions using song exemplars from 13 different strangers for playback, such that each subject was presented with songs from a different stranger to avoid pseudoreplication. I conducted the playback and observation period as above. In some cases, it was necessary to wait longer than 25 min before the subject and neighbors were silent.

After another 25 min, I presented a third playback, again simulating the presence of a neighbor at the shared territorial boundary. I conducted the playback and observation period as above. For each subject, I used the same neighbor song exemplars as above to simulate a neighbor at a shared boundary. Once again, it was necessary in some cases to wait longer than 25 min for the subject to become silent before the playback began.

I recorded the response variables latency to approach, closest approach, latency to sing, and number of songs. These variables tended to be correlated and were combined using principal component analysis to calculate a composite score for statistical analysis. I used the first principal component scores in a Wilcoxon signed-ranks test to compare playbacks and treatments. Power analyses were performed following Cohen (1977).

To determine if invasions by neighbors and strangers had different effects on subject birds, I examined the response of a subject to a neighbor at a shared boundary before and after an invasion by that neighbor and a stranger. In this way, for both treatments, I was able to determine if subjects responded differently to a neighbor at a territory boundary after a simulated intrusion. These methods differed from those of Godard (1993) in several respects, primarily in that the intrusions I used were shorter in duration. I examine the influence of these methodological differences in the Discussion.

RESULTS

Neighbor invasion trials

There was little difference in a subject's response to playbacks of neighbors at a boundary before and after a simulated in-

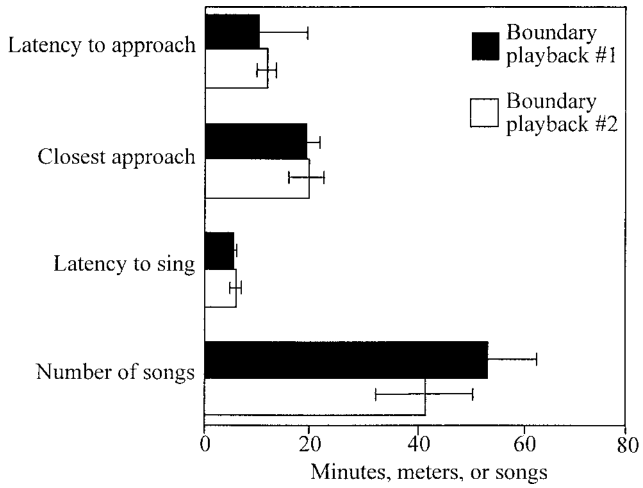

Figure 1
Means (±SE) of responses by subjects to the first (filled bars) and second (open bars) playbacks of neighbors at the correct boundary in the neighbor invasion (NNN) trials. Responses are latency to approach, closest approach, latency to sing, and number of songs.

trusion by that neighbor (Figure 1). The mean responses suggest that after the simulated intrusion, subjects responded to a neighbor with a slower latency to approach, similar closest approach and latency to sing, and a lower song output. The principal component loadings for the response variables are in Table 1. Comparing the scores of the first principal component showed no difference in the subjects' response to neighbors before and after a simulated neighbor intrusion (Figure 2; Wilcoxon matched-pairs test: $Z = -0.078$, $p = .937$). Comparing the response to a neighbor before and during an invasion clearly shows that subjects responded more strongly to the invasion (Figure 2; Wilcoxon matched-pairs test: $Z = -2.197$, $p = .028$).

Stranger invasion trials

Unlike the NNN trials, there were significant differences in the subjects' response to neighbors at the boundary before and after an intrusion by a stranger. After the intrusion by a stranger, subjects responded to neighbors with shorter latency to approach, closer approach, a shorter latency to sing, and more songs (Figure 3). Comparing the first principal component scores, I found that subjects responded significantly more strongly to neighbors after an intrusion by a stranger (Figure 2; Wilcoxon matched-pairs test: $Z = -2.981$, $p = .003$).

Godard (1993) found an increase in response after both neighbor and stranger invasions, as might be expected. However, the magnitude of the change in response was much greater after the neighbor invasion. Surprisingly, I found no increase in aggression after neighbor invasions, but to facilitate a comparison with Godard's (1993) results, I also analyzed these results by comparing the magnitude of the mean difference in response to neighbors before and after invasions in the two trials. Comparing these two means, I found a significantly greater change in response after the stranger invasions than after neighbor invasions (Wilcoxon matched-pairs test: $Z = 2.197$, $p = .028$).

Table 1
Loadings of the different response measures on the first principal component for responses to playback

Response measures	Loadings
Latency to approach	0.933
Closest approach	−0.932
Latency to sing	−0.402
Number of songs	−0.033

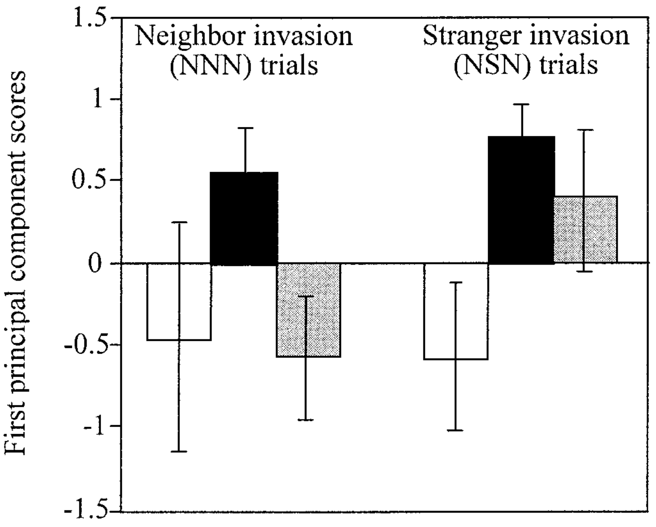

Figure 2
Means (±SE) first principal component scores for responses by subjects to neighbor invasion trials and stranger invasion trials. Bars shown are responses to playbacks of neighbors at a boundary before an invasion (open bars), to the invasion playbacks at the center of the subjects' territories (black bars), and playbacks of neighbors at a boundary after an invasion (gray bars).

Comparison of invasions by neighbors and strangers

There was no clear difference in the way subjects responded to playbacks of neighbors or strangers at the center of the territory (Figure 4). There was a trend to approach strangers' playbacks more slowly, but also to approach more closely. Comparing the first principal component scores, however, there was no significant difference in the subject's response

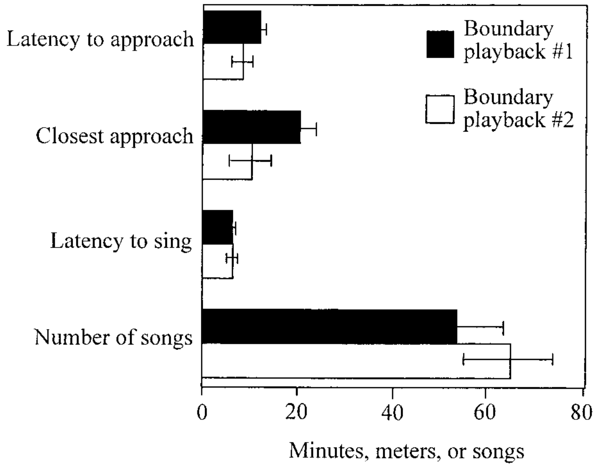

Figure 3
Means (±SE) of responses by subjects to the first (filled bars) and second (open bars) playbacks of neighbors at the correct boundary in the stranger invasion (NSN) trials. Responses are latency to approach, closest approach, latency to sing, and number of songs.

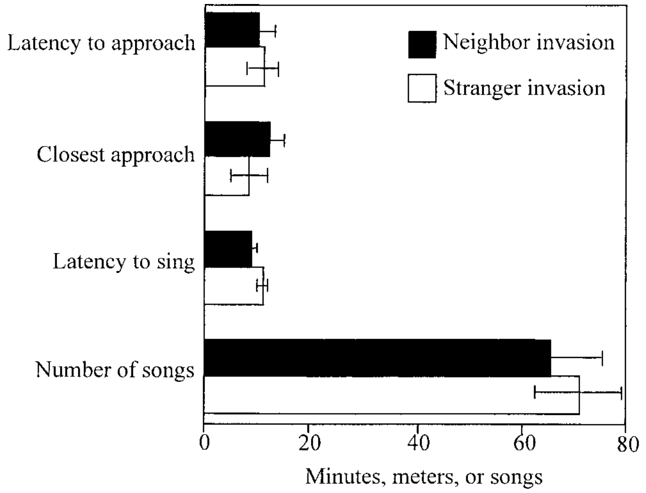

Figure 4
Means (±SE) of responses by subjects to playbacks of invasions by neighbors (open bars) and strangers (filled bars) at the center of the subjects' territories. Responses are latency to approach, closest approach, latency to sing, and number of songs.

to neighbors and strangers at the center of the territory (Figure 2; Wilcoxon matched-pairs test: $Z = -0.863$, $p = .388$).

As mentioned above, it was sometimes necessary to wait longer than 25 min after the invasion playback for the subject to be silent and for the next playback to begin. I considered the possibility that males responding for longer periods of time (longer than 25 min) might also respond more strongly to subsequent playbacks. However, there was no significant correlation between the strength of a subject's response to a playback at the center of his territory and his subsequent response to a neighbor at the boundary after the invasion (NNN trials $r_s = .266$; NSN trials $r_s = .378$). Thus, the strength of a subject's response to an invasion did not predict the strength of response to subsequent playbacks of neighbors.

The responses of the neighbors to playbacks on the territories of the subjects were noted as well. Previous experiments have demonstrated no consistent difference in the way neighbors respond to playbacks of themselves or of strange birds (Hyman, unpublished data). In the present study, neighbors frequently counter-sang with subjects responding to playback, but in no trial simulating a playback at a boundary did a neighbor respond more strongly that the intended subject. In this sense, there was no evidence of any defensive coalitions being established. Thus, the responses of neighbors were not considered to have had any consistent effect on the behavior of subjects.

DISCUSSION

I examined the response of territorial males to two kinds of simulated invasions: The NNN trials simulated an intrusion by a neighbor deep into the subject's territory. The simulated invasions elicited a high level of aggression, but there was no continuing effect in the form of a significant change in the subject's response to the neighbor at the boundary after the intrusion. Thus, subjects evidently did not retaliate against defecting neighbors.

The NSN trials simulated an intrusion by a stranger. If Carolina wrens use their discrimination abilities to establish dear enemy cooperation with neighbors, intrusions by strangers should have no effect on the subjects' relationships with neighbors. Contrary to this prediction, subjects responded significantly more strongly to neighbors at the boundary after an intrusion by a stranger.

The statistical power of the NNN trials to detect a difference of the size found in the NSN trial is high (power = 0.81, following Cohen, 1977), consistent with the fact that a significant effect was detected with the same birds and the same sample size in the NSN trials. Therefore, I have confidence that there was not an undetected difference in the subjects' responses to neighbors after an invasion. At the least, the magnitude of the increase in response after stranger invasions is much greater than any possible increase in response to neighbor invasions.

There was no significant difference in subjects' initial responses to invasions by neighbors or strangers. The power of this test to detect a difference of the size seen in the NSN trials was not as high (power = 0.66). The lack of a difference in response to neighbor or stranger invasions does not imply that Carolina wrens are not dear enemies, however. A differential response to neighbors and strangers is clearly observed at a boundary (Hyman, 2001), but not at the center of a territory. This is consistent with the idea that neighbors at a boundary represent less of a threat than do strangers. The relative threat of a neighbor increases after he invades the territory, and an invading neighbor could represent as great a threat as an invading stranger (Stoddard, 1996).

The only other study to examine responses of subjects to cooperating or defecting neighbors, found that hooded warblers responded more strongly to a neighbor after the neighbor intruded, but not after a stranger intruded (Godard, 1993). It appears that hooded warblers use strategies like tit-for-tat, responding specifically to defecting neighbors with higher aggression. Carolina wrens thus differed from hooded warblers in a similar experiment in that wrens did not show a simple tit-for-tat response by becoming more aggressive toward defecting neighbors. Instead, they increased their response to neighbors after invasions by strangers. Carolina wrens discriminate between the songs of neighbors and strangers (Hyman, 2001; Shy and Morton, 1986). Thus, it is unlikely that the increase in response to neighbors after stranger invasions is caused by confusion about the identity of the intruder. Additionally, the differential response after invasions by neighbors and strangers indicates a clear ability to discriminate.

My methods followed those of Godard (1993), but with a few differences. First, Godard simulated a neighbor at a boundary with a playback located 10 m inside the subject's territory. My boundary playbacks were located 5 m beyond the subject's territorial boundary. Second, Godard performed two intrusion playbacks per trial, whereas I simulated only a single intrusion. Finally, during the intrusions, Godard played songs until the subject approached within 10 m, whereas in the present study, all intrusion playbacks lasted 45 s. These differences make it likely that subjects in the present study were provoked to a lesser degree, which could explain the lack of increased aggression toward intruding neighbors, but not the increased level of aggression toward neighbors after an intrusion by a stranger.

Ecological differences between Carolina wrens and hooded warblers might account for the behavioral differences in response to neighbors and strangers. Carolina wrens and hooded warblers differ considerably in terms of the length of interaction of neighbors and the likelihood of encountering strangers. Neighboring territorial hooded warblers interact over the course of 3–4 months on their breeding grounds (Evans Ogden and Stutchbury, 1994). Territory owners might encounter strangers regularly because young birds settle territories in the spring, and males unsuccessful in attracting a mate may switch territories (Wiley RH, personal communication). In year-round territorial Carolina wrens, young birds settle on territories in their first fall (Haggerty and Morton, 1995). Thus, Carolina wrens in spring have been neighbors from 7 months to several years, and intruding adult strangers in spring are rare. The increased length of interaction between neighboring Carolina wrens could select for a more forgiving strategy, overlooking the occasional intrusion as soon as the neighbor returns to his territory. For Carolina wrens, the intrusion of an unknown competitor might cause such high alarm that an increased aggressive response carries over toward all potential rivals, including neighbors. In this sense, the increase in response would not be a specific adaptation directed toward neighbors, but rather, subjects reacting aggressively toward neighbors could still be reacting to the earlier invasion by a stranger. Additionally, all territory owners in a neighborhood might react differently after an invasion by a stranger. An invasion by a stranger could suggest that a territory owner is at severe risk for territory loss. If neighbors come to probe the subject's ability to defend his territory, subjects might need to reassert their territorial or social status, as either neighbors or mates could be eavesdropping on these interactions (McGregor and Dabelsteen, 1996; Naguib et al., 1999; Otter et al., 1999). However, I found no evidence that the strength of subjects' reaction toward stranger invasions predicted his subsequent response to neighbors at a boundary, though it is possible that responses to invasions by neighbors and strangers differed in ways I did not measure.

There is also a difference in the type of threat posed by invading neighbors and strangers. Carolina wrens and hooded warblers also differ in their extrapair breeding behavior. In multiple studies of hooded warblers, 18–47% of females had at least one extrapair young, and the extrapair father is often a neighbor (Evans Ogden and Stutchbury, 1994). Carolina wrens apparently do not engage in extrapair copulations (Haggerty et al., 2001). Short-term invasions by neighbors could result in loss of paternity in hooded warblers, but not in Carolina wrens. For hooded warblers, the threat of cuckoldry by neighbors might represent a greater threat than invasions by strangers. For Carolina wrens, invading strangers might be a more significant threat because they present an unprecedented threat to usurp a male's territory. In both species, the pattern of aggression might simply reflect a continuing aggressive response after the most threatening intrusion.

The acceptance of mutual territorial boundaries in Carolina wrens requires territory owners to forgo the possible benefits of larger territories. If we define this scenario as a game where cooperation means showing low aggression at boundaries and defection means showing high aggression and trying to expand territory boundaries, the payoffs would be as follows. A wren able to expand his territory (defector) without challenge from a neighbor (cooperator) clearly has a higher payoff than any male who cooperates. Mutually cooperating males achieve dear enemy benefits, while continually defecting males would be in a constant fight over territory boundaries. Finally, mutually defecting males would be expected to do better than a cooperator paired with a defector because the cooperator would inevitably lose the benefits of holding a territory if intruders are unchallenged. Thus, in this scenario, the payoffs fit the conditions for the Prisoner's Dilemma. The lack of increased aggression toward defecting neighbors does not necessarily indicate that neighboring Carolina wrens are not in a Prisoner's Dilemma. Rather, the failure to increase aggression toward intruding neighbors could indicate that Carolina wrens either do not use tit-for-tat at all or use more forgiving strategies than hooded warblers, such as generous tit-for-tat (Nowak and Sigmund, 1992), which allows for occasional unchallenged defections by neighbors.

Ydenberg et al. (1988) proposed the asymmetric war of attrition rather than reciprocal altruism to explain the dear enemy effect. In this model, extended fighting occurs when unfamiliar pairs of competitors both think they are likely to win a contest. Familiar neighbors rarely engage in escalated fights because they make educated assessments of the likely outcome of a fight. This model, or additionally, the ''fighting-to-learn'' model proposed by Getty (1989), are not necessarily alternatives to reciprocal altruism models of the dear enemy effect. These models provide proximate explanations for why neighbors stop fighting over shared boundaries, but they do not take into account mutual benefits that accrue from a reduction in aggression between established neighbors. The mechanism that results in lower aggression toward a neighbor does not necessarily account for the evolution of reciprocally lowered aggression between neighbors. The Prisoner's Dilemma provides a framework to understand when reciprocal restraint can evolve.

It is worth emphasizing that dear enemies in some species have not agreed to a truce in all aspects of their behavior. Radio-tracking studies show that territorial neighbors make frequent foraging trips into neighboring territories (Jansen, 1999; Zach and Falls, 1979), and DNA fingerprinting reveals that neighbors are competitors for extrapair copulations in most species (Kempenaers et al., 1999; Langefors et al., 1998; Westneat, 1990). These areas of competition do not prevent neighbors from attaining dear enemy cooperation, suggesting that the benefits of dear enemy cooperation must be strong. Possible benefits of dear enemy cooperation, including decreased fighting (Eason and Hannon, 1994; Logan and Wingfield, 1990), establishing defensive coalitions (Elfstrom, 1997; Getty, 1987), and avoiding the appearance of territory instability that may attract floaters (Beletsky, 1992), could lead to increased reproductive success (Beletsky and Orians, 1989). The widespread existence of the dear enemy effect might be explained by the variety of benefits available to familiar, cooperative neighbors. However, the strategies that territorial animals use to achieve dear enemy cooperation might differ considerably, depending on the possible benefits and on the population dynamics that underlie the formation of territorial neighborhoods.

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