Indirect reciprocity: song sparrows distrust aggressive neighbours based on eavesdropping

Çağlar Akçay [a,*], Veronica A. Reed [b], S. Elizabeth Campbell [a], Christopher N. Templeton [b,1], Michael D. Beecher [a,b]

[a] Department of Psychology, University of Washington
[b] Department of Biology, University of Washington

ARTICLE INFO

The evolution of cooperation between unrelated individuals has been a central issue in evolutionary biology. The main problem in most theories of cooperation is how a cooperative player selects individuals to 'trust' so that he does not get exploited by noncooperators. While early models emphasized the role of direct experience with individuals in deciding who to trust, more recent work has shown that individuals can eavesdrop on interactions between other individuals to identify cooperators and noncooperators. This second route to cooperation is called indirect reciprocity. In spatially structured populations with repeated interactions between players, both sources of information (direct experience and observed reputation) are readily available. Most models and empirical studies to date, however, have considered indirect reciprocity only in one-shot interactions when direct experience is not available. We examined the role of indirect reciprocity in the maintenance of mutual restraint in aggression (Dear Enemy cooperation) between territorial male song sparrows, *Melospiza melodia*. We found that territory owners eavesdropped on simulated defections by a neighbour (intrusions onto a third bird's territory) and subsequently retaliated against these defecting neighbours. Taken together with our previous results, these results suggest that both direct and indirect reciprocity can be at work in repeated-interaction scenarios, and together lead to emergence of cooperation.

The evolution of cooperation in circumstances where unrelated individuals are expected to be in fierce competition is a persistent puzzle in evolutionary biology. When cooperation is potentially costly, the emergence and stability of a cooperative strategy depends on how it fares against noncooperating strategies. This is the case in the classic one-shot version of the Prisoner's Dilemma game: two players face a situation where mutual cooperation would yield a higher payoff for both players than mutual defection, yet at the same time, each player's best strategy is defecting whatever the other player does (Axelrod & Hamilton 1981; Axelrod 1984), hence the dilemma. For many years, the Prisoner's Dilemma has been the main model for the study of evolution and maintenance of cooperation.

One of the most striking examples of emergence of cooperation in the Prisoner's Dilemma, given by Axelrod in his classic book (Axelrod 1984), was displayed by soldiers during the WWI trench

warfare, who, despite their orders, developed a partial 'live and let live' truce between the trenches, in which both sides were deliberately ineffective in inflicting casualties on the other side (which in turn prompted some 'evolutionary thinking' from the commanders to disrupt this spontaneous emergence of cooperation). Such mutual restraint, however, is not unique to humans. Many territorial animals show a similar phenomenon, called the 'Dear Enemy' effect (Fisher 1954; Temeles 1994), which is the mutual restraint in aggression shown by neighbouring territory owners despite being in direct competition for mating opportunities, resources and space. For instance, although male song sparrows, *Melospiza melodia*, fight rigorously during territory establishment, they decrease aggression towards their neighbours once territory boundaries have been established (Stoddard et al. 1991; Stoddard 1996).

Why should a territorial animal show restraint in aggression towards his neighbour? Mutual restraint would be mutually beneficial because territory owners are freed of the necessity and consequent costs of continued aggression along their borders. However, a neighbour that shows restraint can be exploited by a neighbour that does not reciprocate, but instead expands his territory uncontested (Getty 1987). Thus, to avoid paying the cost of exploitation, territory holders have to adopt a strategy where they

* Correspondence: Ç. Akçay, Department of Psychology, University of Washington, Box 351525, Seattle, WA 98195, U.S.A.
E-mail address: caglar@u.washington.edu (Ç. Akçay).
[1] C. N. Templeton is now at the School of Biology, University of St Andrews, St Andrews, Fife, KY16 9TS, U.K.

can discriminate between 'trustworthy' (cooperative) and 'untrustworthy' (defecting) neighbours, and be aggressive only towards the latter. One element of this strategy is to use direct experience with the neighbour in determining whether to cooperate with him or not; that is, cooperate as long as your neighbour does too, but retaliate if your neighbour stops cooperating (e.g. intrudes on your territory). In fact, individual recognition of neighbours and the Dear Enemy effect has been repeatedly demonstrated in territorial songbirds (Stoddard 1996), and more recently, several studies have demonstrated that territory owners selectively increase aggression against neighbours that have recently increased aggression towards them (Godard 1993; Olendorf et al. 2004; Akçay et al. 2009). Most relevant to the current study, we demonstrated that male song sparrows increase aggression towards neighbours that have recently intruded on their territory, compared to neutral neighbours, which were not involved in the intrusion. This strategy of territory holders is reminiscent of the classic Tit-for-Tat strategy in the repeated Prisoner's Dilemma game (Axelrod & Hamilton 1981; Getty 1987). Strategies such as Tit for Tat, and variants of it (e.g. Nowak & Sigmund 1992), have been termed direct reciprocity, since they involve the use of direct experience with a potential partner in determining actions of the player.

Another more recent line of theoretical research has suggested a second basis for cooperation, when direct experience cannot be used because players only interact once with each other but have had the opportunity to observe the potential partner interacting with other individuals. In such cases, the player can choose to cooperate or not based on information gained in eavesdropping on the potential partner or his 'reputation' (Nowak & Sigmund 1998, 2005). Since the decision to cooperate or not involves the use of eavesdropped or indirectly acquired information, these strategies are termed indirect reciprocity (Alexander 1987).

Indirect reciprocity may be a particularly effective mechanism for maintaining mutual restraint between territorial neighbours because many territorial systems afford an extensive communication network where territory holders can eavesdrop on interactions between other neighbouring territory owners (McGregor 1993; Peake 2005). In particular, if a territory owner eavesdrops on an intrusion by neighbour A on neighbour B's territory, he can infer that neighbour A has defected and is pursuing an aggressive strategy, and that if A is untrustworthy in one relationship, he is likely to be untrustworthy in other relationships as well. Then, so long as our territory owner is able to distinguish between the defector and the victim, he would be expected to retaliate or increase vigilance against the defector. The threat of retaliation based on 'reputation', just like the Tit-for-Tat strategy based on direct experience, can maintain the mutual restraint between neighbours. Note that here, the eavesdropping territory owner judges the reputation of the neighbour (i.e. whether or not he's a defector) through directly observing him in an interaction with another neighbour (as opposed to the reputations being socially transmitted through gossip; see Sommerfeld et al. 2007).

Despite the many recent studies on eavesdropping in territorial systems (Peake 2005), indirect reciprocity between territory holders has not been demonstrated before. This is because most empirical studies (Peake 2005) of eavesdropping in territorial defence have focused on interactions where eavesdropping individuals obtain information on complete, or almost complete (Peake et al. 2002), strangers that they have never encountered before. Such a strategy was adopted with the aim of removing the confound of previous experience with the opponent from the experimental design and thus demonstrating that acquiring information about an opponent's trustworthiness solely via eavesdropping is possible. A similar situation exists in the theoretical literature, where the vast majority of modelling effort has been directed to testing whether reputations can be used effectively in one-shot interactions to maintain cooperation. Thus, to the best of our knowledge, there is no empirical evidence of indirect reciprocity between familiar neighbours.

We have previously shown that song sparrows recognize their neighbours (Stoddard et al. 1991) and retaliate against neighbours that have recently intruded on their own territory (Akçay et al. 2009), providing evidence for a Tit-for-Tat-like strategy. Here, we ask (1) whether a bird will eavesdrop on a simulated aggressive interaction between two of his neighbours in which one of the neighbours (the defector) intrudes upon the other neighbour (the victim), and (2) whether the bird will then respond to the defector by increasing vigilance and aggression towards the simulated defector. Subjects were radiotagged before the experiment, which allowed us to both confirm that the subject was in a position to overhear an intrusion occurring outside his territory and record his behaviour in response to the intrusion. Each trial started with a simulated intrusion by a neighbour (the defector) into the territory of another neighbour (the victim; see Fig. 1 for the experimental design). Thirty minutes after the simulated intrusion, we played songs of the defector or the victim from their respective territory boundaries, followed 15 min later by songs of the other one (the order counterbalanced across subjects). Note that in our experimental design we compared responses to two neighbours that were involved in an aggressive interaction in the victim's territory. The design thus provides a strong test of whether subjects can distinguish the roles of victim and defector. If the subject had indeed eavesdropped upon the intrusion and was able to correctly assign the roles of defector and victim, then subsequently he should respond more aggressively to the defector than to the victim when we simulated them singing from their respective boundaries.
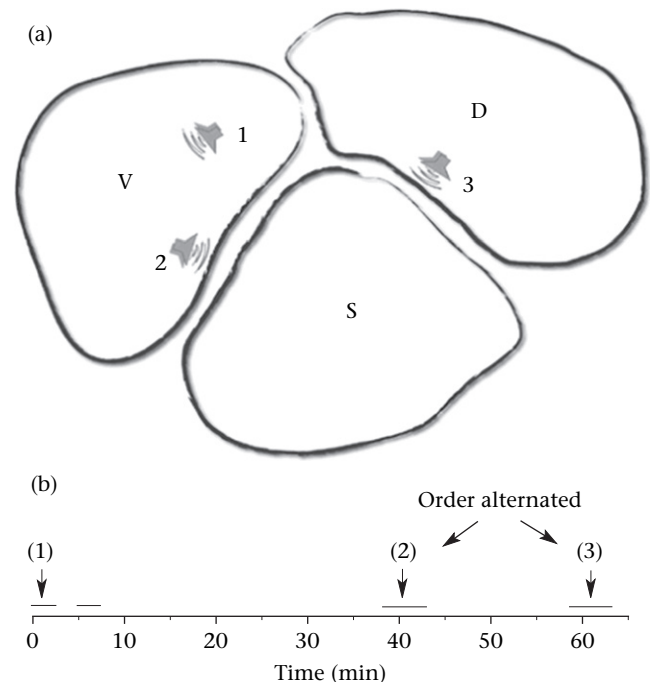
Figure 1. (a) Schematic of the experimental design and (b) the timeline of playbacks. Shapes delineate hypothetical territory boundaries of three neighbouring song sparrows. Each trial started with the simulated intrusion (1) where defector (D) songs were played from inside the victim's (V) territory. The subject (S) was subsequently tested with two boundary playbacks playing a victim's and defector's songs from their respective boundaries (2 and 3). The order for the boundary playbacks was counterbalanced across subjects (see Methods for details).

METHODS

Study Site and Subjects

The study was conducted in Discovery Park, Seattle, Washington, U.S.A. Ten males that held territories in Spring 2009 were selected as subjects in this experiment. Each subject's territory was mapped through extensive observation of movement patterns and singing behaviour (for a minimum of 10 h per male) on a large-scale map. Subjects had a median number of four neighbours (range 3–5). For each subject we selected two neighbours at random to serve as stimulus birds. In all but one case, these two neighbours also shared a boundary with each other.

Radiotelemetry

Radiotelemetry allowed us to locate the subject and record his behaviour during the trials. We fitted a male with small radio-transmitter (BD-2, Holohil Systems Ltd, Carp, Ontario, Canada) that was attached using a loop-harness (Rappole & Tipton 1991). The radiotransmitters weighed 1.00 g, which was less than 5% of the body mass of the bird. The radiotransmitters were removed after the experiment. Radiotagged birds were tracked with radio receivers (R-1000 with 3-element Yagi-antenna, Communication Specialists, Orange, CA, U.S.A.).

Stimuli

We recorded the song repertoires of males with Marantz PMD660 solid state recorders and Sennheiser ME66/K6 shotgun microphones. The repertoires were examined in Syrinx (John Burt, www.syrinxpc.com, Seattle, WA, U.S.A.). We selected one song per neighbour to serve as the stimulus based on the quality of recording. We then made a stimulus tape that contained 10 repetitions of a single rendition of the selected song with 10 s silence in between each repetition. Song sparrow songs last approximately 3 s, and thus the playback stimuli lasted approximately 120 s from the onset of the first song to the termination of the last song.

Procedure

The trials were conducted between 0700 and 1300 hours, between 11 and 14 May 2009. We did not test neighbours on the same day. Two observers equipped with radio receivers located the subject through triangulation before the trial and followed the movements and observed the behaviour of the subject during the playback and post-trial periods. One of these observers was situated towards the boundary of the stimulus bird during the intrusion playback, and alerted other experimenters if the stimulus bird sang during the playback, in which case the trial was terminated (to be repeated another day). A third observer controlled the playback from a portable music player (iPod Touch, Apple Inc.) attached to the speaker via a 20 m cable and recorded the trials using the same recording equipment as above. This observer was also responsible for monitoring the response of the victim to the intrusion and monitoring the stimulus birds in the boundary playbacks. All three observers communicated via walkie-talkie during the trials.

We sought to carry out all the playbacks while the stimulus bird was silent. Although the surest way to do this would be to remove the stimulus bird from the territory, doing so would create a major disturbance in the neighbouring territories of the subject, including song playback to net the stimulus birds. The latter problem would be particularly detrimental for our study as we were interested in the eavesdropping of the subjects and we did not want to create

a situation indicating that the subject's neighbours were under intrusion pressure from a strange bird. Therefore, we chose to leave the birds in their territories and abort any trials where a stimulus bird sang or appeared within view of the subject.

The stimulus bird interfered by singing during the playback in only one trial (during the intrusion stage), which was aborted and repeated 2 days later, at which point the stimulus bird did not interfere. We simulated an intrusion on the victim's territory by the defector using a nondirectional speaker (Pignose Model No. 7-100R) placed well inside the territory ($\sim$20 m away from the boundary with the subject) playing the defector's songs. The subject was within earshot (within 50 m of the speaker) at the start of all simulated intrusions. The playback loop was played twice, each lasting about 2 min, with 3 min in between the playbacks, simulating a persistent intrusion. Thus, the simulated intrusion trial lasted 7 min from the onset of the first playback to end of the last playback. We adjusted the speaker volume to normal amplitudes of song sparrow singing by ear.

Following the intrusion, we set up a directional speaker (see Burt et al. 2001) just inside the boundary ($<$5 m) of the stimulus bird with the subject on the stimulus bird's side, facing into subject's territory. We started the boundary playbacks 30 min after the end of the intrusion playback. The boundary playback lasted approximately 2 min and we continued to follow the subject's behaviour for 3 min after the playback ended. Fifteen minutes later, we did the other boundary playback. Half of the subjects received the boundary playback from the victim's boundary (playing victim's songs) first, followed by the boundary playback from the defector's boundary (playing defector's songs). The order was reversed for the other half of the subjects (the order of trials was determined by coin flip in the first trial and by alternating the order on every subsequent trial). We used the same playback tape in defector boundary playbacks and the simulated intrusion playbacks.

Response Measures

During the simulated intrusion we did not expect to observe an overt aggressive response by the subject because the intrusion was not directed at him, but we did expect him to eavesdrop on the interaction. Thus, we recorded whether he was in earshot of the intrusion, whether or not he approached the boundary of the victim during the intrusion and his closest approach to this boundary during the simulated intrusion.

For the subject's response to boundary playbacks and the victim's response to the intrusion we used four behavioural measures: latency to approach, closest approach, number of flights and number of songs. Note that these response measures are, in principle, available not only to experimenters but also to potential song sparrow eavesdroppers that can locate their neighbours from their vocalizations (Klump 2000). Latency to approach was defined as the first flight towards the speaker, and if the subject never made a flight towards the speaker during the playback (i.e. did not approach), we assigned a latency of 120 s to that trial, corresponding to the duration of the playback. In these cases of no approach in the boundary playbacks we used the real distance of the bird (located through radiotelemetry) from the speaker as the closest approach.

Data Analysis

All response measures except the number of songs in boundary playbacks were correlated with each other (all Kendall's $|\tau| > 0.45$, $P < 0.02$). As expected, number of songs, which does not reflect aggression in this species (Stoddard et al. 1991), did not differ between the two conditions (mean $\pm$ SD: 2.9 ± 3.3 versus

Table 1
Loading coefficients for the principal component analysis

Variable	Coefficient
Number of flights	0.883
Closest approach	−0.868
Latency to approach	−0.702

2.4 ± 3.0; randomization test, 100 000 runs: $P = 0.62$). We entered the three remaining measures (number of flights, closest approach and latency to approach) into a principal components analysis (PCA, correlation matrix, unrotated). The first principal component (PC1) explained 67.5% of the variation, and was taken as a measure of aggression, with higher scores indicating higher levels of aggression (see Table 1 for loading coefficients). We performed nonparametric tests on the aggression scores. Statistical tests were two tailed and were performed in SPSS 14.0 (SPSS Inc., Chicago, IL,

U.S.A.). Randomization tests were conducted in Mathematica 7 (Wolfram Research, Champaign, IL, U.S.A.).

RESULTS

As predicted, subjects responded more strongly to defectors than to victims when these birds were simulated singing from their respective boundaries postintrusion (Fig. 2). Eight of 10 subjects approached the defector boundary playback, whereas only three subjects approached the victim boundary playback. Subjects approached defectors sooner (mean $\pm$ SD: 44 ± 42 versus 93 ± 43 s), gave more flights (2.9 ± 2.8 versus 0.8 ± 1.5) and approached closer (19.5 ± 10.1 versus 30 ± 7.4 m). The same pattern was present in the overall (PC1) aggression scores: subjects responded significantly more aggressively to defector boundary playback (0.196 ± 0.90) compared to victim boundary playback (-0.712 ± 0.56; randomization test, 100 000 runs: $P = 0.004$).
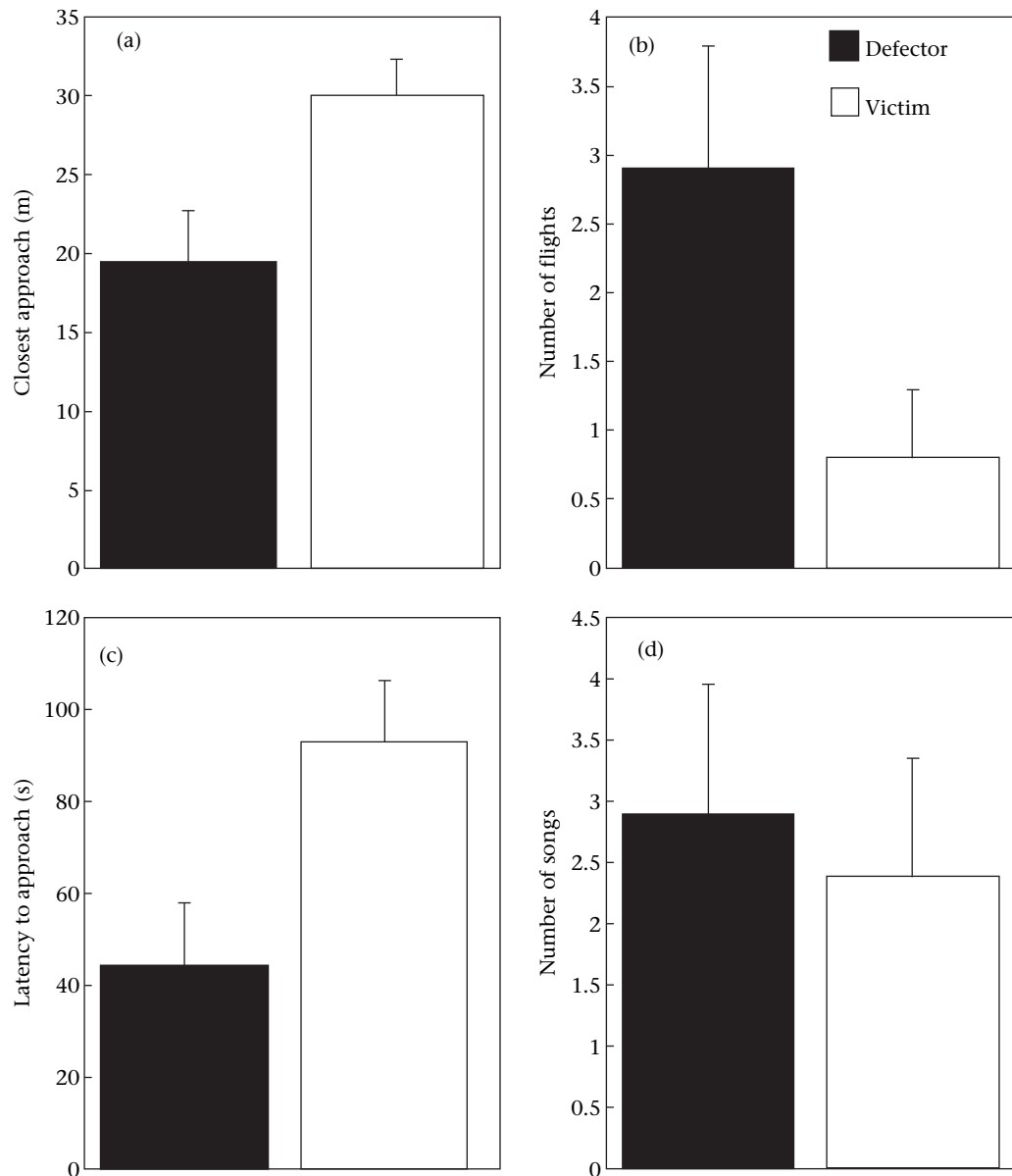

Figure 2. Mean + SE responses of subjects to boundary playbacks. All variables except number of songs were entered into a principal components analysis (PCA). Number of songs did not differ significantly between conditions (see Methods).

During the simulated intrusion, eight of 10 subjects approached the boundary of the victim to an average closest approach of 15.5 m (one subject actually intruded on the territory, and we took his closest approach as 0 m). The remaining two subjects did not move during the intrusion but were within earshot of the speaker (within 50 m of the speaker) and thus we can be certain that they overheard the interaction. Furthermore, subjects' closest approach to the boundary predicted the strength of their response to the defector boundary playback: the closer subjects approached the boundary of the victim during intrusion, the stronger they responded to the defector boundary playback (Kendall rank correlation: $\tau = -0.71$, $N = 10$, $P = 0.007$; Fig. 3a). Their closest approach, however, did not predict their response to the victim boundary playback ($\tau = 0.10$, $N = 10$, $P = 0.70$), indicating that subjects' approach during the intrusion did not simply reflect general responsiveness.

DISCUSSION

We found that eavesdropping territory holders retaliated against their neighbours that were simulated intruding on another neighbour, evidence that territory holders use recent interactions
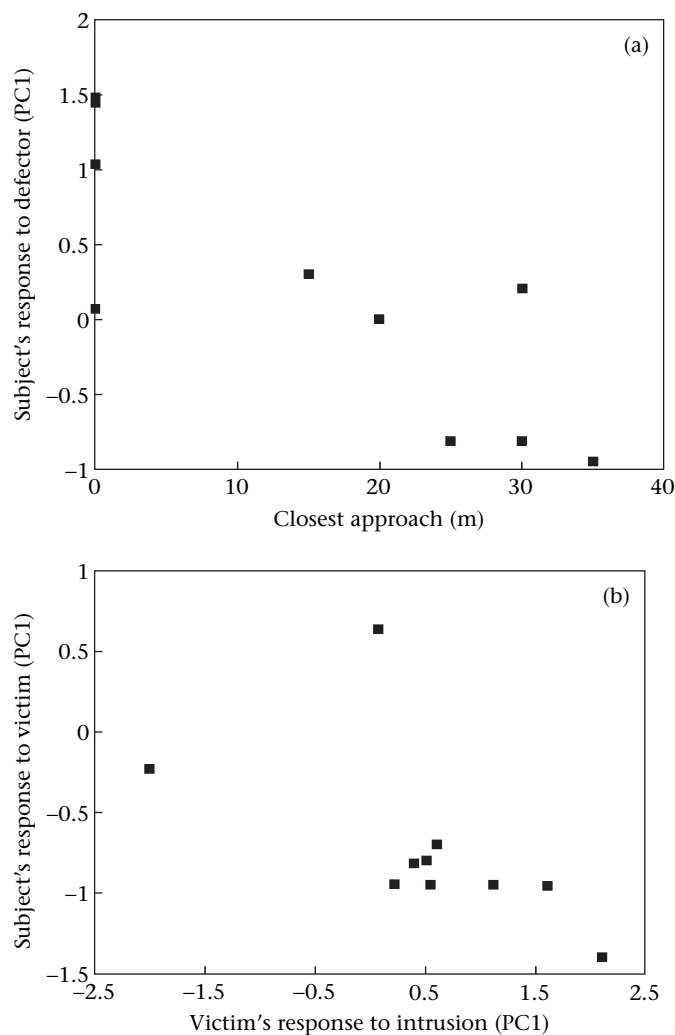
Figure 3. (a) Subject's response (closest approach to the boundary) to intrusion during the defector boundary playback. (b) Subject's response to the victim boundary playbacks relative to the victim's response to intrusion. PC1 refers to the first principal component derived from the principal component analysis.

of their neighbours with others (i.e. reputations) in choosing whether to continue the mutual restraint or not. Indirect reciprocity has previously been shown only between unfamiliar individuals in one-shot interactions (Wedekind & Milinski 2000; Milinski et al. 2002; Bshary & Grutter 2006). To the best of our knowledge, this is the first demonstration of indirect reciprocity between familiar individuals in a repeated-interaction situation, one in which we have previously also shown direct reciprocity (Akçay et al. 2009). Therefore, we suggest both direct and indirect reciprocity help to maintain the mutual restraint between neighbours. Below we discuss the implications of these results. First, however, we address a potential criticism of our experimental design.

We simulated an intrusion by a randomly selected neighbour (the 'defector') on another neighbour (the 'victim'). Because song sparrows typically sing little when they approach an intruder on their territory, this manipulation creates an asymmetry in which more songs will be heard from the simulated intruder (playback speaker) than from the victim. Thus, an alternative explanation for our results is that it was the recent singing activity of the simulated intruder during the intrusion, rather than the simulated intrusion (the defection) itself, that caused the subject to respond more strongly to the defector in the boundary tests. Under this 'activity hypothesis', had we not simulated any intrusion at all, but simply had one neighbour or the other singing in his own territory, the subject would have responded more strongly to whichever one had previously been singing more. According to this hypothesis, the fact that the defector was intruding on another territory has no relevance. We think this hypothesis fails to explain our results for several reasons. First, song sparrow males regularly sing from inside their territories, often at higher rates than those simulated in the current study, and if song sparrows increased aggression towards their neighbours every time they engaged in a bout of singing from their own territory, this would lead to a vicious cycle of escalation between neighbours, and thus to the absence of the Dear Enemy phenomenon we are trying to explain in the first place. Second, our design specifically included the victim boundary playback as the control condition to compare against defector boundary playback. The victim's behaviour, while not controlled quantitatively, provides a natural control condition as song sparrows typically defend their territories rigorously during an intrusion (Akçay et al. 2009). Victims were typically quite active during the intrusion trials. On average, victims approached within 5.2 m of the speaker, gave 8.5 flights and 4.4 songs, and showed a response latency of 97 s. There was a negative correlation between how strongly the victim responded to playback and the subsequent response of the subject to victim boundary playback (Kendall rank correlation: $\tau = -0.55$, $N = 10$, $P = 0.03$; Fig. 3b). There was a similar tendency for a negative correlation between the song output of the victim and the subject's subsequent response to the victim boundary playback ($\tau = -0.48$, $N = 10$, $P = 0.07$). Both of these results suggest just the opposite of what one might expect if subjects were simply responding to the high level of singing by the defector prior to the boundary playbacks irrespective of the location of singing. Taken together with the above considerations, we can rule out the activity hypothesis as a plausible explanation of our data.

Is It Indirect Reciprocity?

Territory holders do not automatically enter the Dear Enemy relationship. The mutual restraint between neighbours is a result of costly interactions during the negotiation of the territory boundaries. Song sparrows engage in intense and costly fights during territory establishment. These fights, in which both neighbours

challenge each other repeatedly by intruding onto each other's territories, continue until they settle upon a boundary where presumably neither of them can drive the other back any further, as predicted in aggressive pressure models (Adams 1998, 2001), or where neither has sufficient incentive to do so (Pereira et al. 2003). These 'boundary negotiations' (Maynard Smith 1982) typically happen at the onset of the breeding season, and once the boundary is established the neighbours display restraint in aggression. Thus, the boundary establishment process can be considered as negotiating a truce that allows neighbours to allocate time and energy for other activities such as foraging and pursuing matings instead of fighting.

Once established, mutual restraint is beneficial to both parties, just as mutual cooperation is more beneficial to both players than is mutual defection in the repeated Prisoner's Dilemma game. However, unilateral violation of the truce can happen anytime, as, for instance, when a nest placed too close to the edge of a territory by the neighbour's mate prompts an attempt at expansion by the neighbour (Burt & Vehrencamp 2005), or when an adjacent territory holder dies and is replaced by a new one (Stoddard 1996). When the truce is violated, a territory holder might suffer a cost, unless he responds with increased aggression himself. Increasing aggression against an aggressive neighbour is in the best immediate interest of a player, consistent with a conditional strategy that calls for defection when the opponent defects (Axelrod & Hamilton 1981; Pollock & Dugatkin 1992). This retaliation is similar to the withholding of help from players with bad reputations by human subjects in indirect reciprocity games: they neither pay an immediate cost by refusing to help and keeping the money for themselves (Milinski et al. 2002), nor do they inflict a direct cost on the opponent by withholding help.

Reliability of Reputation

As mentioned above, most studies, theoretical and empirical alike, have restricted their analysis of the effect of reputations to one-shot interactions, primarily to rule out direct reciprocity (but see Roberts 2008). One further reason for this strategy is the general assumption that reputation will be trumped by direct experience when both are available, as direct experience is assumed to be more reliable than reputation (Roberts 2008). It is interesting to compare our results with the results from our previous study that examined direct reciprocity (Akçay et al. 2009). In our previous study, we used an almost identical design to the current one, except that the intrusion was staged directly in a subject's territory, and we subsequently compared the responses of the subject to boundary playbacks of the intruder and a neutral neighbour. Having used identical boundary playback procedures and the same measures we can put the boundary playback data into a common PCA. Comparing the experiments we found that responses to the aggressive neighbours (i.e. birds that were simulated to intrude) in both studies were very similar, as were responses to the nonaggressive neighbours (i.e. the neutral neighbour and the victim; see Fig. 4). The effect sizes of the two studies were similar and large (Akçay et al. 2009: Cohen's $d = 1.28$; current study: Cohen's $d = 1.20$). Thus, the effects of direct experience and eavesdropping, at least with respect to subjects' subsequent behaviour, were not distinguishable.

In the current study, song sparrows acquired information about their neighbour's reputation by direct observation of an intrusion by the defector onto the victim's territory. When gaining information by first-hand eavesdropping (versus gossip), errors may be less likely. Nevertheless we found that the closer subjects approached the boundary of the victim during intrusion, the stronger they subsequently responded to defector playback (Fig. 4a), implying that the birds that moved closer gained more accurate information about the nature of the interaction.

A second problem with reputations stems from the fact that simply observing a defection may not be a reliable guide to the strategies of the individual involved. For example, observing two neighbours displaying aggression at the territory boundary is potentially ambiguous, as one of them might be truly defecting when the other is playing a Tit-for-Tat strategy, which also calls for increased aggression as retaliation. Aggression would be considered 'justified' if it simply represents retaliation. If, however, retaliators face aggression by eavesdroppers, it would destabilize mutual restraint in a chain reaction. So, the question that an eavesdropper faces is when should he infer that an aggressive opponent is a 'bad guy'? Indeed theoretical studies have shown that
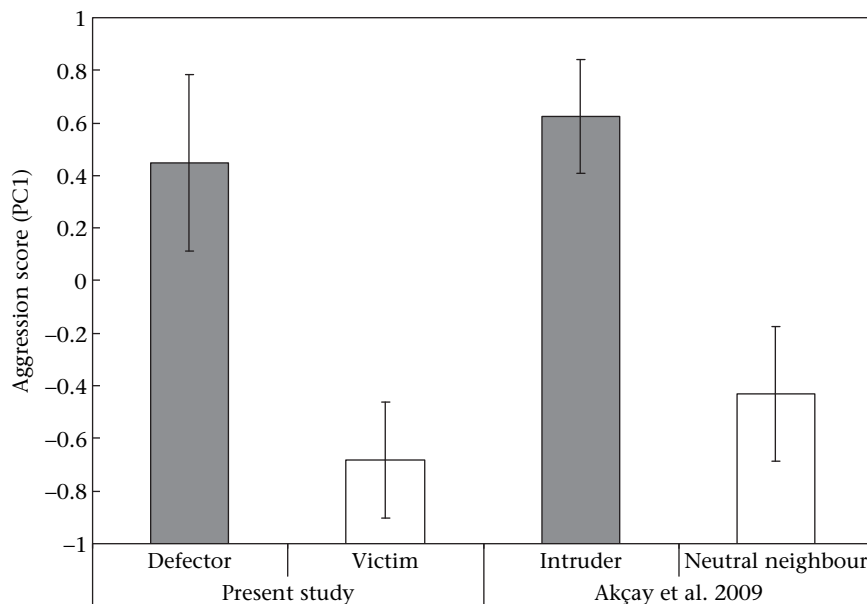
Figure 4. Comparison of results from the present study and those of Akçay et al. (2009). The common PCA (unrotated, correlation matrix) included the same three response variables from each study, and the first component, taken here as an aggression score, explained 67% of variance. Higher scores indicate higher levels of aggression.

indirect reciprocity results in high levels of cooperation when individuals have complex assessment rules that allow them to distinguish between justified and unjustified defections (Ohtsuki & Iwasa 2004, 2006). Without prior knowledge of the history of interactions between the eavesdropped individuals, however, it would be impossible to distinguish justified and unjustified defections (Panchanathan & Boyd 2003; Nowak & Sigmund 2005). Keeping track of such knowledge in unstructured populations where interactions with strangers is the rule rather than exception may require complex cognitive processes as well as reliable reputation mechanisms, relying perhaps on social transfer of information (i.e. gossip) (Nowak & Sigmund 2005).

We suggest, however, that in spatially constrained interactions where each individual interacts repeatedly with a limited number of neighbours, relatively simple rules of thumb can be used to accurately keep track of who is 'bad' and who is 'good', and thus, repeated interactions can facilitate cooperation through indirect reciprocity. We further suggest that empirical studies and theoretical models of eavesdropping should consider games with repeated interactions where information from direct experience can be combined with reputation. We have shown that song sparrows use both direct experience with Akçay et al. (2009) and reputations of their neighbours in determining who to trust. Many systems in nature may be expected to show the same combination of strategies.

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