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Male red-winged blackbirds distrust unreliable and sexually attractive neighbours

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In many species, territorial neighbours fight to establish their mutual border and then develop a truce, known as the dear-enemy phenomenon, characterized by reduced vigilance and aggression along the border. We present evidence that among male red-winged blackbirds (*Agelaius phoeniceus*) the dear-enemy relationship is a form of reciprocal conditional cooperation that is stabilized, at least in part, by retaliation against cheaters. Simulated intrusions by randomly chosen neighbours were punished by a targeted increase in vigilance and aggression that persists for days. We interpret this increase in vigilance towards trespassers as a manifestation of distrust. The conditional decrease in vigilance and aggression is tempered by each neighbour's probability of cuckolding the focal male. Male red-winged blackbirds maintained greater vigilance and aggression towards sexually attractive neighbours that were more successful at extra-pair fertilizations (EPFs). It is unlikely that males directly observed neighbours copulating with their mates. They were more likely to assess a neighbour's ability to achieve extra-pair copulations using surrogate cues that correlate with success at EPFs, including body size. Our results suggest that red-winged blackbirds use rules that incorporate their neighbour's behaviour and quality in their territorial interactions with one another. Our results expand our understanding of cooperation for animals and for humans as well.

Keywords: cooperation; reciprocity; territoriality; dear-enemy relationship; red-winged blackbirds (*Agelaius phoeniceus*)

1. INTRODUCTION

> In the absence of trust … many opportunities for mutually beneficial co-operation would have to be foregone… .
> (Arrow 1970, p. 20)

In most territorial species, adjacent neighbours fight to establish territorial borders and divide the resources. This setting would not appear to be a promising place to look for mutually beneficial cooperation. However, in many species, established neighbours settle into a truce, known as the dear-enemy phenomenon, characterized by reduced vigilance and aggression along their common border (Fisher 1954). We hypothesize that the dear-enemy phenomenon is an expression of reciprocal conditional cooperation (Getty 1987; Langen *et al.* 2000). Cooperation is a beneficial outcome that requires potentially costly collective action (Dugatkin 1997). In the dear-enemy phenomenon the beneficial outcome is a reduction in the time, energy and possibly health costs of continued vigilance and aggression along the border. The collective action is mutual restraint from trespassing and challenging. The potential cost is the risk of being cheated by a neighbour that takes advantage of this 'trust' and does not refrain from trespassing. We interpret reduced vigilance as a manifestation of trust (Rapoport 1971; Barr 2003), and we refer to trespassing dear enemies as unreliable.

There is considerable interest in the role of reciprocity in stabilizing cooperative relationships in nature (Trivers 1971; Axelrod & Hamilton 1981; Dugatkin 1997), and there are many apparent examples of 'tit-for-tat-like' reciprocity in animal and human interactions (Packer 1977; Seyfarth & Cheney 1984; Wilkinson 1984; Milinski 1987; Dugatkin & Alfieri 1991; Godard 1993; Wedekind & Milinski 1996; Stopka & Graciasova 2001). However, the relative importance of reciprocity in stabilizing cooperative relationships in nature remains controversial (Mesterton Gibbons & Dugatkin 1997; Stephens *et al.* 1997; Rapaport 2001; Sigmund *et al.* 2001) and difficult to demonstrate experimentally.

In this study, we use simulated intrusions to test the hypothesis that the dear-enemy relationship between neighbouring territorial male red-winged blackbird (*Agelaius phoeniceus*) is an expression of reciprocal conditional cooperation that is stabilized, at least in part, by retaliation against cheaters. If the dear-enemy relationship were strictly a result of by-product mutualism or kin selection, the reduced vigilance would not be fragile to cheating (Rothstein & Pierotti 1988; Dugatkin 1997).

In our experimental design, which is modified from Godard (1993), subjects are randomly chosen to be the victims of simulated cheating by randomly chosen neighbours. Random sampling implies that the average responses of the experimental and control subjects are representative of the sampled population. If our experimental and control subjects deploy tactics that are conditional on the neighbour's behaviour then we can infer that the neighbour's tactics are also conditional, and that neighbours are engaged in form of game. If there is mutual conditional trust that is fragile to cheating, and cheating is punished at some cost to both players, then the players are expressing 'tit-for-tat-like' reciprocity. We refer to

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simulated trespassers as unreliable and we interpret escalated vigilance and aggression as distrust.

Mate guarding is an important and costly aspect of territorial behaviour in many animals (Komdeur 2001) and neighbours are often the greatest threat to cuckold the territory holder (Gibbs *et al.* 1990). Previous evidence indicates that red-winged blackbirds appear to assess the quality of males on nearby territories (Beletsky & Orians 1987; Freeman 1987). We hypothesized that, in addition to conditional cooperation with their neighbours based on their neighbours' behaviour, territorial males should remain more vigilant and aggressive towards particular neighbours that are a greater threat to cuckold them. We refer to neighbours with higher success at cuckoldry as sexually attractive. We used molecular paternity analysis combined with morphological measurements and observations of territorial behaviour to test the hypothesis that in male red-winged blackbirds, the conditional reduction in vigilance and aggression that characterizes the dear-enemy relationship is tempered by the variable threat of cuckoldry.

2. MATERIAL AND METHODS

(a) *Background*

We conducted this study during the breeding seasons of 1998 and 1999 at the Experimental Pond Facility at the Kellogg Biological Station (Hickory Corners, MI, USA). The site consisted of a 3 × 6 array of circular ponds 30 m in diameter. The margin of each pond was densely vegetated with cattails (*Typha latifolia*) and was consistently colonized by red-winged blackbirds. One to four males settled on each pond and each male attracted between one and eight females onto its territory.

(b) *Experimental tests for reciprocity*

To test whether dear-enemy cooperation is conditional and fragile to cheating, in 1999 we simulated intrusions by territorial males onto another (focal) male's territory. If red-winged blackbirds use tit-for-tat-like strategies in their territorial interactions, then perceived intrusions by a neighbour should result in increased aggression towards the recorded song of that neighbour soon after the simulated intrusion. Simulated intrusions by a neighbour should also increase aggression towards that neighbour the day following the simulated intrusion. Perceived intrusion by a non-neighbour should result in no change in aggression towards the neighbour's song or towards the neighbour (Rothstein & Pierotti 1988; Godard 1993; Komdeur 2001). All experiments were reviewed by the Animal Use and Care Committee of Michigan State University, and met all relevant guidelines and legislation.

We first recorded the territorial songs of all territorial males between 06.00 and 10.00 on calm days in early April using a Sony Audio Acoustica 815a shotgun microphone and a Marantz PMD222 tape recorder. We uploaded several examples of each male's territorial song into .aud files at 16-bit resolution. We standardized all songs to equal maximum amplitude using Cool Edit sound editing software. We constructed playback files for each male by splicing 10 s of silence between each example of a male's song (minimum of four examples per male) resulting in a song rate of six songs per minute. This is within our observed range of male singing rate.

We randomly assigned focal males into either the experimental group (simulated intrusion by an established adjacent neighbour) or the control group (simulated intrusion by a randomly chosen territorial male from a non-adjacent territory). Intrusion was simulated by trapping and temporarily removing the neighbour, and then playing 3 min of recorded song from either the neighbour (experimental group) or a non-neighbour (control group) 5–10 m inside the subject's territory. To avoid pseudoreplication, we used each male's song only once as a neighbour and once as a stranger (Kroodsma 1990; Kroodsma *et al.* 2001). Simulated intrusions were performed during the first week of egg laying. We measured aggression towards 3 min recorded songs from the neighbour 45 min before (pre-intrusion), during and 45 min after (post-intrusion) simulated intrusions (figure 1*a*). We quantified aggression towards the recorded song by recording the latency to approach the speaker, closeness to the speaker and the number of songs, song displays, 'teer' calls, hovers and dive attacks directed at the speaker.

In addition to the response to the neighbour's recorded song, we also observed the degree of vigilance and aggression of each male towards all of its neighbours before and after the intrusion. Pre- and post-intrusion observations consisted of 20 min observations of natural male behaviour taken approximately a week prior to nesting (pre-trial) and the day following simulated intrusions (post-trial; figure 1*b*). Observations were performed after a 3 min acclimation period between 06.00 and 10.00 from a blind positioned 10 m from the territory. We kept a continuous record of the subject and determined the amount of time spent within 5 m of each of its territorial boundaries, the amount of time the subject spent foraging and the amount of time the subject spent off the territory. We also determined the number of songs, counter-songs and song displays performed at each neighbour's border.

(c) *Tests for sensitivity to the threat of cuckoldry*

Territorial residents should increase vigilance and aggression towards unreliable neighbours caught trespassing. They should also be more wary of sexually attractive neighbours that are more successful at gaining extra-pair fertilizations (EPFs) and are therefore more likely to cuckold them. To test for this, in 1998 we used paternity analysis combined with morphological measurements and observations of territorial behaviour (described in § 2b) performed the week that nesting began, to determine if males respond more aggressively towards neighbours that have cuckolded them. We also determined if males behaved more aggressively towards neighbours that were better able to obtain EPFs from females across the neighbourhood.

We collected blood from all 22 territorial males and 252 offspring in 93 nests on their territories. We also measured culmen length, wing chord, tarsus length and weight for all territorial males at the same time we collected blood. We determined paternity of nestlings using six highly variable microsatellite loci (Dawson *et al.* 1997; Gibbs *et al.* 1997; Hughes *et al.* 1998). DNA was extracted and amplified using methods outlined in Olendorf *et al.* (2004). The PCR product was run on 6% polyacrylamide gels and visualized using an FMBIO gel scanner. All gels were scored by hand by two authors (R.O. and K.S.) and verified using FMBIO image analysis software. We used the program Cervus (Marshall *et al.* 1998) to generate paternity exclusions or maximum-likelihood estimates of paternity. As previous work has shown that non-territorial males rarely gain fertilizations, we included only territorial males as potential fathers. Assuming error-free assignment of alleles, we estimated the probability of false inclusion (assigning the wrong father to

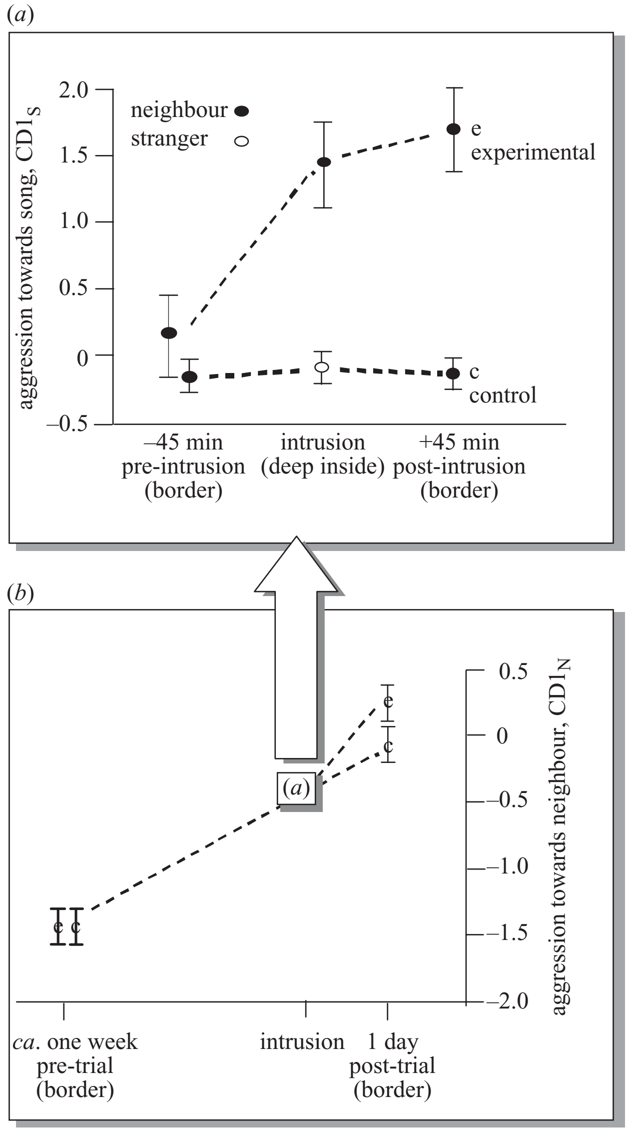

Figure 1. The experimental design and results for the simulated defection experiment. (*a*) Aggression and vigilance towards song playback within trials ($CD1_S$): the neighbour's song at the border pre-intrusion; the neighbour's (experimental) or non-neighbour's (control) song during the intrusion; the neighbour's song back at the border post-intrusion. The time of each playback relative to the intrusion is shown on the *x*-axis along with the position of the speaker (at the border or deep inside the focal male's territory). (*b*) Aggression and vigilance towards the neighbouring male ($CD1_N$) pre- and post-intrusion: *ca.* one week before the intrusion (pre-intrusion) and then again 1 day after the intrusion (post-intrusion). The rectangle labelled (*a*) indicates the approximate time that the playback trial was conducted relative to the pre- and post-trial observations. Error bars show standard error. $n = 6$ in both treatments.

a nestling) to be 0.7%. We were able to assign a father to 250 out of the 252 offspring from which we obtained blood (Gibbs *et al.* 1990).

(d) *Statistical analysis*

We used correspondence analysis to reduce the redundant dependent variables to a few orthogonal variables (ter Braak 1985). In this instance, correspondence analysis is more appropriate than the more common principal component analysis because some of the dependent variables cannot occur simultaneously or are not linearly related. We performed two separate correspondence analyses. The first analysis included each male's reaction to recorded song and resulted in two correspondent dimensions: $CD1_S$ and $CD2_S$ (correspondent dimensions are analogous to principal component axes). $CD1_S$ accounted for 50.9% of the variation in male response to recorded song. The second analysis included each male's vigilance and aggression directed towards neighbours following simulated intrusions from both 1998 and 1999. The second analysis resulted in two correspondent dimensions: $CD1_N$ and $CD2_N$. $CD1_N$ accounted for 48.1% of the variation in the responses to neighbours. In both cases, aggressive behaviours load positively onto the corresponding CD1, so we used the $CD1_S$ as our measures of aggressive response towards recorded song and $CD1_N$ as our measure of aggression and vigilance towards a neighbour (table 1). $CD2_N$ and $CD2_S$ never differed significantly among treatments for any of the analyses and are not discussed further.

Table 1. Aggression towards song in 1999 intrusion trials. (The first two correspondence dimensions, their component loading and percentage of variance explained by the correspondence analyses. (*a*) Vigilance and aggression by 12 males towards recorded songs of neighbours and non-neighbours in the 1999 experimental intrusion trials. (*b*) Vigilance and aggression by 37 males towards neighbours in 1998 and 1999.)

(*a*)	$CD1_S$	$CD2_S$
latency of response	−0.56	−0.43
closest approach	−0.55	−0.34
songs	0.05	0.21
song displays	0.51	0.68
calls	0.68	−0.48
hovers	0.72	−0.38
dives attacks	0.77	−0.23
variation explained (%)	50.85	28.40

(*b*)	$CD1_N$	$CD2_N$
time spent at border	0.29	0.77
time spent foraging	−0.56	−0.65
time spent off territory	−0.24	−0.05
songs at border	0.81	−0.07
counter songs	0.48	−0.05
displays	0.57	−0.08
variation explained (%)	48.13	25.35

We ensured that the data were sufficiently normal for parametric analysis by examining normal cumulative probability plots and by plotting the residuals of each test with the mean to ensure homoscedasticity. We used repeated-measures ANOVA to analyse the simulated defection experiment as we subjected each male to multiple playbacks. As each male had three to seven neighbours, we grouped interactions within male using either a nested ANOVA or an ANCOVA.

3. RESULTS

Our simulated defection experiment shows that red-winged blackbirds use tit-for-tat-like strategies in their dear-enemy relationships. Experimental and control males exhibited equally low levels of aggression towards the neighbour's song played at the border during the pre-intrusion playback (figure 1*a*). Dear-enemy relationships were already established. During the intrusion playback, subjects were very aggressive towards recordings of the neighbour but not towards the non-neighbour (figure 1*a*), showing that neighbours were treated as a greater threat than wandering strangers (consistent with their relative threat to cuckold the subjects). Post-intrusion, subjects escalated aggression towards the neighbour's song along the border in the experimental treatment but not in the control treatment (figure 1*a*; $CD1_S$, repeated-measures ANOVA: treatment $F_{1,11} = 12.914$, $p < 0.005$; playback $F_{2,22} = 0.066$, $p > 0.05$; treatment × playback $F_{2,22} = 15.103$, $p < 0.001$).

Males from both treatments were equally vigilant and aggressive towards their neighbours during pre-intrusion observations (figure 1*b*). Experimental intrusion by a neighbour, however, resulted in a greater increase in vigilance and aggression towards that neighbour the day following simulated intrusion, relative to the increase found in control intrusions (figure 1*b*; $CD1_N$ repeated-measures ANOVA: treatment $F_{1,11} = 2.147$, $p > 0.05$; observation $F_{1,11} = 15.551$, $p < 0.001$; treatment × observation $F_{1,11} = 17.425$, $p < 0.005$). Experimental intrusion did not alter a focal male's behaviour towards other adjacent neighbours whose song was never played back ($CD1_N$ repeated-measures ANOVA: treatment $F_{1,11} = 0.874$, $p > 0.05$; observation $F_{1,11} = 1.002$, $p > 0.05$; treatment × observation $F_{1,11} = 1.873$, $p > 0.05$).

Males in both treatments increased their aggression as the nesting cycle progressed from the pre- to post-trial period, but control groups increased their aggression to a lesser extent than experimental males (figure 1*b*). The general increase in aggressiveness over time is probably a result of increased fertility by the females and greater risk of cuckoldry during the second observational period (Tobias & Seddon 2000).

To determine whether vigilance and aggression are related to risks of cuckoldry, we analysed interactions between pairs of neighbouring males. Males behaved more aggressively towards males that had cuckolded them compared to males that had not (figure 2; $CD1_N$, nested ANOVA: male $F_{18,19} = 1.24$, $p > 0.05$; cuckoldry(male) $F_{19,42} = 2.32$, $p < 0.05$). There was also a positive relationship between aggression towards a neighbour and that neighbour's ability to gain EPFs across the population (figure 3; $CD1_N$, ANCOVA; male $F_{19,59} = 0.826$, $p > 0.05$; neighbour's EPFs $F_{1,59} = 4.465$, $p < 0.05$; male × neighbour's EPFs $F_{19,59} = 0.828$, $p > 0.05$).

Males may be able to estimate a neighbour's sexual attractiveness through physical characteristics. We generated a measure of male size by performing a principal component analysis on four aspects of male size (culmen length, wing chord, tarsus length and weight). The first principal component (PC1) accounted for 45% of the variance and each of the four aspects of male size loaded positively on it. We therefore use PC1 as our measure of male size. Male size (PC1) correlated positively with the number of EPFs associated with each male ($r_{21} = 0.54$, $p < 0.025$). Although males tended to increase aggression towards larger neighbours, there was considerable variation in each male's response to the size of its neighbours (figure 4, $CD1_N$, ANCOVA; male $F_{19,57} = 2.205$, $p > 0.05$; neighbour's size $F_{1,57} = 2.378$, $p < 0.05$; male × neighbour's size $F_{19,57} = 2.334$, $p < 0.01$).

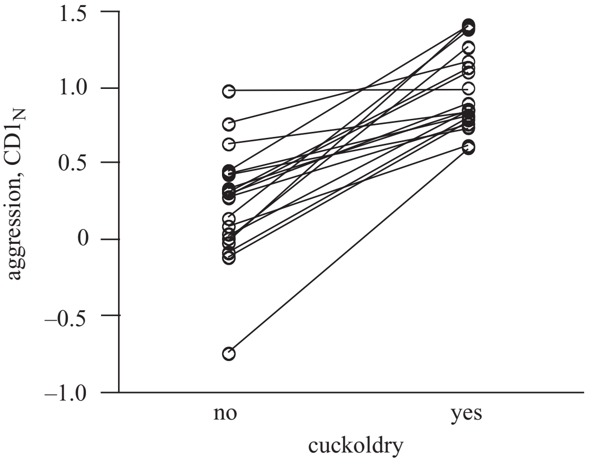

Figure 2. Average vigilance and aggression ($CD1_N$) by territorial males towards neighbours who sired young on their territories through EPF (cuckoldry yes) and those that did not (cuckoldry no). Each line represents one male and each dot represents the average aggression by a subject towards neighbours in that category. Each male had three to seven neighbours and there were 99 pairwise interactions included. Three males are not shown because one was cuckolded by all of its neighbours and two males were not cuckolded by any of their neighbours. $n = 19$ males.

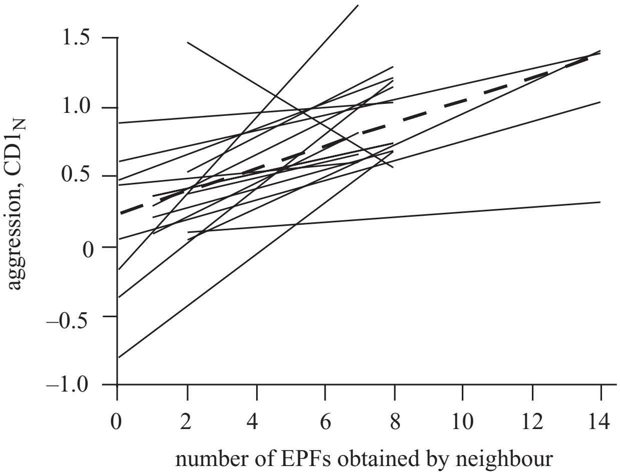

Figure 3. Aggression by territorial males in response to the total number of EPFs obtained by a neighbour across the entire population ($n = 99$ pairwise interactions, each male had between three and seven neighbours). The thick dashed line shows the overall trend; the thin solid lines show the trend lines for each individual male ($n = 22$).

4. DISCUSSION

Our simulated intrusion experiments show that reduced vigilance and aggression between dear enemies is a form of conditional cooperation that is fragile to cheating, which is punished by retaliation (Axelrod & Hamilton 1981; Getty 1987; Rothstein & Pierotti 1988). Males increased aggression both towards playbacks of their neighbour's song as well as towards their actual neighbour following simulated intrusion by that neighbour. In addition,

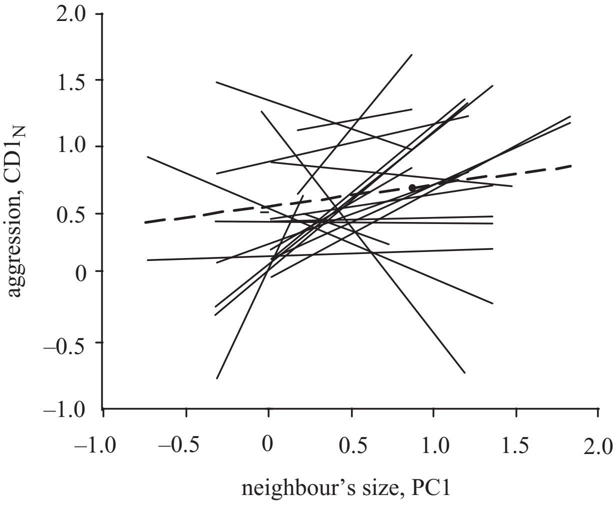

Figure 4. Aggression by territorial males in response to their neighbours size (PC1). The thick dashed line shows the overall trend; the thin solid lines show the trend lines for each individual male ($n = 22$ males, 99 pairwise interactions, each male had three to seven neighbours).

observations of territorial behaviour combined with paternity analysis show that male red-winged blackbirds maintain higher vigilance and aggression towards sexually attractive neighbours that are more likely to cuckold them. In essence, male red-winged blackbirds seem to use multiple criteria in determining the level of aggression they direct to individual neighbours.

It could be argued that the increased aggression displayed towards neighbours who appeared to have cheated was a result of a general increase of aggression by the focal male directed towards all neighbours in response to a territorial invasion. However, observations of focal male behaviour towards other neighbouring males show that the increase in aggression was directed only towards the neighbour that appeared to have cheated. These results show that reduced vigilance and aggression among dear-enemy neighbours is conditional on each neighbour reliably refraining from trespassing. The experimental design implies that the relationship is reciprocal. This pattern is reasonably described as 'tit-for-tat-like' reciprocity (Rothstein & Pierotti 1988).

Males behaved more aggressively towards neighbours that had cuckolded them, regardless of the simulated trespassing. Both males and females are known to make forays in search of extra-pair copulations. However, extra-pair copulations are cryptic and it is unlikely that a male can directly observe most extra-pair copulations between females from his territory and neighbouring males (Gray 1996, 1997). There is also no evidence that males can recognize the paternity of particular young in the nest (Kempenaers & Sheldon 1996). However, a male may be able to assess a neighbour's ability to gain extra-pair copulations (Nowak & Sigmund 1998; Komdeur 2001; Thusius *et al.* 2001). We reason that the total number of EPFs obtained by a male should correlate with his sexual attractiveness to females. Sexual attractiveness to females should be apparent to other males, and those males might be more hostile towards sexually attractive neighbours. We found that males do behave more aggressively towards neighbours that are most successful at obtaining EPFs.

We also found that larger males gain more EPFs. This finding is consistent with several other studies which suggest that sexual dimorphism in Icterids is a result of sexual selection (Searcy 1979*a*,*b*; Rohwer *et al.* 1996). Although we found that males are significantly more aggressive towards larger neighbours, this relationship left considerable variance unaccounted for. There are several potential sources of noise in the relationship between size and aggression. First, males may use many cues to assess a neighbour's ability to achieve extra-pair copulations. For instance epaulet size and colour, territory quality and behavioural cues such as nest defence effort are all potential cues that could convey information about a male's sexiness (Searcy 1979*a*; Eckert & Weatherhead 1987; Milks & Picman 1994). Second, the relative size of neighbours may be important. Larger males may be more aggressive than smaller males towards large neighbours. Finally, only a few points (3–7) characterized each male's behaviour towards its neighbours. We therefore probably had little power to consistently detect a relationship within males.

In this study, we used simulated defections to show that male red-winged blackbirds exhibit a reciprocal relationship with their neighbour wherein neighbouring males reduce aggression and vigilance with each other, but increase these behaviours in response to perceived defections. We also show that males modulate their willingness to reduce aggression with their neighbours in response to either the neighbour's cuckoldry or the neighbour's perceived 'sexiness'. Future studies that can tease these two hypotheses apart are needed. These results show that male red-winged blackbirds seem capable of using a surprisingly complex set of factors in their social interaction with their neighbours.

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