

Enemies are not always dear: male song sparrows adjust dear enemy effect expression in response to female fertility



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The dear enemy effect arises when territorial animals respond more intensely to unfamiliar strangers than to familiar neighbours. This widespread behavioural phenomenon occurs because strangers represent a threat to both an animal's territory and parentage, whereas neighbours represent a threat only to parentage. Recent research in birds demonstrates some flexibility in the dear enemy effect across the breeding season. Given that neighbours often sire extrapair young, male animals may benefit by responding more aggressively to neighbours during periods of female fertility. Here we investigate the hypothesis that the dear enemy effect varies with female fertility by testing the prediction that male birds will respond more strongly to neighbours when their own mates are fertile than when they are not fertile. We conducted a playback experiment with wild song sparrows, *Melospiza melodia*, repeating playback sessions to paired territorial males over the course of a breeding season, including periods when females were fertile and periods when they were not. Male song sparrows displayed a dear enemy effect only when their social mate was not fertile. We conclude that male song sparrows adjust behaviour towards neighbours based on their own mate's fertility status, presumably because neighbours threaten a territorial male's parentage during his breeding partner's fertile period. When paternity is not at stake, reduced aggression towards neighbours may enhance fitness, but when paternity is at stake, normal levels of aggression towards neighbours may be favoured as a mate-guarding tactic.

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When an animal encounters a conspecific rival, it must choose an appropriate response. If the rival represents a strong threat to the animal's resources or reproductive success, then the animal may respond aggressively; if the rival represents a weak threat, then the animal may respond less aggressively or not at all. In territorial animals, unfamiliar rivals usually represent a greater threat because they may usurp an animal's territory or threaten an animal's paternity by copulating with its mate (in species that engage in extrapair copulations). Neighbours, in contrast, already occupy a territory of their own and therefore only threaten an animal's paternity (Temeles, 1994). Therefore, territorial male animals often respond more aggressively to unfamiliar individuals (strangers) than to familiar individuals (neighbours). This phenomenon is known as the 'dear enemy effect' (Fisher, 1954). Decreased aggression towards neighbours allows animals to spend

more time on important tasks such as foraging, nest building, or caring for young instead of engaging in costly territorial disputes. The dear enemy effect has been documented in diverse animal taxa, including insects (e.g. Langen, Tripet, & Nonacs, 2000), birds (e.g. Hardouin, Tabel, & Bretagnolle, 2006), mammals (e.g. Monclús, Saavedra, & de Miguel, 2014), reptiles (e.g. Whiting, 1999), crustaceans (e.g. Booksmythe, Jennions, & Backwell, 2010), fish (e.g. McGregor & Westby, 1992) and amphibians (e.g. Feng et al., 2009).

Recent research on neighbour–stranger discrimination has revealed that the level of aggression displayed towards conspecific neighbours varies across the breeding season. Male skylarks, *Alauda arvensis*, responded more strongly to strangers than to neighbours in the middle of a breeding season (i.e. after hatching of first brood) but displayed no difference in response during the beginning (i.e. territory establishment) or end of the breeding season (i.e. after hatching of second brood; Briefer, Rybak, & Aubin, 2008). Additionally, winter wrens, *Troglodytes troglodytes*, increased their responses to neighbours versus strangers at the beginning of the breeding season but displayed no difference in response during the middle or end of the breeding season (Courvoisier, Camacho-Schlenker, & Aubin, 2014). According to the

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threat-level hypothesis (Temeles, 1994), these results may be explained by a change in threat level during different stages of the breeding season. Although these studies have found differences in responses to neighbours and strangers across a breeding season, they did not directly investigate the underlying causes for these differences. Currently, the causes of the flexibility of the dear enemy effect across a breeding season are poorly understood.

In many bird species, most extrapair offspring are sired by neighbouring males (e.g. Gibbs et al., 1990; Griffith, Owens, & Thuman, 2002; Hill, Akçay, Campbell, & Beecher, 2011; Mennill, Ramsay, Boag, & Ratcliffe, 2004). Therefore, during periods of female fertility, a neighbouring male should represent a greater threat to a male's paternity than at other times of the year. Consequently, a territorial male animal may benefit from responding aggressively to neighbouring males during his female's fertile period in order to protect his paternity. Conversely, neighbours should not be as threatening to a male during periods where his female is not fertile because they no longer threaten his paternity (see Fig. 1). Neighbours are expected to benefit from decreased aggression towards one another during these periods so they can focus on foraging or provisioning young. Strangers, in contrast, should represent an equivalent threat across a breeding season because the loss of a breeding territory will always result in reduced reproductive success. We hypothesize that male expression of the dear enemy effect should vary with female fertility: the dear enemy effect should be present when females are not fertile but should be absent when females are fertile.

In this study, we tested this hypothesis by conducting repeated playback of neighbour and stranger songs during different breeding stages in song sparrows, *Melospiza melodia*. Song sparrows are temperate-breeding songbirds that are known to display the dear enemy effect (Harris & Lemon, 1972; Kroodsmas, 1976; Stoddard, Beecher, Horning, & Campbell, 1991; Stoddard, Beecher, Horning, & Willis, 1990). This species has moderately high rates of extrapair fertilization (e.g. 24% of chicks, 36.1% of broods, Hill et al., 2011; 10.5% of chicks, 20–40% of broods, Major & Barber, 2004; 27.9% of chicks, O'Connor et al., 2006; 28% of chicks, 44% of broods, Sardell,

Keller, Arcese, Bucher, & Reid, 2010), and neighbours are the typical extrapair sires (Hill et al., 2011). We predicted that if dear enemy effect expression is influenced by female fertility, then male song sparrows would respond more intensely (e.g. more flights, more time spent near the loudspeaker) to strangers than to neighbours during periods when females were not fertile, but respond similarly to neighbours and strangers during periods when females were fertile. However, if dear enemy effect expression is not driven by female fertility status, we expected that male song sparrows would not differ in their aggression towards neighbours in a way that varies with female fertility.

METHODS

Study Site and Study Species

We conducted this experiment at the Queen's University Biological Station (44°34'N, 76°19'W) north of Kingston, Ontario, Canada. Our playback experiments took place between 18 April and 22 May 2015 and between 8 April and 15 May 2016; these periods correspond roughly to pair formation through nest building, egg laying and incubation in our study population. Our subjects were 29 focal male song sparrows (19 in 2015 and 10 in 2016) living in fields and marshes in the vicinity of the research station. Of our 29 subjects, 25 were banded with unique combinations of coloured leg bands and a Canadian Wildlife Services numbered band to facilitate individual identification. For the remaining four unbanded males, we distinguished between individuals based on recordings of their individually distinctive song types, as well as their territorial position. Sharing of complete song types between neighbours is rare for song sparrows in eastern North America (Hughes, Anderson, Searcy, Bottensek, & Nowicki, 2007; although see Foote & Barber, 2007), including in our study population (Stewart & MacDougall-Shackleton, 2008) and therefore distinguishing between individuals based on unique song types is not difficult. From the original 29 playback subjects, we excluded two individuals that did not respond to any playback trials, three individuals that never paired with a female, and two individuals that moved their breeding territory part-way through the study period. After these exclusions we were left with 22 males for our analyses.

Playback Stimuli

We created playback stimuli that allowed us to simulate song bouts of neighbours and strangers for each of our playback subjects. We considered neighbours to be birds that occupied a territory adjacent to the playback subject (i.e. some portion of their territory boundary was shared) and we considered strangers to be birds that occupied a territory at a different site, at least 2 km away from the focal bird. Some birds used for stranger stimuli were the same as birds used for neighbour stimuli at different sites. We had a total of 26 birds that we used for playback stimuli, eight were used twice (once as a neighbour and once as a stranger), six were used three times (either twice as a stranger and once as a neighbour or twice as a neighbour and once as a stranger), and three were used four times (twice as neighbours and twice as strangers). Male song sparrows in this population usually move less than 200 m between breeding attempts (Potvin, Crawford, MacDougall-Shackleton, & MacDougall-Shackleton, 2015) so it is very unlikely that focal males would have previously encountered these stranger stimuli.

To create playback stimuli, we collected recordings of song sparrows between 0600 hours and 1200 hours during early and mid-April using a directional microphone (Sennheiser ME67/K6) connected to a solid-state digital recorder (Marantz PMD660, 44.1 kHz sampling rate, 16-bit encoding, WAVE format). Birds were usually recorded

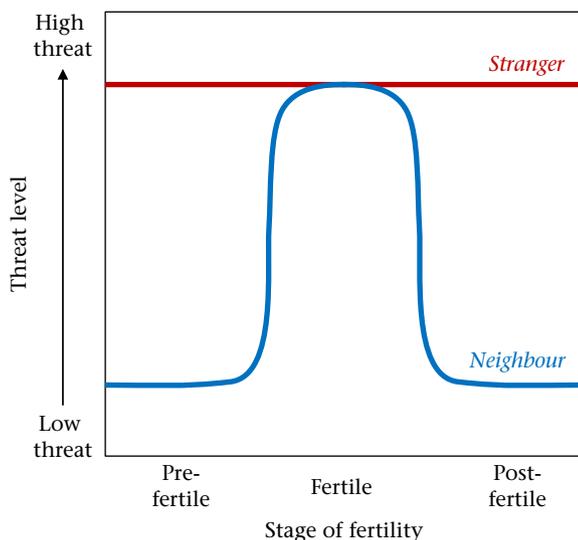


Figure 1. Visual model representing the relative threat posed by stranger males versus neighbour males to a territorial male, in relation to his partner's stage of fertility. Stranger males represent a constant threat to a territorial male over a breeding season because they always threaten a male's territory ownership. Neighbouring males, on the other hand, do not represent a threat to territory ownership after territories are established; instead they only represent a threat when a territorial male's partner is fertile because it can engage in extrapair copulations with a male's mate.

singing spontaneous territorial songs, however in a few instances we used a short playback (<30 s) to motivate birds to sing. From each recording of each male, we extracted five songs, each of a different song type, choosing the recordings with the lowest level of background noise (based on visual inspection of sound spectrograms generated in Audition 3.0 software, Adobe, San Jose, CA). For each song we applied an 800 Hz high-pass filter to remove low-frequency background noise. In a few recordings, higher-frequency noise was present; we reduced it to background levels using the lasso tool and the amplify function of Audition. After filtering sounds, we normalized all playback stimuli to -1 dB; we standardized the amplitude of our loudspeaker (model: Scorpion TX200, FOXPRO Inc., Lewistown, PA, U.S.A.) so that the peak amplitude of each stimulus was 75 dB at a distance of 1 m from the speaker (sound level meter: Casella Cel-240; C weighting, fast response). We then repeated each song at a rate of one song every 10 s (as in [Stoddard et al., 1990](#)), for a total stimulus track duration of 3 min.

For every bird that we simulated with playback, we created five different stimuli, each with a different song type from the same recorded male (although in two cases we were only able to collect four well-recorded song types). Across repeated trials to each subject, we used one of the five (or four in two cases) different stimuli for each of the simulated intruders, and on consecutive trials we would use stimuli that had not been used previously. All focal birds received playback from the same neighbour bird and stranger bird during all trials. However, in three instances, the neighbour lost its territory to a different bird in the middle of the experimental period; in these cases, we changed the neighbour stimulus to simulate the current neighbour, thereby maintaining an experimental design of 'neighbour versus stranger'.

Playback Experiment

We mapped the territories of our focal birds during their arrival from migration in early April. An observer followed focal birds around their territories for at least 90 min, taking careful note of locations where each bird sang, and logging these points into a GPS (Garmin GPS60). We set up our playback loudspeaker 10 m inside the subject's territory, nearest to the boundary with the neighbour that we were simulating with playback. We chose to place the loudspeaker slightly inside the territory in order to minimize the chance of interference from the neighbour. The loudspeaker occupied the same position for both neighbour and stranger trials. For most birds, we broadcast playback from the same location within each bird's territory across the entire season. In three instances, however, territory borders changed over the course of the experiment. In these instances we moved the speaker to maintain a position 10 m from the edge of the focal bird's territory (average distance moved in these three cases: 5 m). We placed the loudspeaker in a sound baffle made of a 20-inch (51 cm) diameter plastic parabola lined with 2-inch (5 cm) thick foam and a camouflage-coloured fabric. This baffle diminished the noise behind the loudspeaker, in order to further reduce interference from the neighbour. We did not conduct playback to neighbouring birds on the same day; subjects had to be at least one territory apart, and have different neighbours used for playback stimuli to receive playback on the same day.

We carried out playback experiments between 0630 hours and 1300 hours. An observer sat at a position 20 m away from the loudspeaker and dictated the focal bird's behaviour into a microphone, to serve as a record of the birds' response to playback. Playback trials began once both the focal bird and the neighbouring bird were not singing and when the focal bird was greater than

15 m away from the loudspeaker. The playback period lasted 3 min and was followed by a 5 min post-playback observation period. We focused our analysis solely on the 3 min playback period because most birds began countersinging with their neighbours during the post-playback period. After 20 min had elapsed from the end of the first playback trial, the subject received the second treatment (i.e. neighbour or stranger). We alternated the order of presentation of the neighbour and stranger stimuli, such that each bird received the neighbour or stranger playback first an equal number of times.

To ensure that we tested each focal male across all breeding stages, we conducted multiple, frequent playbacks over the breeding season. This was necessary because we were often unsure of the breeding stage of our focal males until the incubation period, when we found most of our nests. By backdating (see below), this allowed us to assign each playback session to a specific breeding stage in our analyses. We revisited each bird every 3–7 days to present both neighbour and stranger playback trials. We conducted 5.5 ± 0.24 (mean \pm SE; range 3–7) neighbour and stranger playbacks to each individual.

Fertility

We tracked the breeding stage of focal pairs by observing male and female behaviour and monitoring active nests. We found 17 nests from our 22 subjects (song sparrows are secretive nesters, and even with considerable effort we could not find all nests). For the five subjects where we were unable to locate nests, we observed female behaviour to determine breeding stage: if we saw a female with nest material, we assumed she was in the nest-building stage; if we saw a female foraging for short periods of time separated by 30–40 min in the morning, we assumed she was incubating. For the 17 subjects with known nests, we used the method outlined in [Nice \(1943\)](#) to backdate nests when we did not have complete data from nest building. We assigned breeding stage length as follows: nest building (2–4 days), egg laying (4–5 days; 4 days for nests with 4 eggs, and 5 days for nests with 5 eggs), and incubation (12–13 days). No playbacks took place during the post-incubation period. Sperm storage in song sparrows has not been quantified so we assumed the fertile period for the female to begin 6 days prior to the laying of the first egg and considered it to end on the day the penultimate egg had been laid (as in [Akçay et al., 2012](#)). Since the lengths of breeding stages are not rigidly defined, there were some instances where we were unable to assign birds to a breeding stage during a playback trial (e.g. if we found the nest during incubation and it had been depredated before it hatched); we excluded such trials from analysis.

Sample Size and Statistical Analysis

We excluded several trials from our final analyses due to interference by neighbours, lack of response by focal birds to both neighbour and stranger playback (i.e. the subject was not seen or heard for the duration of either trial), and lack of sufficient information to determine fertility status (see section on [Fertility](#)). After exclusion, we had 84 neighbour and stranger trials during the pre-fertile period derived from 20 focal birds, 62 neighbour and stranger trials during the fertile period derived from 22 focal birds, and 56 neighbour and stranger trials during the post-fertile period derived from 20 focal birds.

We conducted principal components analysis (PCA) using SPSS 20.0 (SPSS Inc., Chicago, IL, U.S.A.) to create composite variables that summarized our intercorrelated measurement variables of birds' responses to playback. We included four variables in this analysis:

number of flights, closest approach to the loudspeaker, latency to approach within 10 m of the loudspeaker and time spent within 10 m of the loudspeaker. We chose to include only physical response variables and not vocal response variables because these are widely recognized to be indicators of aggression in song sparrows (Searcy, Akçay, Nowicki, & Beecher, 2014; Searcy & Beecher, 2009). PCA identified one principal component factor with an eigenvalue above 1, explaining 69.8% of the variance in behavioural measures, which we retained for analysis (Table 1). This principal component (PC1) was positively associated with number of flights and time spent within 10 m of the speaker, and negatively associated with closest approach distance and latency to approach. Accordingly, we interpreted high positive values of PC1 as reflecting high aggression.

We used multiple regression in base R (version 3.2.3, R Core Team, 2015) to compare aggression elicited by neighbour versus stranger playback. Playback results from each period (pre-fertile, fertile, post-fertile) were analysed separately. We used stimulus identity (neighbour/stranger) as our predictor variable while controlling for subject identity, number of treatments (i.e. how many times each bird had been subject to playback trials) and order of stimulus presentation (i.e. whether the neighbour treatment was first or second on that day). We used *q-q* plots to confirm that model residuals were normally distributed, and plotted residuals to confirm that the data were homoscedastic. *P* values were considered significant when they were less than or equal to 0.05.

All methods involving animals were approved by the University of Windsor Animal Care Committee (AUPP number 13-15).

RESULTS

Male song sparrows displayed higher aggression towards strangers than towards neighbours, consistent with a dear enemy effect, during their female's pre-fertile period (ANOVA: $F_{1,18} = 9.0$,

Table 1

Factor loadings for PC1 ('male aggression score') derived from principal component analysis of territorial response to playback

Variables	PC1
Closest approach	-0.86
Latency to approach within 10 m	-0.92
Time spent within 10 m	0.79
Number of flights	0.76
Eigenvalue	2.80
% Variance explained	69.8%

This component was the only PC with an eigenvalue >1, so only PC1 was retained for analysis.

$P = 0.004$; Table 2, Fig. 2) and post-fertile period (ANOVA: $F_{1,20} = 7.9$, $P = 0.009$; Table 2, Fig. 2). During the female's fertile period, however, male song sparrows responded similarly to neighbour and stranger playback (ANOVA: $F_{1,18} = 0.4$, $P = 0.55$; Table 2, Fig. 2). Subject identity also had an effect on response to playback during the fertile period ($P = 0.0001$) and post-fertile period ($P < 0.0001$) but not during the pre-fertile period ($P = 0.14$).

DISCUSSION

We found that male song sparrows show flexibility in the dear enemy effect, in that the strength of territorial response to neighbour versus stranger song varies with female fertility. Male song sparrows displayed a dear enemy effect when their female was in the pre-fertile and post-fertile stages, but not when their female was fertile. These results are consistent with our prediction that male song sparrows increase aggression towards neighbours during periods of female fertility, presumably to protect their paternity.

The difference in expression of the dear enemy effect across different breeding stages suggests that male song sparrows exhibit a mate-guarding tactic wherein they increase aggression towards

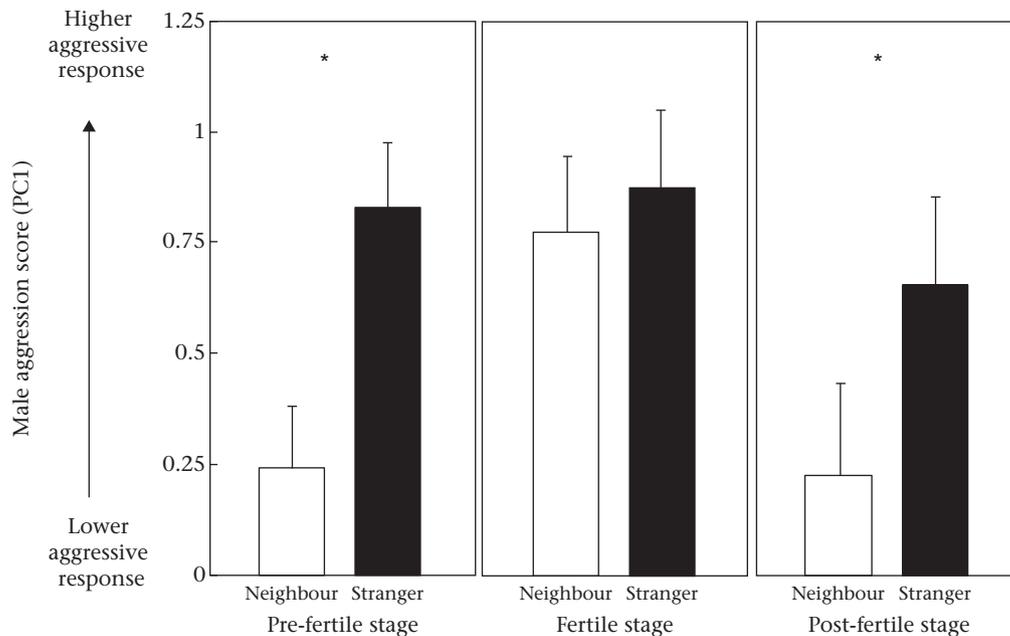


Figure 2. Responses of male song sparrows to simulated territorial intrusions by neighbours (white bars) and strangers (black bars) during their mate's pre-fertile, fertile and post-fertile periods. Male aggression scores are a principal component score that summarizes four behavioural measurements of birds' responses to playback. Data are presented as means \pm SE.

Table 2

Male song sparrows varied expression of the dear enemy effect with their female's fertility

	df	F	P
Pre-fertile			
Stimulus identity	1	9.0	0.004
Subject identity	19	1.5	0.14
Order	1	0.2	0.69
Number of treatments	1	2.8	0.10
Fertile			
Stimulus identity	1	0.36	0.55
Subject identity	21	3.9	0.0001
Order	1	1.7	0.20
Number of treatments	1	0.007	0.93
Post-fertile			
Stimulus identity	1	7.9	0.009
Subject identity	18	7.6	<0.0001
Order	1	0.51	0.48
Number of treatments	1	2.2	0.15

We analysed these data using a multiple regression. Significant *P* values are shown in bold.

neighbours during periods when extrapair paternity is an increased risk. Indeed, song sparrows have moderately high rates of extrapair paternity and neighbours are most often the sires of extrapair offspring in this species (e.g. Hill et al., 2011). Therefore, guarding against paternity loss to rival neighbouring males is presumably important. It is possible that increased aggression towards neighbours in song sparrows ensures a male's paternity through discouraging the neighbouring male from intruding, and possibly by demonstrating the male's quality to its mate. In another temperate songbird, the black-capped chickadee, *Poecile atricapillus*, females engaged in more extrapair copulations if their high-ranking mate lost a singing contest with a playback-simulated male during her fertile period than if their high-ranking mate won such a singing contest (Mennill, Ratcliffe, & Boag, 2002). Thus it may benefit a male bird to respond strongly to rival males during their female's fertile period and win contests in order to ensure their paternity. However, during periods when a male's own mate is not fertile, the male may benefit by foraging, prospecting for extrapair copulations with other females or provisioning young rather than engaging in costly aggressive behaviour with a neighbour. Future work could include genetic analysis of parentage to determine whether male song sparrows that are more aggressive to neighbours during their female's fertile period benefit by losing less paternity in their own nests.

During the pre-fertile period, male birds establish territories and negotiate boundaries with neighbours. Neighbouring males should act aggressively towards each other until boundaries are firmly established (Briefer et al., 2008). This is likely the case very early in the breeding season after birds arrive from their wintering grounds. It is important to note that our study began roughly 2–3 weeks after song sparrows had arrived on their breeding grounds from migration; by this time territories appeared to be stable and we did not observe aggressive encounters between established neighbours. During the fertile period, male song sparrows engage in frequent copulations with their mate (Nice, 1943), and thus mate guarding to ensure paternity is important during this time. During the post-fertile period (defined as the incubation period in our study), territories are well established and neighbours have little reason to display aggression towards each other, as they do not generally pose a threat to a territory or to paternity. In fact, males may be attempting to attract neighbouring females during this period to seek out extrapair copulations (Foote & Barber, 2009). Various factors such as recent intrusions (Akçay et al., 2009), relatedness (Akçay, Swift, Reed, & Dickinson, 2013),

neighbour aggression (Hyman & Hughes, 2006) and male quality (Sandoval, 2011) can affect male response to neighbours in songbirds, however female fertility appears to also play an important role.

Eliassen and Jørgensen (2014) hypothesized that by engaging in extrapair copulations, females create a cooperative neighbourhood, wherein males are incentivized to cooperate with nearby males because a male may have extrapair offspring in his neighbours' nests. Females then benefit from this if males engage in more cooperative behaviours and fewer aggressive interactions. From this hypothesis, the authors suggested that males should display a dear enemy effect when females are not fertile. Our results are consistent with this idea as we found that male song sparrows show a dear enemy effect when their female is not fertile, but do not show a dear enemy effect when their female is fertile. Note, however, that evolution of a cooperative neighbourhood by extrapair copulations incurs a cost through a period of time (i.e. during the fertile period) when neighbours are very aggressive and uncooperative towards each other in order to protect their own paternity. Alternatively, males may reduce aggression towards each other during their mate's nonfertile periods because males can only secure extrapair copulations during neighbouring females' fertile periods. As a result, high aggression during nonfertile periods provides a substantially lower benefit than high aggression during the fertile period. The cooperative neighbourhood hypothesis also fails to explain why males display a dear enemy effect during the pre-fertile period, when extrapair fertilizations are not yet possible, and it fails to explain why the dear enemy effect occurs in animals that are not known to have extrapair copulations (e.g. little owls, *Athene noctua*: Hardouin et al., 2006; Muller, Epplen, & Lubjuhn, 2001).

We developed a visual model of the relative threat of neighbours versus strangers over the course of a female's breeding period (Fig. 1). We speculated that neighbours and strangers would pose similar levels of threat during the female fertile period. This position was supported by our results given that male song sparrows responded equally aggressively to neighbour and stranger playback during this period. However, a more comprehensive method of examining the true relative threat levels of neighbours and strangers during this time period may be through an experimental design similar to Stoddard et al. (1990), wherein male song sparrows were presented with neighbour and stranger playback simultaneously and the observers noted the amount of time males spent near each speaker. This design forces males to choose which stimulus to respond to and may elucidate which class of conspecifics are more threatening during this time period. If strangers are a higher threat during the fertile period, we would expect males to focus their response on stranger playback; if neighbours are a higher threat during this period, we would expect males to focus their response on neighbour playback; if neighbours and strangers were an equal threat during this period, we would expect males to focus their response on both playbacks.

The results from this study have implications for the experimental design of future investigations of the dear enemy effect. It is important for researchers to take breeding stage of subjects into consideration when conducting dear enemy effect studies or, by extension, any studies involving neighbour playback. As shown here, a study conducted during an animal's fertile period may yield a negative result even though these animals may display the dear enemy effect during the nonfertile periods. In conjunction with Briefer et al. (2008) and Courvoisier et al. (2014), our study provides evidence that the social interactions between territorial birds are dynamic over a breeding season. The dear enemy effect appears to be a fluid phenomenon that is partially determined by the breeding stage of females.

Conclusions

Song sparrows displayed a dear enemy effect during the pre-fertile and post-fertile period but not during the fertile period. Our results suggest that whereas territorial male song sparrows respond with consistent high rates of aggression towards unfamiliar strangers, their response to neighbouring males is more aggressive during their female's fertile period than it is outside the fertile period. Thus, male song sparrows appear to balance the costs of territorial defence with the necessity of defending paternity. Future work could investigate whether males that are more aggressive to neighbours during their female's fertile periods have fewer extrapair offspring in their own nest.

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