Animal Behaviour 126 (2017) 17–22

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

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

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ARTICLE INFO

Article history:
Received 29 August 2016
Initial acceptance 23 September 2016
Final acceptance 21 November 2016

MS. number: A16-00761

Keywords:
dear enemy effect
fertility status
fitness
mate guarding
Melospiza melodia
neighbour–stranger discrimination
paternity
song sparrow
territoriality

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.

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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http://dx.doi.org/10.1016/j.anbehav.2017.01.009
0003-3472/

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; Kroodsma, 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.

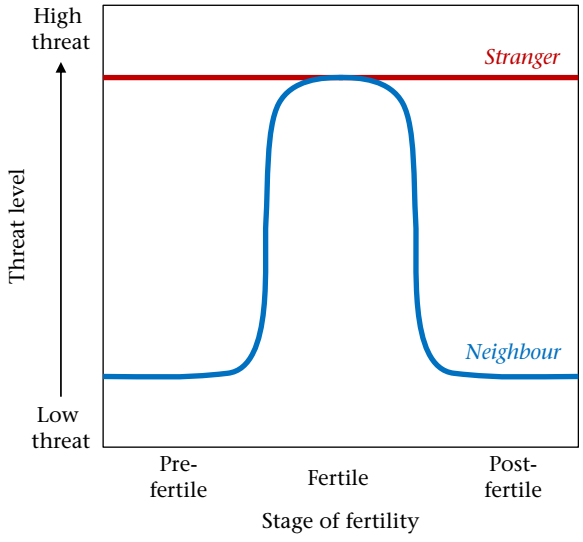

Figure 1. Visual model representing the relative threat posed by stranger males versus neighbour males to a territorial male, in relation to his partner's stage of fertility. Stranger males represent a constant threat to a territorial male over a breeding season because they always threaten a male's 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.

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