



Male song sparrows have elevated testosterone in response to neighbors versus strangers



Christopher Moser-Purdy^{a,*}, Scott A. MacDougall-Shackleton^b, Frances Bonier^c, Brendan A. Graham^a, Andrea C. Boyer^b, Daniel J. Mennill^{a,*}

^a Department of Biological Sciences, University of Windsor, Windsor, ON N9B 3P4, Canada

^b Department of Biology, Western University, London, ON N6G 1G9, Canada

^c Biology Department, Queen's University, Kingston, ON K7L 3N6, Canada

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ABSTRACT

Upon hearing a conspecific signal, animals must assess their relationship with the signaller and respond appropriately. Territorial animals usually respond more aggressively to strangers than neighbors in a phenomenon known as the “dear enemy effect”. This phenomenon likely evolved because strangers represent a threat to an animal's territory tenure and parentage, whereas neighbors only represent a threat to an animal's parentage because they already possess a territory (providing territory boundaries are established and stable). Although the dear enemy effect has been widely documented using behavioral response variables, little research has been conducted on the physiological responses of animals to neighbors versus strangers. We sought to investigate whether the dear enemy effect is observed physiologically by exposing territorial male song sparrows (*Melospiza melodia*) to playback simulating a neighbor or a stranger, and then collecting blood samples to measure plasma testosterone levels. We predicted that song sparrows would exhibit increased testosterone levels after exposure to stranger playback compared to neighbor playback, due to the role testosterone plays in regulating aggression. Contrary to our prediction, we found that song sparrows had higher testosterone levels after exposure to neighbor playback compared to stranger playback. We discuss several explanations for our result, notably that corticosterone may regulate the dear enemy effect in male song sparrows and this may inhibit plasma testosterone. Future studies will benefit from examining corticosterone in addition to testosterone, to better understand the hormonal underpinnings of the dear enemy effect.

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1. Introduction

Territorial animals interact with many types of conspecific individuals. Upon encountering a conspecific individual, an animal must assess its threat level and respond appropriately. Across a wide range of animal taxa, territorial interactions are more intense when a resident animal encounters an unfamiliar stranger versus a familiar neighbor (Temeles, 1994). This phenomenon is known as the “dear enemy effect” (Fisher, 1954). Strangers are thought to pose a higher threat of territory takeover than neighbors who, by definition, already possess a territory and therefore might be less likely to usurp the resident animal's territory (Getty, 1987). Because neighbors may be less of a threat, the establishment of a less aggressive relationship between neighbors allows individuals to maximize their fitness by focusing effort on activities such as foraging and provisioning for young instead of costly aggressive

encounters. The dear enemy effect has been reported in many animal taxa including birds (e.g. Hardouin et al., 2006), mammals (e.g. Rosell et al., 2008), insects (e.g. Langen et al., 2000), frogs (e.g. Lesbarrères and Lodé, 2002), lizards (e.g. Whiting, 1999), fish (McGregor and Westby, 1992), and crustaceans (Booksmythe et al., 2010).

The dear enemy effect has been well studied using physical and acoustic measures of behavioral response (Temeles, 1994). In contrast, physiological responses to neighbor and stranger stimuli are almost completely unknown (but see Aires et al., 2015). Under the Challenge Hypothesis, territorial male animals are predicted to increase their testosterone levels in response to a territorial challenge (Wingfield et al., 1990). Testosterone is a steroid hormone that often regulates aggression in vertebrates. For example, experimentally increased testosterone causes increased aggression toward conspecific individuals (e.g. Wingfield, 1994; Mougeot et al., 2005) and testosterone levels often increase during simulated territorial intrusions (e.g. Hau et al., 2000; Wingfield and Wada, 1989). Given that testosterone can modulate responses to territorial challenges, and given that strangers might pose a heightened threat in comparison to neighbors, we predicted that

* Corresponding authors.

E-mail addresses: cmoserpurdy@rogers.com (C. Moser-Purdy), dmennill@uwindsor.ca (D.J. Mennill).

individuals will increase circulating testosterone levels when exposed to a stranger more than when exposed to a neighbor. This increase in testosterone may mediate the behavioral responses observed in dear enemy effect studies. Only one study has previously examined this potential hormonal mechanism of the dear enemy effect by examining a tropical fish species. Mozambique tilapia (*Oreochromis mossambicus*) showed an increased level of 11-ketotestosterone in response to presentation of a stranger in comparison to a neighbor (Aires et al., 2015). It is unknown whether any other vertebrates have a similar endocrine response to challenges from neighbors versus strangers.

We used song playback to study the role of testosterone in mediating the dear enemy effect in territorial male song sparrows (*Melospiza melodia*). We exposed territorial males to playback simulating either an unfamiliar stranger or an established territorial neighbor and then sampled their testosterone levels, to test the prediction that birds would show heightened testosterone during confrontation with a stranger. Song sparrows are an ideal study system for this experiment given that multiple previous studies show that they display the behavioral response predicted by the dear enemy hypothesis (Harris and Lemon, 1976; Kroodsmas, 1976; Moser-Purdy et al., 2017; Stoddard et al., 1990; Stoddard et al., 1991) and because they increase testosterone when challenged by conspecifics during breeding (Wingfield and Wada, 1989).

2. Methods

2.1. Study site and species

We presented territorial male song sparrows with experimental playback of recordings of conspecific song at the Queen's University Biological Station (44° 34' N, 76° 19' W; Ontario, Canada). During April of 2016 we recorded birds and mapped territories; we spent ≥ 90 min observing each bird, over multiple days, and we logged each of his song posts using a Global Positioning System (Garmin 60CS). From May 4 to May 19, 2016 we conducted playback experiments on 22 paired male song sparrows. All birds had established territories and were paired at the time of playback (i.e., each male was observed affiliating with a female over extended periods, regularly foraging together and moving around their territory together), as determined during observations in April and early May. Four birds were banded from studies in previous years with unique combinations of colored bands and a Canadian Wildlife Service numbered band. In addition, we banded 12 of the birds we caught in 2016; these birds were banded after the post-playback blood collection, rather than before playback. We did not want to capture the birds prior to playback, exposing our subjects to a potentially stressful event and reducing our ability to capture them a second time for blood collection after playback. We had no difficulty identifying birds, regardless of whether or not they were banded, based on location, behavior, and individually distinctive songs (song sharing is low in Eastern populations of song sparrows; Hughes et al., 2007; Stewart and

MacDougall-Shackleton, 2008; although see Foote and Barber, 2007). Testosterone levels did not differ among birds from different banding cohorts (i.e., banded in 2015, banded in 2016, or unbanded; Spearman's rank correlation: $\rho = 0.30$, $p = 0.18$, $N = 22$).

2.2. Playback stimuli

To construct playback stimuli we recorded spontaneous bouts of singing from male song sparrows. We used an omni-directional microphone (model: Sennheiser ME62/K6) mounted inside of a parabolic reflector (model: Telinga MK2) connected to a solid-state digital recorder (model: Marantz PMD660, 44.1 kHz sampling rate, 16-bit encoding, WAVE format). We collected five song types from each male to use in constructing playback stimuli. We isolated five songs that showed no overlapping background noise (assessed visually based on spectrograms generated in Audition 3.0, Adobe, San Jose, CA), and we normalized each song to -1 dB using the "normalize" feature of Audition 3.0. Each stimulus was 30 min in length and consisted of five song types played at a rate of one song every 10 s (this is a natural singing rate for this population based on our preliminary observations). One song type was broadcast for 3 min before switching to a different song type (this too was within the range of natural song type switching in our population). We cycled through each of the five song types twice for a total of 30 min (Fig. 1). Each stimulus set was composed of different song types from the same bird.

To create neighbor stimuli, we collected a recording of the neighbor from a bird adjacent to each playback subject. To create stranger stimuli, we collected a recording from a bird at least 2 km away from the focal bird. We had 14 stimuli in total: four were used twice (three were used once as a neighbor and once as a stranger, one was used twice as a stranger) and two were used three times (twice as a neighbor and once as a stranger).

In addition to neighbor and stranger stimuli used during the playback phase of the experiment, we also created a capture stimulus for the capture phase of the experiment (see below). A separate stimulus was necessary because the subjects' responses to neighbor playback did not incite sufficiently close approaches to permit capture. Songs for the capture stimulus were collected from a bird > 5 km away from all of our playback subjects. We designed the capture stimulus to be highly aggressive and thereby incite rapid, close approach to the loud-speaker so that we could capture birds in a mist net. The stimulus consisted of five song types from the same bird, each played five times separated by 2 s of silence, and with 8 s of song sparrow calls inserted prior to each change in song type. We used the same capture stimulus for all birds.

2.3. Playback experiment

We presented each of the 22 subjects with 30 min of stranger playback ($N = 10$) or neighbor playback ($N = 12$) (Fig. 1). After this 30-min

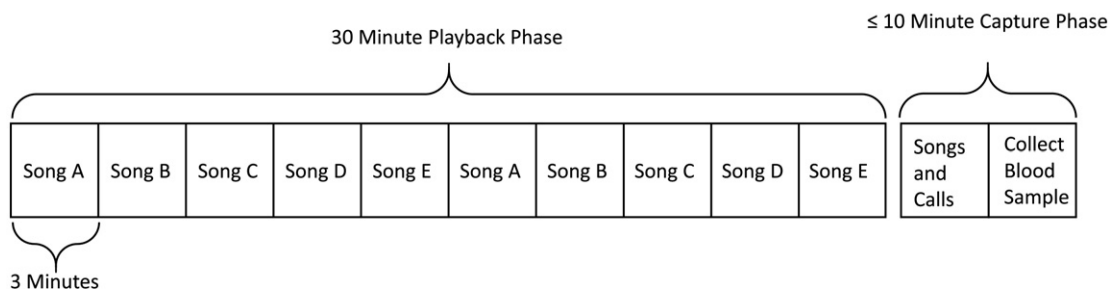


Fig. 1. Schematic representation of the experimental procedure used to study androgen responses to neighbor or stranger playback in song sparrows. Birds received 30 min of playback consisting of either neighbor or stranger songs, with each song type played for a 3-minute bout. Five song types were used for each playback stimulus and a bout of each song type was repeated once. Following the 30-minute playback phase we began the capture phase. During the capture phase, we played a capture stimulus to facilitate rapid capture of the subject, followed by the collection of a blood sample within 10 min (except in three cases, see *Hormone Analysis* for details).

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