Delayed song maturation and territorial aggression in a songbird

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Abstract

Asymmetries in competitive ability can determine the outcome of social interactions in animals and are often expressed through differences in sexual traits. Competitive ability (resource holding potential, RHP), trait expression and ultimately reproductive success may vary with an individual’s age or experience. In some species, reproductively mature males delay acquisition of some adult traits and thereby signal their young age. Theory on animal contests predicts that individuals assess the RHP of an opponent relative to their own, such that escalation is more common between evenly matched opponents. Here, we test predictions from this theory on animal contests by simulating young and old males that differ in RHP. We simulated white-crowned sparrows (Zonotrichia leucophrys) intruding into the territory of a recruit or return. Playback of a song repertoire simulating a young male (recruit) elicited a weaker response from established territory holders (return), but a stronger response from recruits. Playback of a single song type simulating an older male elicited the opposite responses. This indicates that males distinguished between simulated young and old intruders based on song, and responded differently depending on their own experience. Our study highlights the possibility that receiver as well as sender traits should be considered when interpreting animal interactions.

Keywords: mutual assessment; birdsong; delayed maturation; sexual traits; Zonotrichia leucophrys

1. INTRODUCTION

Animals often compete with conspecifics over limited resources, such as territories and mating opportunities [1]. Asymmetries in competitive ability and motivation may determine the outcome of these contests [2]. To avoid interactions with clearly superior competitors and to minimize risk of injury, animals may use traits to assess their rival’s competitive ability or resource holding potential (RHP) relative to their own, and direct aggression at individuals of similar or lesser RHP [3,4]. Such mutual assessment as predicted by game theory has been shown in a few species [5,6]. Here, we test experimentally whether a songbird uses an acoustic trait in mutual assessment.


RHP is commonly a correlate of body size or experience [7]. Older individuals often have a competitive advantage over younger conspecifics [8]. In some species, second-year (SY) males are markedly different from after-second-year (ASY) males with respect to delayed acquisition of an adult secondary sexual character [9]. Such delayed trait maturation presents an evolutionary puzzle, because elaborate adult-like traits are commonly preferred by females and are thus crucial for reproduction in these reproductively mature males. However, young individuals may benefit from reduced aggression in interactions with old individuals [10]. Delayed maturation in plumage occurs commonly in birds [11,12]. In some species, song traits differ between young and old males [9].

Song in oscine birds is commonly learned in the first year of life, ending with crystallized song [13]. Some close-ended learning species, which acquire new songs solely early in life, delay completion of the final song repertoire until the first breeding season [14]. Around half of SY male Puget Sound white-crowned sparrows Zonotrichia leucophrys pugetensis sing several song types early in the breeding season, before selectively retaining a single adult song type that is retained for the remainder of life [15,16]. Males that overproduce songs at the beginning of their first breeding season are more likely to share songs with a territorial neighbour than recruits that do not overproduce [16] and song sharing is important in acquiring a social mate [17]. The incidence of song overproduction differs significantly between age classes and can thus signal the singer’s age [15].

To test whether males vary the strength of response to a territorial intruder depending on their relative RHP, we simulated intrusions by SY and ASY males to recruits and returns. Based on the mutual assessment hypothesis, we predict a strong response by a territory holder to an intruder of similar RHP and a weak response to an intruder that differs in RHP, i.e. one that signals a different age.

2. MATERIAL AND METHODS

We studied a migratory population of territorial male Puget Sound white-crowned sparrows at Bullard’s Beach State Park, Oregon in 2008–2011. Details of the study site and song recording procedure are given in Nelson & Poels [18]. We differentiated between males new to the study area (recruits) and returns, which were banded males that had defended a territory in the area in a previous year [19]. Recruits could reliably be aged as SY males because they have shorter wings than ASY males and brown-and-tan crown coloration [16,20]. Recruits did not have prior breeding experience at the study site.

(a) Song playback experiment

We performed a playback experiment to 16 unpaired males, eight recruits and eight returns. We mapped territories by observing song posts on days prior to testing and placed a loudspeaker 10–15 m inside the territory boundary to simulate a newly arrived male intruding into the test subject’s territory. All subjects sang a single song type each. Test subjects received two treatments of 16 songs each on one morning between 07.00 and 11.15 h Pacific Time, with a 1 h interval between treatments (details in the electronic supplementary material). In one treatment, we presented the subject with two song types, where one type was the same as the subject’s song type (figure 1). Most overproducing males share one song type with a territory neighbour, i.e. sing the same note complex [16]. Some close-ended learning species, which acquire new songs solely early in life, delay completion of the final song repertoire until the first breeding season [14]. Around half of SY male Puget Sound white-crowned sparrows Zonotrichia leucophrys pugetensis sing several song types early in the breeding season, before selectively retaining a single adult song type that is retained for the remainder of life [15,16]. Males that overproduce songs at the beginning of their first breeding season are more likely to share songs with a territorial neighbour than recruits that do not overproduce [16] and song sharing is important in acquiring a social mate [17]. The incidence of song overproduction differs significantly between age classes and can thus signal the singer’s age [15].

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Figure 1. Examples of sonograms of songs of a subject male and the two stimuli (repertoire of two song types and single song type) presented to this subject during playback. Songs consist of four phrases; note complex (NC) and trill notes are underlined in the subject’s song.

Figure 2. Response of recruits (white bars) and returns (gray bars) of white-crowned sparrows to playback of a repertoire or single song type as measured by (a) PC1 and (b) mean approach distance. Median and interquartile range are shown. PC2 and the other five response measures are shown. PC2 and the other five response measures are shown in the electronic supplementary material.

3. RESULTS

The three approach distance measures (latency to approach, closest and mean approach distance) were strongly positively correlated ($r \geq 0.75$) with PC1. The number of flights and mean song rate were positively correlated ($r \geq 0.54$) with PC2. Trill length was moderately negatively correlated with both PC1 and PC2 ($r = -0.57$ and $r = -0.44$, respectively). Overall, PC1 and PC2 explained 65.3 per cent of the variance in the response variables.

For PC1, the statistical interaction between treatment and subject's age was significant ($F_{1,14} = 15.0$, $p = 0.002$; figure 2a). The response difference was greatest in mean approach distance: seven of eight returns approached closer to the single song type than to the repertoire playback, while all recruits showed the opposite response (figure 2b). Main effects of age ($F_{1,14} = 2.83$, $p = 0.12$) or treatment ($F_{1,14} = 1.53$, $p = 0.24$) were not significant. As measured by PC2, returns and recruits gave similar song and flight responses to the two stimuli (treatment: $F_{1,14} = 0.60$, $p = 0.45$; age: $F_{1,14} = 0.01$, $p = 0.91$; treatment $\times$ age: $F_{1,14} = 1.40$, $p = 0.26$; figures in the electronic supplementary material).

4. DISCUSSION

Results from our playback experiment support the mutual assessment hypothesis. A repertoire of two song types, common only among SY males as a result of delayed maturation, elicited a weaker territorial response from established than young territory holders. In contrast, a single song type elicited a stronger response from young than from old males.

Our results indicate that males assessed the threat of the simulated intruder relative to their own RHP based on a song trait. This confirms findings that individuals assess an opponent’s fighting ability based on traits that are associated with size, age or experience [8,22]. Furthermore, our results agree with theory, in that most escalated interactions occur among individuals of similar competitive ability [4]. To an established older male, song overproduction may signal an SY male without competitive experience who is of little threat, either to his territory or in terms of losing paternity [23]. In contrast, to a recruit on territory for the first time, another young male who is most likely in search of a territory is a strong threat and an equal competitor.

A difference in approach but not singing behaviour or flights is in accordance with previous studies [19]. Approach behaviour is generally a good proxy for aggressive response and possible attack [24]. Our measure of approach here also takes into account how long an individual stayed close to the opponent, which reflects contest duration. Thus, our results support theory that predicts long conflicts when contestants are equal [4]. Dependence of strength of response on the RHP of both the signaler and receiver in a signalling interaction may be more common than currently recognized [25,26].
In the case of song development studied here, song overproduction only signals young age during the short period at the beginning of the breeding season. Any benefits that SY males may gain from reduced aggression from returns is transitory, because most SY males go through the selective song attrition process within one to two weeks after arrival on the breeding grounds [15]. Similarly, many SY males go through the final steps of their crown moult in the same time period as they overproduce [16]. The majority of SY males retain a song type that is shared with territorial neighbours [16]. During the process of overproduction, song can be used as a signal of age.

Here, we have shown in a songbird mutual assessment based on a song trait that reflects age. Contests, where individuals compete aggressively and directly against one another, are ubiquitous in animals. Our results highlight the importance of considering receiver as well as sender traits when interpreting territorial interactions.

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