ANIMAL BEHAVIOUR, 2008, **75**, 1603–1610
doi:10.1016/j.anbehav.2007.09.038

ARTICLES

Sexual selection on aggressiveness in females: evidence from an experimental test with tree swallows

KIMBERLY A. ROSVALL
Department of Biology, Duke University

(Received 16 July 2007; initial acceptance 17 August 2007;
final acceptance 24 September 2007; published online 25 March 2008; MS. number: A10817)

While much research has focused on the evolution of conspicuous male displays, ornaments and behaviours, less is understood about the evolution of similar traits in females. To determine whether females express these traits as nonadaptive by-products of sexual selection favouring the same traits in males or whether females are directly selected to express such traits, the benefits of these traits must be understood. The prevalence of aggression in female–female competition suggests that females may experience direct sexual selection for aggressiveness, but data are lacking. I used the tree swallow, *Tachycineta bicolor*, to test the hypothesis that selection directly favours aggressiveness in females during intrasexual competition over nesting sites. After assaying the aggressiveness of a population of tree swallows, I experimentally reduced the number of nesting cavities, a resource required for female reproductive success. More aggressive females were more likely to obtain nesting cavities after the experimental reduction, while female age and male aggressiveness did not predict nesting cavity acquisition. Aggressive behaviour in female tree swallows is therefore beneficial in the context of female–female competition for a critical breeding resource. These results indicate that the processes favouring aggressiveness in intrasexual competition among females may not be very different from the processes shaping aggressive behaviour in males.

Keywords: aggressiveness; cavity nester; female aggression; female–female competition; intrasexual competition; nestbox; sexual selection; *Tachycineta bicolor*; tree swallow

Decades of work have illustrated how mate choice and intrasexual competition may drive the evolution of conspicuous male traits (Darwin 1871; Fisher 1958; Andersson 1994). Much less is understood, however, about the evolution of conspicuous female displays, ornaments and behaviours (Clutton-Brock 2007). A key question is whether females express these traits as nonadaptive by-products of sexual selection favouring the same traits in males, or whether such traits are a consequence of direct selection on females themselves. With females and males sharing most of their genome, conspicuous traits may exist in both sexes through genetic correlation, in spite of only having functional significance in one sex (Lande 1980; Lande & Arnold 1983). Alternatively, females may experience direct sexual selection for conspicuous traits if they function in the context of female–female competition or male mate choice (Amundsen 2000). Because sexually selected traits are often costly to produce or maintain (Zahavi 1975, 1977; Hamilton & Zuk 1982; Folstad & Karter 1992; Fitzpatrick et al. 1995), understanding the benefits of these traits is critical to determining whether or not females experience direct selection to express these traits.

Previous work on sexually selected traits in females has focused on the function of ornamentation and vocalization (Ritchison 1983; Langmore 1998; Amundsen 2000; Amundsen & Parn 2006); less attention has been given to the function of female traits used in aggressive interactions, despite the prevalence of such interactions. Female aggressiveness may be beneficial in the context of female–female competition over resources or males in a variety of taxa (e.g. Jaeger et al. 1982; Gowaty & Wagner 1988; Rauch 1988; Summers 1989; Berglund et al. 1993; Kopachena & Falls 1993; Slagsvold & Lifjeld 1994; Walter & Trillmich 1994; Palombit et al. 2001; Jawor et al. 2006).

Correspondence: K. A. Rosvall, Department of Biology, Duke University, Box 90338, Durham, NC 27708, U.S.A. (email: kar23@duke.edu).

0003–3472/08/$34.00/0

Among birds, more aggressive females are more likely to be monogamously mated (Slagsvold 1993; Sandell 1998) and therefore may receive more direct benefits from their mates than if polygynously mated, especially as a secondary female (e.g. Searcy & Yasukawa 1996). Intrasexual aggression among females also may function to prevent territory eviction, brood parasitism, infanticide or extrapair mating by a social mate (Møller 1987; Gowaty & Wagner 1988; Roberts & Searcy 1988; Dunn & Hannon 1991; Slagsvold & Lifjeld 1994). While past studies have used settlement patterns and temporal variation in female aggression to infer that aggressive behaviour may facilitate territory or nest site acquisition, there has not been a direct test of whether more aggressive females are more likely to breed overall. Sexual selection for aggressive competition among females may be particularly important in species that are obligate secondary cavity nesters if more aggressive females can competitively exclude other females from potential nesting sites. Here, I provide experimental evidence that more aggressive females can outcompete less aggressive females during intrasexual competition over limited nesting sites, suggesting that female aggressiveness is directly favoured by sexual selection.

I used the tree swallow, *Tachycineta bicolor*, to test the hypothesis that selection directly favours aggressiveness in females. Tree swallows require a cavity for nesting but cannot excavate one on their own (Robertson et al. 1992), and cavities of the appropriate size in the appropriate habitat are limited (Holroyd 1975). Accordingly, at least 25% of tree swallows behave as nonterritorial floaters (Stutchbury & Robertson 1985; Kempenaers et al. 2001), which are reproductively mature individuals who do not breed because they do not have access to a nesting site (Brown 1969). Most of these floaters are 1-year-old ‘subadult’ females (47–79%; Stutchbury & Robertson 1985). Previous work in this species has documented intense aggressive interactions among females, with females sometimes killing other females or their offspring, presumably to acquire a nesting site (Chek & Robertson 1991). Fights among females range from brief aerial chases to intense fights in which the participants tumble to the ground while grappling with and pecking each other (Robertson et al. 1992). The relative scarcity of cavities and relative excess of females make tree swallows an ideal system for asking whether aggressiveness in the context of female–female competition over nesting sites is favoured directly by sexual selection. To test this hypothesis, I experimentally reduced cavity availability in a population of individuals whose aggressiveness had been quantified previously. This manipulation effectively increased competition for nestboxes, forcing individuals to compete for a critical limited resource required for reproductive success. If selection directly favours aggressiveness in females, more aggressive females should be more likely to obtain a nesting cavity.

METHODS

Study Site and Population

I performed this study on a population of tree swallows breeding in nestboxes near Linesville, Pennsylvania, U.S.A. (41°40′N, 80°26′W). This site was initiated in 2004 and consists of 37 nestboxes dispersed over approximately 23 ha of ponds and lawns. Behavioural trials used to validate the method of assaying aggressiveness were performed in May 2005. Aggression assays for the experimental manipulation were performed between 20 April and 1 May 2006, and the nestbox reduction took place on 1 May 2006. Because this population is relatively recently established and had experienced high predation the previous year, it had a higher proportion of subadult females (55%) than is typical of more established populations (6–35%; Robertson et al. 1992). This high proportion of subadult females defending nestboxes provided a unique opportunity to further explore age-related differences in nestbox acquisition.

Males and females were captured using mist nets or nestbox traps (Stutchbury & Robertson 1986). Individuals were sexed by the presence of cloacal protuberance or brood patch, wing chord length (Stutchbury & Robertson 1987c), behavioural cues (e.g. nest building for a female) and plumage coloration. Tree swallows have female-biased delayed plumage maturation, where 1-year-old females have a distinct brown subadult plumage that differs markedly from the blue-green plumage of adult females and all males (Robertson et al. 1992). Females were classified as either subadult or adult based on the percentage of blue in their upper plumage: females whose plumage was less than 50% blue were considered subadult and females with more than 90% blue plumage were considered adult (Hussell 1983). No intermediate females were present at this site. Individuals were banded with one numbered metal band and one plastic colour band (blue for males, red for females). In addition, all individuals were marked with dabs of acrylic paint on their wings and rump for individual identification (Dunn et al. 1994).

Aggression Assay

I measured aggressiveness in both males and females using a standardized behavioural bioassay designed to simulate a territorial intrusion (modified from Winkler 1992). In each trial, a caged intruder was introduced to the focal individual’s territory and placed 1.5 m from the entrance to the nesting cavity for 5 min. The decoy was a live tree swallow captured that morning from a population located 3–5 km away and placed in a cage (30 × 30 × 25 cm) mounted on a tripod. Before the start of a trial, the cage was covered with a dark cloth to keep the decoy calm and to prevent the focal individual from seeing it.

Because there is some evidence that aggression varies based on the sex of the intruder (Stutchbury & Robertson 1987a,b), I tested the aggressiveness of males using a male decoy and tested the aggressiveness of females using a subadult female decoy. This method framed the behavioural assay in the context of intrasexual competition. It is unlikely that using an adult female decoy instead of a subadult would have altered the focal female’s behaviour, as female tree swallows respond equally strongly to intruders of brown and blue plumage (Stutchbury & Robertson