



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.

© 2008 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

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).

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

1987b). Focal female behaviour is also unlikely to have been affected by the behaviour of her mate, as females respond equally strongly with and without their mate present (K. A. Rosvall, unpublished data). All aggression trials were performed between 0600 and 1100 hours. Trials in which the focal individual was absent or not reliably identifiable for more than 50% of the trial were not used in the analysis, nor were trials in which eastern bluebirds, *Sialia sialis*, which are nestbox competitors, attacked the decoy or the focal individual for more than 50% of the trial.

During the 5 min trial, I used a digital voice recorder to document the aggressive behaviours that the focal individual performed towards the decoy. Aggressive behaviours included swooping or hovering within 0.75 m of the cage (i.e. half the distance to the nestbox), or perching or pecking at the cage. Aggression scores were calculated by summing the number of 5 s. intervals during which the focal individual directed any aggressive response at the decoy (i.e. as few as 0, to a maximum of 60).

To validate my method of measuring aggressiveness, I performed repeated trials (range 2–4) on individual females ($N = 10$) using different decoys ($N = 4$). For each female, the first and last of the repeat trials occurred within a 10-day period early in the 2005 breeding season. To meet the assumptions of the models in the validation analysis, aggression scores were natural log transformed. I tested whether decoy identity and female reproductive status affected the aggression score using a backward stepwise general linear model (GLM). Female reproductive status was included as a potential predictor of aggression because trials for the validation analysis were performed at varying times relative to a female's first egg date. Trials occurred, on average, 3.5 ± 1.2 days after first egg date. Neither decoy identity nor female reproductive status were significant predictors of aggression score (GLM, decoy: $F_{3,9} = 0.732$, $P = 0.549$; reproductive status: $F_{1,9} = 0.085$, $P = 0.775$), and thus these variables were removed from future analyses. Only focal bird identity was a significant predictor of aggression score (GLM, female identity: $F_{1,9} = 12.149$, $P < 0.00001$). To determine whether aggression scores captured consistent behavioural responses from focal individuals, I calculated repeatability following Lessells & Boag (1987). Repeatability describes the amount of phenotypic variation that can be ascribed to persistent differences between individuals (Boake 1989; Falconer 1989). Females used in the 2005 validation analysis were not the same females used in the 2006 experimental manipulation because the purpose of these trials was to validate the consistency of the aggression assay, not to measure the repeatability of individual females or the effect of variation in female repeatability on the acquisition of nestboxes.

Experimental Manipulation

At the start of the breeding season in 2006 (i.e. before egg laying), I determined which individuals had acquired nestboxes at my site and I assayed their aggressiveness no more than 10 days before the manipulation. Individuals who were seen repeatedly entering a box, defending it

from other birds or building a nest inside were considered to have acquired that box. Of the 37 nestboxes at my site, 31 were occupied by tree swallows and six were occupied by eastern bluebirds. Several tree swallows were banded early on at nestboxes on the study site but immediately disappeared, thus decreasing the total number of swallows to 27 females and 29 males during the 48 h prior to the manipulation. Therefore, sample sizes for the following analyses differ from 31 primarily because of some transience of potential breeders early in the season. Aggression scores were not obtained from six males because they were absent during more than 50% of their trial, and so these males were eliminated from the analysis. Of the 27 females, one was scored for her aggressiveness 4 days after the manipulation, as an aggression score could not be obtained for her previously. A subset of females ($N = 6$) were scored again at this time, and repeatability was calculated again (Lessells & Boag 1987) to ensure that scores obtained before the manipulation were not different from scores obtained immediately following the manipulation. For the females for which scores were obtained both before and after the manipulation, aggressiveness was highly repeatable ($r = 0.75$, $N = 6$, $F = 7.096$). Therefore, for the one female whose aggression score was recorded after the manipulation, this score is probably an accurate measure of her aggressiveness. In total, 27 females and 23 males were assayed for aggressiveness and are included in the analysis.

After performing aggression assays on males and females defending cavities at the beginning of the breeding season, I experimentally reduced the number of nesting cavities in the population. On the afternoon of 1 May 2006, I put up 15 new nestboxes, dispersed throughout the population. The entrance to each new nestbox was closed with duct tape at this point, making the boxes inaccessible. Each new nestbox was placed equidistant from either two or three other nestboxes, to control for effects of distance on cavity acquisition. At this stage of the breeding season, tree swallows leave their breeding site in the evening to roost overnight at a separate site; females do not sleep in their nestboxes until the completion of nests (Robertson et al. 1992). On the night of 1 May 2006, after all individuals had departed their cavities for their roosting sites, I removed all nestboxes occupied by tree swallows. Cavities occupied by eastern bluebirds were not removed because all six pairs were already either incubating or feeding nestlings, and at my site, I have never observed a tree swallow usurp the cavity of an established bluebird. Overnight, I opened the 15 new cavities by removing the duct tape covers from the entrance holes. At the time of the manipulation, no female had begun egg laying, but all females were in various stages of nest building.

The following morning, birds returned from their roosting sites and were forced to compete for access to a new nesting cavity. Beginning at dawn, I made repeated visits to the 15 new nestboxes to determine which individuals were defending each box. Both males and females were considered to have acquired a nestbox if they were seen repeatedly defending, entering and perching on the nestbox. Female nest-building behaviour also was used to signify nestbox acquisition. Repeat visits to each

nesting cavity in the 2 days following the manipulation indicated no changes in ownership of boxes since the morning of the manipulation, and I considered ownership final for the purpose of analysis. None of the birds that obtained nestboxes after the manipulation were usurped later in the season. Using a Mann–Whitney U test, I compared the aggression scores of individuals that obtained a nestbox and individuals that did not. A nonparametric test was used because aggression scores were not normally distributed. Results are reported as means \pm SE.

Ethical Note

Decoys used in aggression assays showed no signs of stress upon their release and typically resumed normal activities soon after release. At least six of 11 decoys used in this study successfully bred at the study site. Of the remaining five, four were probably floaters captured during early season nestbox intrusions that are common in this species (Stutchbury & Robertson 1987a), and one decoy escaped prior to banding, preventing me from tracking its future activities. To minimize the effect of the nestbox reduction on the breeding population, nine of the original nestboxes were restored 48 h after the manipulation. Seven banded pairs that did not obtain a cavity after the manipulation and two new unbanded pairs acquired these cavities and successfully bred at the study site. All birds at this site and the birds used as decoys bred in relative synchrony with other tree swallows in the surrounding area, indicating that neither the manipulation of nestboxes nor the use of decoys had a significant effect on reproduction. All aspects of this experiment were approved by the Institutional Animal Care and Use Committees at both Duke University (A062-04-02) and the University of Pittsburgh (0404837A-2).

RESULTS

Aggression scores across trials were highly repeatable (repeatability sensu Lessells & Boag 1987: $p < 0.0001$; $r = 0.79$, $N = 10$, $F = 12.149$), indicating reliable and consistent differences between individuals.

Female tree swallows that obtained a cavity after the manipulation had significantly higher aggression scores ($\bar{X} \pm \text{SE} = 31.7 \pm 4.6$) than females that did not obtain a cavity ($\bar{X} \pm \text{SE} = 18.3 \pm 4.0$) (Mann–Whitney U test: $U = 47.5$, $N_1 = 15$, $N_2 = 12$, $P = 0.038$; Fig. 1). For males, however, there was no significant difference in aggressiveness between individuals that obtained a cavity ($\bar{X} \pm \text{SE} = 25.4 \pm 6.2$) and those that did not obtain a cavity ($\bar{X} \pm \text{SE} = 25.6 \pm 5.1$) ($U = 70.0$, $N_1 = 13$, $N_2 = 10$, $P = 0.756$; Fig. 1). All pairs remained together during the manipulation. There was no relationship between the aggression scores of females and the scores of their mates (Spearman rank correlation: $r_s = -0.080$, $N = 21$, $P = 0.73$). Nestbox occupancy was reduced by 48% in accordance with the 48% reduction in the number of cavities, thus confirming the assumption of cavity limitation. As mentioned above, seven banded pairs that did not obtain cavities were seen at the study site during the 48 h following the manipulation, but there was no

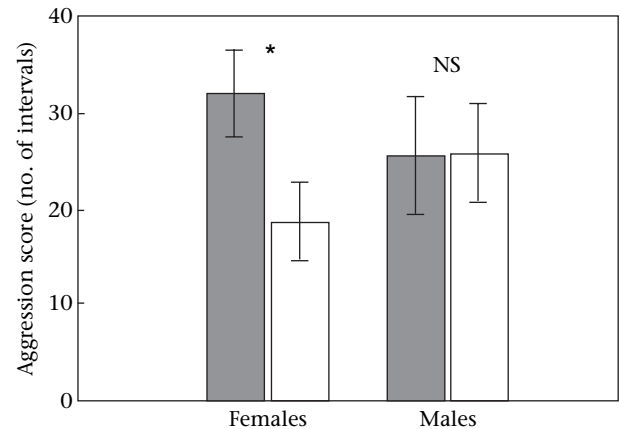


Figure 1. Aggression scores ($\bar{X} \pm \text{SE}$) of females and males that obtained a cavity (■) and those that did not (□).

indication that they were defending an unknown nesting cavity. These seven pairs quickly acquired cavities when nine nestboxes were put back up to minimize the effect of this experiment on the study population, again demonstrating that cavities were limiting.

Aggression scores were not significantly different between female age classes (subadult: $\bar{X} = 25.0 \pm 5.1$; Mann–Whitney U test: $U = 100.5$, adult: $\bar{X} = 26.4 \pm 4.5$; $N_1 = 13$, $N_2 = 14$, $P = 0.645$; Fig. 2), and adult females were no more likely to obtain a nestbox than were subadult females (Chi-square test: $\chi^2_1 = 0.101$, $N_{\text{subadult}} = 7$, $N_{\text{adult}} = 8$, $P = 0.751$).

DISCUSSION

These results provide experimental evidence that aggressive behaviour in female tree swallows is beneficial in securing a cavity and is therefore likely to be directly favoured by sexual selection in the context of female–female competition over nesting sites. After an experimental reduction in nesting cavity availability, more aggressive females acquired cavities, whereas less aggressive females did not. Cavities were indeed limiting, as the number of potential breeders directly tracked the

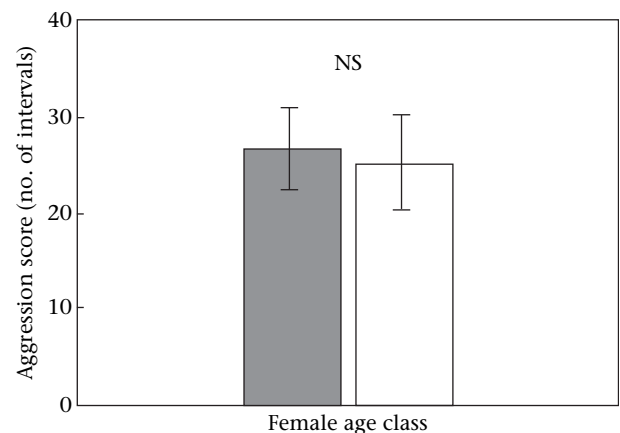


Figure 2. Aggression scores ($\bar{X} \pm \text{SE}$) of adult (■) and subadult (□) females.

adjustment of cavity number. Given that a nesting cavity is essential for female reproductive success and that more aggressive females are more likely to obtain a cavity, these results indicate that aggressiveness is adaptive in female tree swallows and is thus the likely target of direct selection. This study does not capture all variation in reproductive success (e.g. number of offspring); however, it does show that less aggressive females are less likely to obtain a cavity, the equivalent of zero reproductive success, whereas more aggressive females have the opportunity to breed. An alternative interpretation of these data, given that pairs stayed together, could be that male aggressiveness determined cavity acquisition. However, because male aggressiveness did not predict cavity acquisition and because males and females did not mate assortatively by aggressiveness, female aggressiveness was probably the primary determinant of cavity acquisition in this study. This experiment thus provides evidence that female aggressiveness is favoured in the context of female–female competition for a critical breeding resource, much like male–male competition has been cited in the evolution of conspicuous traits and behaviours in males of many species (Andersson 1994). Taken together with studies on the function of female ornamentation (Lebas 2006; Weiss 2006; Pryke 2007; reviewed in Amundsen & Parn 2006) and song in female songbirds (Ritchison 1983; Catchpole & Slater 1995; Searcy & Yasukawa 1995; Langmore 1998), these results suggest that the processes favouring conspicuous traits and behaviours in females may not be very different from the processes affecting these traits in males.

Males typically are regarded as the more competitive sex, but male aggressiveness did not predict cavity acquisition in this study. This result may be explained if females are the more likely target of selection for cavity acquisition in this system. Female tree swallows do not engage in brood parasitism; thus, a cavity is necessary for their reproductive success (Barber et al. 1996; Kempnaers et al. 1999). Male floaters, on the other hand, occasionally reproduce via extrapair fertilizations with resident females (Barber & Robertson 1999; Kempnaers et al. 2001). Other sources of selection on males may have been stronger during the time of the manipulation, such as selection to retain a female. This hypothesis is consistent with my observation that all pairs remained together throughout the manipulation. Although male aggressiveness did not predict cavity acquisition in this experiment, it may influence territory establishment, perhaps before females arrive on the breeding ground.

If males experience selection to be aggressive, indirect selection via genetic correlation may work together with direct selection to favour aggressive behaviour in female tree swallows. To test whether indirect selection via genetic correlation with males also encourages aggressiveness in females, a detailed pedigree would be needed to calculate heritability of aggression score. While I do not have an estimate of heritability, the high repeatability of aggression score in this study suggests a potential for high genetic variance in female aggressiveness, because repeatability provides an upper limit for heritability (Falconer 1989). High repeatability does not necessarily equate to high heritability, however, because repeatability can be

high owing to a large environmental component of inter-individual variance (e.g. maternal or development effects; Falconer 1989). A repeatability value of 0.79 is especially high for a behaviour (see Boag 1983; Boake 1989), indicating that aggression scores were minimally affected by localized or fleeting circumstances. High repeatability of aggressiveness also suggests that this trait may be particularly likely to respond to selection, much like other traits with low variance within individuals and high variance between them (Boake 1989).

Finding that aggressive behaviour is beneficial to females is particularly notable in the face of the costs of aggressiveness that have been well documented in a number of vertebrates (e.g. Folstad & Karter 1992; Walter & Trillmich 1994; Creel 2001; Dijkstra et al. 2007), including birds (Lefelaar & Robertson 1985; Robertson et al. 1986; Duckworth 2006). Females may risk injury or even death during intense aggressive interactions (Lefelaar & Robertson 1985; Robertson et al. 1986). If female aggression is mediated by testosterone (e.g. Langmore et al. 2002; Gill et al. 2007; but see Elekonich & Wingfield 2000; Jawor et al. 2006), aggressive females may also experience increased stress levels or lower immune function (Folstad & Karter 1992; Braude et al. 1999; Wingfield et al. 2001; Ketterson et al. 2005; but see Roberts et al. 2004). Even low-intensity aggressive behaviours may be costly if time and energy spent being aggressive detract from other behaviours essential to survival or reproductive success (e.g. foraging, parental care; Stearns 1992). While the precise costs of aggressiveness are unknown in this system, the benefit to aggressive females over other females is probably substantial (e.g. obtaining a nesting cavity versus not obtaining one).

The high proportion of subadults in this relatively recently established population provided a unique opportunity to examine age-related differences in competitive ability that may be relevant in understanding the evolution of delayed plumage maturation in female tree swallows. While males of many species show delayed plumage maturation, female-biased delayed plumage maturation is extremely rare (Robertson et al. 1992). One widely accepted theory for delayed plumage maturation, the breeding threshold hypothesis, states that young individuals delay full investment in breeding because they are competitively inferior (Studd & Robertson 1985; Rohwer & Butcher 1988). If subadult plumage is used to signal low threat in aggressive interactions, two predictions should hold: (1) subadults should experience reduced aggression from resident females and (2) subadults should be less aggressive. Stutchbury & Robertson (1987b) rejected the first prediction by demonstrating that subadult plumage in female tree swallows evokes reduced aggression from males but not from females. My results further support those of Stutchbury & Robertson (1987b) by rejecting the second key prediction of the hypothesis, that subadult plumage signals low aggressive threat. Subadults were as aggressive and as likely to obtain a nesting cavity based on their aggressiveness as were adults. Although reduced aggressiveness cannot account for the relative scarcity of subadults in established breeding populations of tree swallows, subadults may be inferior in other aspects that deter them from breeding. For example, subadult

females have shorter wings (Stutchbury & Robertson 1987c; K. A. Rosvall, unpublished data), which may make them less efficient at flying (Pennycuik 1968). Subadult females tend to lose more mass during the nestling phase than do adult females (Lozano & Handford 1995), indicating that breeding and provisioning a nest may be more difficult for subadults. Also, because subadult females typically arrive at the breeding ground later than adult females (Robertson et al. 1992), their relative absence from the breeding population may simply be because most territories are already claimed by the time they arrive on the breeding ground.

While more aggressive females were more successful in obtaining nesting cavities, traits other than aggressiveness may have contributed to this outcome. Recent work in several species shows that aggressive behaviour may be part of a correlated behavioural syndrome (Sih et al. 2004). In laboratory and field studies, aggressiveness has been associated with exploratory and dispersal behaviour (Verbeek et al. 1996; Dingemanse et al. 2003; van Oers et al. 2004; Duckworth & Badyaev 2007). If more aggressive birds are also more exploratory, or are more likely to return back from their roosting sites before their neighbours, they may be more likely to find vacancies, and these correlated behaviours may help explain why more aggressive females were more likely to secure nesting cavities. Female tree swallows are likely to be quite exploratory, as they tend to take over naturally vacant cavities within hours of predation or nest abandonment of another female (Stutchbury & Robertson 1987a). Regardless of the exact mechanism by which females obtained cavities in this study, the results still indicate that females that obtained cavities were significantly more aggressive than females that did not. Further work could elucidate the extent to which aggressive and exploratory behaviours are correlated and the mechanism by which these traits are favoured by selection.

Acknowledgments

This work was supported by a National Science Foundation Graduate Research Fellowship, the American Ornithologists' Union and a McKinley Research Award. I am grateful to the Linesville State Fish Hatchery, University of Pittsburgh and Pymatuning Lab of Ecology for use of field sites and space. Many thanks to S. Nowicki for detailed advice in designing and writing up this study. The experiment and manuscript were greatly improved by helpful comments from R. C. Anderson, B. Ballentine, E. P. Derryberry, P. A. Gowaty, J. Hyman, S. Peters, E. A. Vance and two anonymous referees. This is Pymatuning Lab of Ecology publication no. 194.

References

- Amundsen, T. 2000. Why are female birds ornamented? *Trends in Ecology & Evolution*, **15**, 149–155.
- Amundsen, T. & Parn, H. 2006. Female coloration: review of functional and nonfunctional hypotheses. In: *Bird Coloration* (Ed. by G. E. Hill & K. J. McGraw), pp. 280–345. Cambridge, Massachusetts: Harvard University Press.
- Andersson, M. B. 1994. *Sexual Selection*. Princeton, New Jersey: Princeton University Press.
- Barber, C. A. & Robertson, R. J. 1999. Floater males engage in extrapair copulations with resident female tree swallows. *Auk*, **116**, 264–269.
- Barber, C. A., Robertson, R. J. & Boag, P. T. 1996. The high frequency of extrapair paternity in tree swallows is not an artifact of nestboxes. *Behavioral Ecology and Sociobiology*, **38**, 425–430.
- Berglund, A., Magnhagen, C., Bisazza, A., König, B. & Huntingford, F. 1993. Female–female competition over reproduction. *Behavioral Ecology*, **4**, 184–187.
- Boag, P. T. 1983. The heritability of external morphology in Darwin's ground finches (*Geospiza*) on Isla Daphne Major, Galapagos. *Evolution*, **37**, 877–894.
- Boake, C. R. B. 1989. Repeatability: its role in evolutionary studies of mating behavior. *Evolutionary Ecology*, **3**, 173–182.
- Braude, S., Tang-Martinez, Z. & Taylor, G. T. 1999. Stress, testosterone, and the immunoredistribution hypothesis. *Behavioral Ecology*, **10**, 345–350.
- Brown, J. L. 1969. Territorial behavior and population regulation in birds. *Wilson Bulletin*, **81**, 293–329.
- Catchpole, C. K. & Slater, P. J. B. 1995. *Bird Song: Biological Themes and Variations*. New York: Cambridge University Press.
- Chek, A. A. & Robertson, R. J. 1991. Infanticide in female tree swallows: a role for sexual selection. *Condor*, **93**, 454–457.
- Clutton-Brock, T. 2007. Sexual selection in males and female. *Science*, **318**, 1882–1885.
- Creel, S. 2001. Social dominance and stress hormones. *Trends in Ecology & Evolution*, **16**, 491–497.
- Darwin, C. 1871. *The Descent of Man, and Selection in Relation to Sex*. London: Murray.
- Dijkstra, P. D., Hekman, R., Schulz, R. W. & Groothuis, T. G. G. 2007. Social stimulation, nuptial coloration, androgens and immunocompetence in a sexual dimorphic cichlid fish. *Behavioral Ecology and Sociobiology*, **61**, 599–609.
- Dingemanse, N. J., Both, C., van Noordwijk, A. J., Rutten, A. L. & Drent, P. J. 2003. Natal dispersal and personalities in great tits (*Parus major*). *Proceedings of the Royal Society of London, Series B*, **270**, 741–747.
- Duckworth, R. A. 2006. Behavioral correlations across breeding contexts provide a mechanism for a cost of aggression. *Behavioral Ecology*, **17**, 1011–1019.
- Duckworth, R. A. & Badyaev, A. V. 2007. Coupling of dispersal and aggression facilitates the rapid range expansion of a passerine bird. *Proceedings of the National Academy of Sciences, U.S.A.*, **104**, 15017–15022.
- Dunn, P. O. & Hannon, S. J. 1991. Intraspecific competition and the maintenance of monogamy in tree swallows. *Behavioral Ecology*, **2**, 258–266.
- Dunn, P. O., Whittingham, L. A., Lifjeld, J. T., Robertson, R. J. & Boag, P. T. 1994. Effects of breeding density, synchrony, and experience on extrapair paternity in tree swallows. *Behavioral Ecology*, **5**, 123–129.
- Elekovich, M. M. & Wingfield, J. C. 2000. Seasonality and hormonal control of territorial aggression in female song sparrows (Passeriformes: Emberizidae: *Melospiza melodia*). *Ethology*, **106**, 493–510.
- Falconer, D. S. 1989. *Introduction to Quantitative Genetics*. 3rd edn. Essex: Longman Scientific & Technical.
- Fisher, R. A. 1958. *The Genetical Theory of Natural Selection*. New York: Oxford University Press.
- Fitzpatrick, S., Berglund, A. & Rosenqvist, G. 1995. Ornaments or offspring: costs to reproductive success restrict sexual

- selection processes. *Biological Journal of the Linnean Society*, **55**, 251–260.
- Folstad, I. & Karter, A. J. 1992. Parasites, bright males, and the immunocompetence handicap. *American Naturalist*, **139**, 603–622.
- Gill, S. A., Alfson, E. D. & Hau, M. 2007. Context matters: female aggression and testosterone in a year-round territorial neotropical songbird (*Thryothorus leucotis*). *Proceedings of the Royal Society of London, Series B*, **274**, 2187–2194.
- Gowaty, P. A. & Wagner, S. J. 1988. Breeding-season aggression of female and male eastern bluebirds (*Sialia sialis*) to models of potential conspecific and interspecific egg dumpers. *Ethology*, **78**, 238–250.
- Hamilton, W. D. & Zuk, M. 1982. Heritable true fitness and bright birds: a role for parasites? *Science*, **218**, 384–387.
- Holroyd, G. L. 1975. Nest site availability as a factor limiting population size of swallows. *Canadian Field-Naturalist*, **89**, 60–64.
- Hussell, D. J. T. 1983. Age and plumage color in female tree swallows. *Journal of Field Ornithology*, **54**, 312–318.
- Jaeger, R. G., Kalvinsky, D. & Shimizu, N. 1982. Territorial behavior of the red-backed salamander: expulsion of intruders. *Animal Behaviour*, **30**, 490–496.
- Jawor, J. M., Young, R. & Ketterson, E. D. 2006. Females competing to reproduce: dominance matters but testosterone may not. *Hormones and Behavior*, **49**, 362–368.
- Kempnaers, B., Congdon, B., Boag, P. & Robertson, R. J. 1999. Extra-pair paternity and egg hatchability in tree swallows: evidence for the genetic compatibility hypothesis? *Behavioral Ecology*, **10**, 304–311.
- Kempnaers, B., Everding, S., Bishop, C., Boag, P. & Robertson, R. J. 2001. Extra-pair paternity and the reproductive role of male floaters in the tree swallow (*Tachycineta bicolor*). *Behavioral Ecology and Sociobiology*, **49**, 251–259.
- Ketterson, E. D., Nolan, V., Jr. & Sandell, M. 2005. Testosterone in females: mediator of adaptive traits, constraint on sexual dimorphism, or both? *American Naturalist*, **166** (Supplement), S85–S98.
- Kopachena, J. G. & Falls, J. B. 1993. Aggressive performance as a behavioral correlate of plumage polymorphism in the white-throated sparrow (*Zonotrichia albicollis*). *Behaviour*, **124**, 249–266.
- Lande, R. 1980. Sexual dimorphism, sexual selection, and adaptation in polygenic characters. *Evolution*, **34**, 292–305.
- Lande, R. & Arnold, S. J. 1983. The measurement of selection on correlated characters. *Evolution*, **37**, 1210–1226.
- Langmore, N. E. 1998. Functions of duet and solo songs of female birds. *Trends in Ecology & Evolution*, **13**, 136–140.
- Langmore, N. E., Cockrem, J. F. & Candy, E. J. 2002. Competition for male reproductive investment elevates testosterone levels in female dunnocks, *Prunella modularis*. *Proceedings of the Royal Society of London, Series B*, **269**, 2473–2478.
- Lebas, N. R. 2006. Female finery is not for males. *Trends in Ecology & Evolution*, **21**, 170–173.
- Leffelaar, D. & Robertson, R. J. 1985. Nest usurpation and female competition for breeding opportunities by tree swallows. *Wilson Bulletin*, **97**, 221–224.
- Lessells, C. M. & Boag, P. T. 1987. Unrepeatable repeatabilities: a common mistake. *Auk*, **104**, 116–121.
- Lozano, G. A. & Handford, P. T. 1995. A test of an assumption of delayed plumage maturation hypotheses using female tree swallows. *Wilson Bulletin*, **107**, 153–164.
- Møller, A. P. 1987. Intraspecific nest parasitism and antiparasite behavior in swallows, *Hirundo rustica*. *Animal Behaviour*, **35**, 247–254.
- van Oers, K., de Jong, G., Drent, P. J. & van Noordwijk, A. J. 2004. A genetic analysis of avian personality traits: correlated, response to artificial selection. *Behavior Genetics*, **34**, 611–619.
- Palombit, R. A., Cheney, D. L. & Seyfarth, R. M. 2001. Female–female competition for male ‘friends’ in wild chacma baboons, *Papio cynocephalus ursinus*. *Animal Behaviour*, **61**, 1159–1171.
- Pennycuik, C. J. 1968. Power requirements for horizontal flight in the pigeon. *Journal of Experimental Biology*, **49**, 527–555.
- Pryke, S. R. 2007. Fiery red heads: female dominance among head color morphs in the Gouldian finch. *Behavioral Ecology*, **18**, 621–627.
- Rauch, N. 1988. Competition of marine iguana females (*Amblyrhynchus cristatus*) for egg-laying sites. *Behaviour*, **107**, 91–106.
- Ritchison, G. 1983. The function of singing in female black-headed grosbeaks (*Pheucticus melanocephalus*): family-group maintenance. *Auk*, **100**, 105–116.
- Roberts, L. B. & Searcy, W. A. 1988. Dominance relationships in harems of female red-winged blackbirds. *Auk*, **105**, 89–96.
- Roberts, M. L., Buchanan, K. L. & Evans, M. R. 2004. Testing the immunocompetence handicap hypothesis: a review of the evidence. *Animal Behaviour*, **68**, 227–239.
- Robertson, R. J., Gibbs, H. L. & Stutchbury, B. J. 1986. Spitefulness, altruism, and the cost of aggression: evidence against superterritoriality in tree swallows. *Condor*, **88**, 104–105.
- Robertson, R. J., Stutchbury, B. J. & Cohen, R. R. 1992. *Tree swallow (Tachycineta bicolor)*. In: *The Birds of North America*. No. 11. Philadelphia; Washington, D.C.: Academy of Natural Sciences; American Ornithologists’ Union.
- Rohwer, S. & Butcher, G. S. 1988. Winter versus summer explanations of delayed plumage maturation in temperate passerine birds. *American Naturalist*, **131**, 556–572.
- Sandell, M. I. 1998. Female aggression and the maintenance of monogamy: female behaviour predicts male mating status in European starlings. *Proceedings of the Royal Society of London, Series B*, **265**, 1307–1311.
- Searcy, W. A. & Yasukawa, K. 1995. *Polygyny and Sexual Selection in Red-winged Blackbirds*. Princeton, New Jersey: Princeton University Press.
- Searcy, W. A. & Yasukawa, K. 1996. The reproductive success of secondary females relative to that of monogamous and primary females in red-winged blackbirds. *Journal of Avian Biology*, **27**, 225–230.
- Sih, A., Bell, A. M., Johnson, J. C. & Ziemba, R. E. 2004. Behavioral syndromes: an integrative overview. *Quarterly Review of Biology*, **79**, 241–277.
- Slagsvold, T. 1993. Female–female aggression and monogamy in great tits *Parus major*. *Ornis Scandinavica*, **24**, 155–158.
- Slagsvold, T. & Lifjeld, J. T. 1994. Polygyny in birds: the role of competition between females for male parental care. *American Naturalist*, **143**, 59–94.
- Stearns, S. C. 1992. *The Evolution of Life Histories*. Oxford: Oxford University Press.
- Studd, M. V. & Robertson, R. J. 1985. Life-span, competition, and delayed plumage maturation in male passerines: the breeding threshold hypothesis. *American Naturalist*, **126**, 101–115.
- Stutchbury, B. J. & Robertson, R. J. 1985. Floating populations of female tree swallows. *Auk*, **102**, 651–654.
- Stutchbury, B. J. & Robertson, R. J. 1986. A simple trap for catching birds in nest boxes. *Journal of Field Ornithology*, **57**, 64–65.
- Stutchbury, B. J. & Robertson, R. J. 1987a. Behavioral tactics of subadult female floaters in the tree swallow. *Behavioral Ecology and Sociobiology*, **20**, 413–419.

- Stutchbury, B. J. & Robertson, R. J.** 1987b. Signaling subordinate and female status: two hypotheses for the adaptive significance of subadult plumage in female tree swallows. *Auk*, **104**, 717–723.
- Stutchbury, B. J. & Robertson, R. J.** 1987c. Two methods of sexing adult tree swallows before they begin breeding. *Journal of Field Ornithology*, **58**, 236–242.
- Summers, K.** 1989. Sexual selection and intra-female competition in the green poison-dart frog, *Dendrobates auratus*. *Animal Behaviour*, **37**, 797–805.
- Verbeek, M. E. M., Boon, A. & Drent, P. J.** 1996. Exploration, aggressive behavior and dominance in pair-wise confrontations of juvenile male great tits. *Behaviour*, **133**, 945–963.
- Walter, B. & Trillmich, F.** 1994. Female aggression and male peace-keeping in a cichlid fish harem: conflict between and within the sexes in *Lamprologus ocellatus*. *Behavioral Ecology and Sociobiology*, **34**, 105–112.
- Weiss, S. L.** 2006. Female-specific color is a signal of quality in the striped plateau lizard (*Sceloporus virgatus*). *Behavioral Ecology*, **17**, 726–732.
- Wingfield, J. C., Lynn, S. E. & Soma, K. K.** 2001. Avoiding the 'costs' of testosterone: ecological bases of hormone-behavior interactions. *Brain Behavior and Evolution*, **57**, 239–251.
- Winkler, D. W.** 1992. Causes and consequences of variation in parental defense behavior by tree swallows. *Condor*, **94**, 502–520.
- Zahavi, A.** 1975. Mate selection: a selection for a handicap. *Journal of Theoretical Biology*, **53**, 205–214.
- Zahavi, A.** 1977. The cost of honesty (further remarks on the handicap principle). *Journal of Theoretical Biology*, **67**, 603–605.

IN FOCUS

Featured Articles in This Month's *Animal Behaviour*

Female Fighters

Sexual selection, the evolution of adornments for attracting mates and weapons for competing with members of the same gender, continues to pose intriguing behavioural questions. In this issue, Rosvall (pp. 1603–1610) asks whether aggression among female tree swallows occurs as a by-product of sexual selection for aggression among males, or whether there is direct selective value for females who are aggressive.

This question arises because selection on one gender often carries over to affect the other gender. Male mammals have functionless nipples because they share most of their genome with females; nipples occur in both males and females as a result of shared genetic architecture, even though they are functional only in females. In cattle, horns probably function primarily in intermale combat, but are carried by both males and females. In horned breeds, such as Texas Longhorns, both bulls and cows carry large horns, and in breeds selected for minimal horns, such as Polled Herefords, both genders lack horns.

In some cases, male and female characteristics are unlinked, genetically. In peafowl, the male, or peacock, carries an elaborate train of feathers, whereas the female, or peahen, is drab. Siamese fighting fish, *Betta splendens*, provide an example that combines linkage and independence: males bear much larger tails than females, but male and female coloration are at least partially linked, so selection for brightly coloured *Betta* males results in bright female coloration.

These observations lead to two important and interesting questions. First, what level of linkage exists between male and female traits, and second, to what extent does selection pressure on one gender lead to the presence of traits that may be disadvantageous in the other? Strong selection for traits such as horns, coloration or aggressiveness in one gender may actually lead to disadvantageous features for the other.

Tree swallows are monogamous and each pair requires a hole in a tree to nest successfully. The availability of holes in any given area is limited, and a significant proportion, about a quarter, of tree swallows fail to nest because they cannot find appropriate holes in trees. Under these circumstances, the obvious prediction is that aggressive competition for holes is critical to these birds. Less obvious is which gender might engage in this competition.

By manipulating the number of nest holes in the birds' habitat, Rosvall was able to measure the intensity of aggression of males and females, the effect of that aggression on each pair's possession of a nest hole, and differences between the outcomes of male and female behaviour (Fig. 1).

A key initial finding was that individual birds consistently expressed aggressive behaviour. This suggests, but does not prove, that genetic differences underlie the behavioural differences between birds. Pairs with more aggressive females were more likely to possess a hole, whereas the aggressiveness of the male was not correlated with hole ownership. Interestingly, the aggressiveness of males and females in pairs was not correlated, suggesting that aggressive birds do not preferentially choose aggressive mates.

Rosvall concludes that similar processes may affect sexually selected traits in females and males. Clearly, female tree swallows gain a direct advantage from being aggressive and are not just aggressive because selection favours aggression in males. Results like this challenge the stereotype of aggressiveness as a typically male trait.

Michael Breed
Executive Editor



Figure 1. A subadult female tree swallow on an experimental nest-box. Photo: Kimberly Rosvall.