

Maintenance of variation in sexually selected traits in females: a case study using intrasexual aggression in tree swallows *Tachycineta bicolor*

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A fundamental question in evolutionary biology is how phenotypic variation is maintained in the face of selection that ought to deplete that variation. Much research has investigated this question in traits favored via sexual selection in males, with a common solution implicating the condition dependence of sexually selected phenotypes. Despite growing interest in sexual selection on females, it is not clear if the same mechanisms maintain variation in female ornaments, weaponry or other female behaviors targeted by sexual selection. An important step in testing condition dependence in females is thus to identify whether sexually selected female phenotypes are associated with condition and also with potential costs. Here, I examine these two components of condition dependence for a sexually selected behavior, intrasexual aggression, in female tree swallows *Tachycineta bicolor*. I asked whether high levels of intrasexual aggression map onto natural variation in female condition and whether aggression is associated with one potential behavioral cost: performance in a vertically challenging test of flight. More aggressive females were heavier for their body size, heavier for their wing size and showed decreased flight ability, relative to less aggressive females. These findings are consistent with condition dependence, where only females in better condition are able to be highly aggressive. The association between high aggression and reduced flight ability may result from the additional lift required to power these relatively heavier birds. These associations between natural variation in aggressive behavior, morphology and flight ability are consistent with condition dependence because they confirm two basic assumptions of condition dependence: a link between aggression and condition, and a link between aggression and a behavioral cost, the speed of escape flight. As the first study to examine these assumptions for a conspicuous behavior favored by intrasexual selection in females, this study suggests broad relevance of condition dependence.

A long-standing question in evolutionary biology is how variation is maintained in traits that are under selection: variation is the raw material on which selection acts, and yet theory suggests that selection should deplete genetic variation (Darwin 1859, Fisher 1930, Charlesworth 1987, Falconer 1989). Over the years, many solutions to this paradox have been proposed, such as mutation (Lande 1975), balancing selection (Moore and Moore 1999), condition dependence (Rowe and Houle 1996), and variable selective pressures (David et al. 2000, Jia et al. 2000, Danielson-Francois et al. 2006) generating or maintaining trait variance over time. Much research has focused on this puzzle in traits under intersexual selection in males (i.e. the paradox of the lek, Kirkpatrick and Ryan 1991, Tomkins et al. 2004, Cotton and Pomiankowski 2007). Relatively fewer studies have explored the maintenance of variation in sexually selected traits in females, with the exception of female ornaments (Siefferman and Hill 2005, reviewed in Amundsen and Pärn 2006, Weiss 2006, Legagneux et al. 2010), despite growing evidence that sexual selection promotes exaggerated female traits as

well (Amundsen 2000, Clutton-Brock 2007, Kraaijeveld et al. 2007, Clutton-Brock 2009).

One example of a female behavior that appears to be sexually selected occurs in the tree swallow *Tachycineta bicolor*, where high levels of intrasexual aggression are favored in female-female competition over nesting cavities (Rosvall 2008). While there is some debate regarding the application of sexual selection to females (Clutton-Brock 2010, Roughgarden and Akçay 2010), a recent 'consensus view' suggests a solution, where a trait is sexually selected if it influences competition for mates (Shuker 2010, Rosvall in press). Thus, intrasexual selection clearly occurs when two individuals directly compete for a mate, but it also occurs during the many forms of indirect mating competition, e.g. competition for mating resources, such as a territory or nesting site, that are required for an individual to be qualified as a mate, even though competition for these resources occurs prior to (or, in place of) any direct competition to mate (Andersson 1994, Ahnesjö et al. 2001). In line with this view, sexual selection appears to shape female aggression in tree swallows much like

aggression and dominance are selectively advantageous in male–male competition for territories and mates (Brown 1969, Andersson 1994). Females that outcompete other females for nesting cavities have the opportunity to mate and to breed; without acquiring a cavity, a female will neither mate nor breed, since there is essentially no intraspecific brood parasitism in this species (Barber et al. 1996, Kempenaers et al. 1999). Aggressive interactions among females are common in tree swallows, ranging from short aerial chases to vigorous mid-air grappling and tumbling to the ground, and the loser may suffer cavity eviction or even death (Chek and Robertson 1991, Robertson et al. 1992, Rosvall unpubl.). Cavities are a limited resource essential to female mating and reproductive success (Holroyd 1975, Robertson et al. 1992), and thus, the finding that more aggressive females are more likely to obtain a nesting cavity (i.e. a resource required to be qualified to mate) suggests that high levels of aggression are favored via sexual selection (Rosvall 2008).

If more aggressive females are more likely to obtain nesting cavities and are more likely to breed altogether, then why are all females not highly aggressive? Despite apparent directional selection for high aggressiveness in the context of nestbox competition, females with a range of aggressiveness persist in a population every year. For example, in the population studied here, the coefficients of variance for female aggressiveness remain high annually: 59.0% in 2005, 49.9% in 2006, and 50.9% in 2007, with aggression scores ranging from 0 to approximately 55 each year (see Methods for details).

A potential solution to this apparent paradox is that aggressive behavior, like many other sexually-selected phenotypes, is also associated with various production or maintenance costs (reviewed in Andersson 1994, Searcy and Nowicki 2005). Indicator mechanisms of sexual selection predict that either direct costs (e.g. increased risk of predation, parasitism or injury) or indirect costs (e.g. high energetic demands or low immune function) ultimately affect individual fitness, and that they do so differentially based upon an individual's quality or condition (Zahavi 1975, Grafen 1990, Kotiaho 2001). Life history theory suggests that sexually selected phenotypes are often costly, since individuals have limited resources to devote to aspects of mating effort, parental effort and self-maintenance, resulting in evolutionary tradeoffs among these contributors to fitness (Stearns 1992, Roff et al. 2002, Magrath and Komdeur 2003). Condition dependence, where a phenotype is linked with an individual's intrinsic condition or quality, is thus likely to evolve because only the 'best' individuals are able to overcome the costs associated with the phenotype (Price et al. 1993, Johnstone 1995). The condition dependence of sexually selected phenotypes solves the above mentioned paradox because these phenotypes become linked with the many loci determining condition, making trait variance resistant to depletion by selection (Rowe and Houle 1996, Tomkins et al. 2004).

With respect to the maintenance of variation of female aggressive behavior, two key questions emerge: first, are high levels of aggression associated with an underlying aspect of female condition? And, second, is aggression linked, either directly or indirectly, with other behavioral costs that could ultimately result in fitness costs? Regarding

the first question, 'condition' describes an individual's ability to obtain the resources needed to satisfy its energy demands (Rowe and Houle 1996). Thus, if aggressiveness is condition dependent, then variation in female aggressiveness will map onto individual variation in energy reserves. A previous study demonstrated a link between female aggression and female mass (Rosvall 2011), suggesting the potential for condition dependence; however, it is not yet clear if this relationship exists as a side effect of aggressive females having larger structural size, or whether these highly aggressive females are truly in better condition. Here, I use two years of morphological and behavioral data from a population of tree swallows to directly test whether a standard measure of avian condition (i.e. size corrected body mass) predicts variance in female aggression, a key step in determining whether aggressiveness is condition dependent.

Regarding the second question, there are many possible direct and indirect costs that may be associated with aggression, including reduced parental effort, lower immune function, or increased susceptibility to predators (Kopachena and Falls 1993, Zysling et al. 2006, Rosvall 2011). Because tree swallows are aerial insectivores that spend 80% of the day in flight (Robertson et al. 1992), the ability to fly may be an important contributor to self-maintenance, mating effort, or survival through its influence on foraging, aggressive interactions or the ability to flee from predators, respectively. Based upon known trade-offs in flight (Pennycuik 1989, Warrick 1998, Dial 2003), we might expect a female that excels at the rapid aerial chases that characterize swallow aggression to fare comparatively poorly in her ability to generate lift. To capture individual variation in flight speed that is likely to map onto flight efficiency, lift, and ultimately, the ability to flee quickly and escape a predator (Norberg 1990, Kullberg et al. 2002b), I tested females in a portable, vertical flight tube and compared this measure of flight ability to a female's aggressiveness. Collectively, this approach ties together a sexually selected trait with individual condition and with one potential behavioral cost. In doing so, these studies examine two underlying assumptions of condition dependence, and accordingly, they contribute to our understanding of the maintenance of variation in sexually selected traits in females.

Methods

Data for this study were collected in Crawford County, Pennsylvania in the spring of 2005 and 2006. All flight tests took place between April and June 2006. The site consists of approximately 80 pairs of tree swallows nesting in artificial cavities at the Pennsylvania State Gamelands and State Fish Hatchery near Linesville, Pennsylvania (41°40'N, 80°26'W). All females were classified as either subadult (i.e. one-year old) or adult (i.e. older than one year) based on plumage (Hussell 1983). Wing length was measured to the nearest 0.5 mm using a wing rule, tarsus was measured with calipers to the nearest 0.1 mm, and mass was measured to the nearest 0.1 g using a spring-loaded scale. In cases where females were captured in both years ($n=7$ of 65 females), I arbitrarily selected

behavioral and morphological measurements from the first year only, to avoid pseudoreplication. A subset of these females were also used in another study, measuring how female aggressiveness impacts offspring (Rosvall 2011).

I estimated female body condition as the residuals from a regression of body mass on tarsus length because tarsus length positively and significantly co-varied with body mass ($n = 55$, $r_s = 0.30$, $p = 0.028$), and because tarsus provides a stable measure of overall body size that is unlikely to already co-vary with condition (Rising and Somers 1989, Green 2001). Measures of condition such as this one have been used extensively in many songbird species, including tree swallows (Perrins 1965, Ardia 2006, Ardia and Clotfelter 2007, cf. Green 2001), and they provide an estimate of an individual's protein, fat, or muscle reserves (Lozano 1994). I chose this particular measure of condition instead of another proxy for female quality (i.e. breeding date) that has been used in this species (Bowlin and Winkler 2004, Ardia et al. 2006) because reproductive traits such as the timing of breeding are thought not to reflect an individual's acquisition, storage or use of resources (i.e. condition), but instead they reflect the conversion of these resources into offspring, a parameter which is itself likely to be a condition dependent trait (Tomkins et al. 2004).

Another morphological measure that may be relevant to the connection between aggression, condition, and flight ability is wing-loading (body mass/wing area). Without a direct measure of wing area, I used the ratio of body mass/wing length as a proxy for wing-loading. While this proxy should not be interpreted as a true measure of wing-loading, this measure is mathematically proportional to wing-loading (Norberg 1990). For statistical reasons of multicollinearity, I did not use this particular measure in the model examining the morphological predictors of aggressive behavior. Instead, I use this proxy to visually represent the results of the multiple regression (see Statistical analyses) and to place the results in the framework of flight mechanics.

All females were color-banded and marked with small dabs of acrylic paint (approximately 3–5 mm wide) on their wings for individual identification (Dunn et al. 1994). A very thin layer of paint was applied swiftly and evenly to the 7th primary and allowed to dry in a manner that did not alter the shape of flight feathers (unpubl.). While most females in this study were marked with paint earlier in the season, some were not marked until immediately after flight tests. To test the assumption that paint did not affect flight, I compared flight ability between females that did and did not have painted wings at the time of flight trial. Females whose wings were marked with acrylic paint for identification prior to flight trials did not differ from unmarked females in flight ability (unpaired t-test: painted = $1.44 \pm 0.07 \text{ m s}^{-1}$; unpainted = $1.32 \pm 0.05 \text{ m s}^{-1}$, $t = 1.23$, $p = 0.24$), suggesting that this auxiliary marking did not significantly affect flight aerodynamics. Therefore, I pooled both painted and unpainted females in all subsequent analyses.

Flight ability

I measured flight ability using a portable flight tube in the field (modified from Kullberg et al. 2002a, b) that is

thought to capture an individual's ability to quickly flee from a predator. The vertical tube (180 cm tall, 40 cm diameter) was made of semi-transparent plastic and marked with horizontal lines every 20 cm. When released from the hand at the bottom of the tube, birds flew straight up, towards the light, and into a mist-net cage, where I was able to retrieve them for repeat trials. Each bird was tested multiple times (average: 6.0 ± 0.4 trials per bird) consecutively in a short time period (< 5 min). I did repeat trials because some females did not immediately fly straight up the tube on the first attempt. I examined the potential effect of repeat trials on flight speed, and I found that both bird identity and flight trial order significantly affected speed (linear mixed model, $n = 158$ flights, $R_{\text{adj}}^2 = 0.33$; bird as random effect explained 22.1% variance in flight speed; order as fixed effect explained 10.5% variance in flight speed, $F = 10.7$, $p < 0.01$). Post hoc Tukey tests revealed that the order effect was driven by significantly slower speeds in the first attempt than in the fourth and fifth attempts (both $p < 0.05$). No other effects of order were seen. The mean, median and maximum flight speeds were highly correlated (all $r > 0.55$, all $p < 0.018$), and thus, I used the median speed to fly straight up the middle 140 cm of the tube as a proxy for an individual's typical flight ability (m s^{-1}). This approach conservatively estimates flight ability, eliminating the fastest and slowest flights for all individuals and effectively minimizing any effects of performing repeated trials.

Each trial was recorded with a digital camcorder (Canon ZR850). Trials were scored later, watching frame by frame (30 frames s^{-1}) to determine the time to fly up the tube for each individual. Flight trials took place during either the incubation or nestling stages, although there was no difference in flight ability between females tested in these two stages (incubation: $1.35 \pm 0.25 \text{ m s}^{-1}$, $n = 16$; nestling: $1.37 \pm 0.20 \text{ m s}^{-1}$, $n = 12$; unpaired t-test: $t = 0.21$, $p = 0.84$), and so data were pooled for further analyses. Further, because female age is thought to relate to mass and wing length (Desteven 1978, Stutchbury and Robertson 1987b, Lozano and Handford 1995), both traits that could affect flight ability, I tested whether subadult and adult females differed in median flight speed. Finding no difference (adults: $1.38 \pm 0.22 \text{ m s}^{-1}$, $n = 13$; subadults: $1.35 \pm 0.23 \text{ m s}^{-1}$, $n = 16$; unpaired t-test: $t = 0.44$, $p = 0.66$), I pooled age classes for future analyses as well. One female was inadvertently tested twice, during both incubation and nestling stages. To avoid pseudoreplication, I used only the first data point from this female. All other females were tested once for their flight ability.

Aggression

Females were assayed for their aggressiveness using a simulated territorial intrusion with a live, subadult female tree swallow as a decoy. Subadult (i.e. one year-old) female tree swallows often do not obtain nesting cavities, instead frequently intruding at the nesting cavities held by other swallows (Stutchbury and Robertson 1987a). Interactions between these floaters and nestbox owners can escalate to violence or lead to a change in cavity ownership (Leffelaar and Robertson 1985, Chek and Robertson 1991). Thus, a

behavioral bioassay using a subadult female decoy serves as a convenient proxy of a female's aggressive response to a naturalistic and potentially threatening intruder. The decoy was captured from at least 1 km away and placed in a wire cage (approximately 30 cm cube) atop a tripod positioned 1.5 m in front of the focal female's nestbox. Aggression scores were calculated as the number of 5-s intervals of a 5-min trial during which the focal bird responded aggressively by diving at, hovering over, or perching on the cage. Thus, aggression scores ranged from 0 to 60. This measure of female aggressiveness has been shown to be highly repeatable among individuals, and it does not depend on the decoy's identity, the focal female's mate, or the age of the focal female (Rosvall 2008, 2010). Furthermore, response to this behavioral bioassay predicts a female's ability to acquire a nesting site (Rosvall 2008). Aggression was measured during the nestling period for all females. While aggression trials did not always take place during the same breeding stage as flight trials, aggression scores are highly repeatable within a season (Rosvall 2008) and aggression scores between stages are highly correlated (Rosvall unpubl.).

Statistical analyses

Due to issues of multicollinearity, body mass, body condition (i.e. the residuals of body mass on tarsus) and the proxy for wing-loading (i.e. wing length/body mass) cannot be entered into the same model. Instead, I used a multiple regression to test for a relationship between female aggression and morphological variables: body mass, wing length and tarsus length. The interaction between mass and tarsus was entered to test whether mass relative to structural size (i.e. an approximation of body condition) predicted aggressiveness. Thus, the statistical model examines condition dependence through the interaction between mass and tarsus (Table 1); for visual purposes, I also show the relationship between aggression and body condition measured as the residuals of mass on tarsus (Fig. 1). Likewise, the interaction between mass and wing length was included to test whether mass relative to wing length predicted aggressive behavior. This interaction provides a window into whether or not the relationships between mass and aggression varies based upon wing length, and thus it sheds insight onto the relationship between wing-loading and aggression. To visually represent this effect, I also graph the relationship between aggression and a proxy for wing-loading (mass/wing length; Fig. 1). Because tarsus and wing length were not significant as main effects but they were a part of significant interactions, these parameters were entered into the model as excluded terms, thus eliminating

their individual contribution to the least squares means (Ratner 2003, Howell 2009). Because of the potential for correlations among predictor variables, I used variance inflation factors (VIF) to examine the degree of multicollinearity in the model. All aggression scores were square-root transformed to achieve normality.

To test for a relationship between flight ability and aggressiveness, I used Spearman rank correlations. To examine whether morphological measures account for any links between flight ability and aggressiveness, I used multiple regression to test whether the same morphological features that predicted aggression in the larger dataset also predict flight ability in the subset of females tested for flight ability.

Results

Female mass, the interaction between female mass and wing, and the interaction between female mass and tarsus significantly predicted aggressiveness, but wing length and tarsus length did not (whole model: $R_{adj}^2 = 0.28$, $n = 54$ females, $F\text{-ratio} = 7.79$, $p < 0.0002$, Fig. 1, Table 1). All variance inflation factors for these parameters were low (Table 1) and far below the conservative cutoff of 5 (Menard 2002), meaning that parameter estimates and standard errors were minimally influenced by other independent variables in the model. More aggressive females were heavier altogether, and they were heavier for their body size and heavier for their wing size, compared to less aggressive females. There was no relationship between female aggressiveness and either wing length or tarsus length.

In a vertical test of flight ability, females that were more aggressive flew at significantly lower median speeds (Fig. 2: $r_s = -0.62$, $p < 0.005$, $n = 20$), demonstrating a negative relationship between aggressiveness and take-off speed in vertical flight. The multiple regression testing for a direct link between morphological features and flight ability revealed no significant relationships in the subset of females tested for flight ability (whole model: $R_{adj}^2 = -0.04$, $n = 27$ females, $F\text{-ratio} = 0.79$, $p = 0.57$; mass: $F = 1.42$, $p = 0.25$; tarsus: $F = 0.35$, $p = 0.56$; mass \times tarsus: $F = 0.01$, $p = 0.92$; mass \times wing: $F = 0.11$, $p = 0.74$).

Discussion

Aggressive females have higher body condition and reduced vertical flight ability, but do these findings support

Table 1. Multiple regression of aggressive behavior, based upon morphological measures: $R_{adj}^2 = 0.28$, $n = 54$ females, $F\text{-ratio} = 7.79$, $p = 0.0002$. Tarsus and wing length were non-significant on their own (ns), and they were thus entered as excluded effects in the model because they were components of significant interactions with mass. VIF = variance inflation factor. *indicates significant effects at $p < 0.05$.

Source	t	F-ratio	VIF	p
Body mass	1.52	7.64	1.02	0.0080*
Tarsus length		excluded		ns
Wing length		excluded		ns
Mass \times tarsus (proxy for condition)	2.34	5.49	1.18	0.023*
Mass \times wing (proxy for wing-loading)	3.84	14.78	1.16	0.0003*

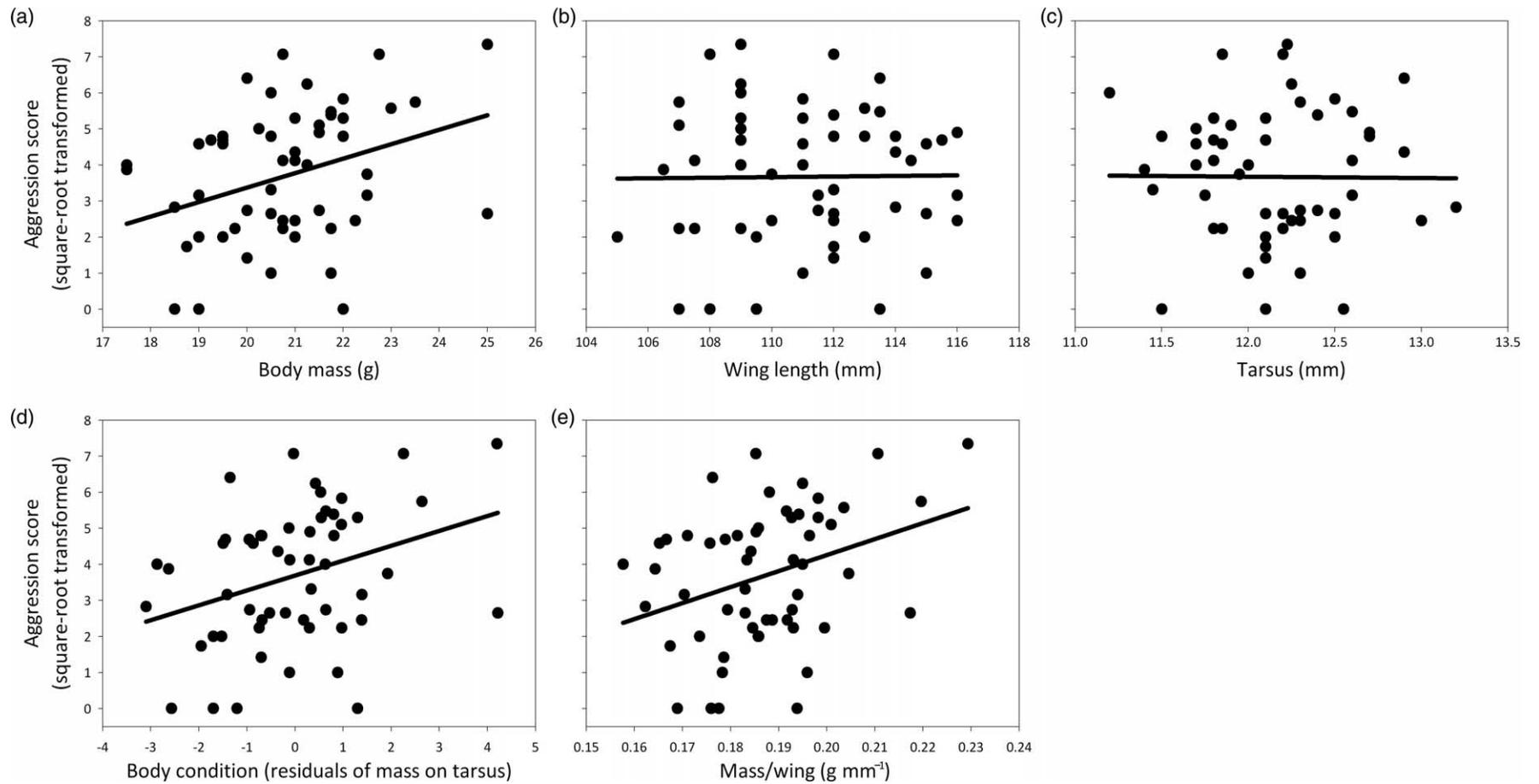


Figure 1. Visual representations of the relationship between female aggressiveness and (a) mass, (b) wing length, (c) tarsus length, (d) body condition, shown as the residuals of a regression of mass on tarsus, (e) a proxy for wing-loading, shown as the ratio of body mass/wing size. For formal statistics on these relationships, see Table 1.

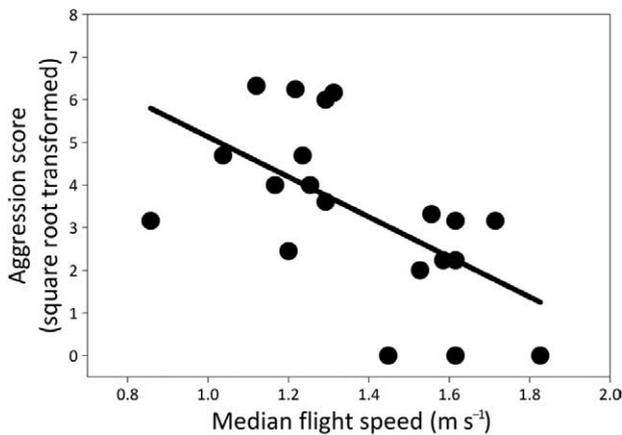


Figure 2. More aggressive females flew significantly slower during a test of vertically-challenging flight ($r_s = -0.62$, $p < 0.005$, $n = 20$).

condition dependence? The demonstrated positive correlations between female aggression and body condition are consistent with one of the key assumptions of condition dependence, that sexually selected phenotypes are inherently linked with underlying individual variation in condition, making phenotypic variance resistant to depletion from directional selection. Positive co-variation between aggressiveness, mass and a standard measure of condition suggests that high levels of aggressiveness are limited to only females in the best condition, similar to many sexually-selected traits in males (Andersson 1994) and ornamentation in females (Siefferman and Hill 2005, reviewed in Amundsen and Pärn 2006, Weiss 2006, Legagneux et al. 2010). The rapid aerial chases and dive-bombs that characterize tree swallow aggressive interactions also suggest that this behavior is likely to be energetically expensive. Condition dependence rests upon the assumption that relatively heavier females retain supplementary energy reserves that permit them to be more aggressive. While I do not have direct measures from this study, other work shows that changes in relative body mass correlate with pectoral mass and fat content (Witter and Cuthill 1993, Kullberg et al. 2002b, Dietz et al. 2007). It is not clear whether these reserves would improve endurance during a protracted battle, as in male–male endurance rivalries (Andersson 1994, Shuster and Wade 2003), or whether higher body condition simply allows individuals to take part in energetically-expensive activities in general, including these intense aggressive encounters.

An important caveat to these findings is that these field measures of behavior and morphology cannot disentangle cause and effect. Thus, despite these strong correlations, it is not clear whether greater condition directly facilitates aggression, whether increased aggression improves condition, or whether a third variable instead links the two. If aggressive behavior is a part of an overarching behavioral syndrome (Sih et al. 2004), then aggressive females may also outcompete other females in competition over food, and females that are already more aggressive will thus be better able to increase their body mass. Testosterone (T) provides another potential mechanistic connection between body condition and aggression, since high T has been experimentally linked with increased aggressive behavior

in female songbirds (Zysling et al. 2006, Sandell 2007), and this androgen also promotes lean muscle mass as well as increased muscle fiber size and number (Wade and Gray 1979, Regnier and Herrera 1993, Herbst and Bhasin 2004). Experimental manipulations of either aggressiveness or condition are necessary to fully explore condition dependence, although the correlations presented here provide an important first step. Regardless of the precise mechanism linking aggression and condition, these positive relationships between aggression and condition suggest that, like aggression and dominance in males, inter-individual variation in female aggressiveness in tree swallows is associated with inter-individual variation in condition, thus reducing the extent to which directional selection can deplete variance in aggressiveness (Rowe and Houle 1996, Tomkins et al. 2004).

A second essential aspect of condition dependence, that sexually selected traits are costly to the trait bearer, was also supported here. Finding that more aggressive females have greater relative body mass also means that those females carry relatively heavier loads than less aggressive females. In line with this view, more aggressive females showed greater mass relative to their wing length (i.e. suggesting greater wing-loading), and they were less proficient at vertically challenging flight. Unlike the positive correlations between aggression and body condition, these findings suggest a potential behavioral or energetic cost associated with aggression, or possibly, with the body types associated with high aggressiveness. Indeed, heavier birds or birds with greater wing-loading often do exhibit increased energy expenditure in flight (Engel et al. 2006, Schmidt-Wellenburg et al. 2007, Bowlin and Wikelski 2008, Schmidt-Wellenburg et al. 2008), and this finding may thus demonstrate an indirect (energetic) cost of being a heavy, aggressive female. Costs such as these are essential components of condition dependence and indicator mechanisms of sexual selection (Zahavi 1975, Grafen 1990, Kotiaho 2001).

In the subset of females that were tested for flight ability, however, these morphological features do not predict flight speed, suggesting that condition may not provide a direct mechanistic link between increased aggression and decreased flight take-off speed. One potential explanation for this negative result may be decreased statistical power in this more limited sample of birds. Indeed, a post hoc Levene's test comparing variance in mass measured on the day of flight trials versus mass measured for the larger population of birds demonstrates significantly higher variance in the larger population (SD for population mass = 1.6 g, SD for flight-tested birds' mass = 0.9 g, $F = 7.72$, $p < 0.01$). A second possible interpretation of this negative result is that morphology does not directly mediate the link between female aggression and vertical flight ability, with a third, unmeasured variable accounting for this connection (e.g. metabolic or hormonal status). This apparently mass-independent variation in flight performance also may reflect other behavioral differences among females, e.g. co-variation between high levels of aggression and reduced motivation or reactivity in a challenging situation (Sih et al. 2004, Koolhaas et al. 2007). In either case, though, being aggressive is associated with lower flight performance, suggesting that more aggressive

females are less adept at performance in vertically challenging flight. This apparent cost associated with aggressive behavior is consistent with the second assumption of condition dependence (i.e. direct or indirect costs associated with the sexually selected trait). For this behavioral cost to translate into an evolutionary cost of aggression, however, these females would also need to suffer a survival or reproductive cost due to reduced ability to forage or escape a predator caused by lower vertical take-off speed or lower flight efficiency (Pennycuik 1989, Chandler and Mulvihill 1992, Warrick 1998, Hedenström and Rosen 2001, Veasey et al. 2001, Kullberg et al. 2002b).

As suggested at the outset, it would be overly simplistic to assume that performance during vertically challenging flight is the only relevant aspect of flight for any bird. Indeed, known morphometric tradeoffs between different aspects of flight ability may counter this particular cost associated with aggressive behavior. For example, both within- and among- species comparisons demonstrate that the same morphologies that require increased generation of lift to overcome the force of gravity (i.e. heavier mass, shorter wings) also promote greater maneuverability in flight (Pennycuik 1989, Warrick 1998, Dial 2003). Mathematically speaking, if heavier females have larger muscles, they may be able to generate a larger power margin in flight, making steep dives and acceleration less energetically expensive (but see Dietz et al. 2007). Shorter wings are likewise advantageous for maneuverability, by reducing the feasible turning radius. Each of these components of flight ability are likely to be relevant to a tree swallow, with an increase in the mass-specific power margin aiding in the steep dives often seen during extended chases (Rosvall unpubl.) and increased maneuverability improving foraging capabilities (Bowlin and Winkler 2004). Stated another way, a female with greater mass per unit wing is also a female with smaller wings per unit mass. Short wings, therefore, may make it more difficult for a female to generate the lift needed to excel in this power-demanding vertical flight test, but short wings may also tighten aerial turning radius, allowing improved maneuverability in both foraging and social contexts. In short, a lower flight take-off speed might only reflect a cost in one context that is tempered by flight strengths in other contexts.

Collectively, these studies identify links between aggressive behavior, morphology and flight ability in female tree swallows that are consistent with condition dependence. These findings expand our understanding of the mechanisms that maintain phenotypic variation, since the current study is one of a few to examine the underlying mechanisms maintaining variation in a sexually selected trait in females (cf. female ornamentation references above). As a consequence, these results attest to the broad relevance of condition dependence and balancing selection in maintaining phenotypic variance.

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