

# Do males offset the cost of female aggression? An experimental test in a biparental songbird

Kimberly A. Rosvall

Department of Biology, Duke University, Box 90338, Durham, NC 27708, USA

Aggressive behavior in females is thought to be costly due to a trade-off between aggression and parental care. In biparental systems, resolution of this trade-off may depend on the extent to which males mitigate the cost of female aggression. Using a population of tree swallows (*Tachycineta bicolor*) in which intrasexual aggression has been shown to be beneficial to females in acquiring a nesting cavity, but costly in terms of offspring quality, I asked if the cost of female aggression is offset by her partner. First, I determined if pairs mate disassortatively by aggressiveness and whether the degree of dissimilarity of aggressiveness correlates with parameters of reproductive success. I then experimentally handicapped males to test whether female aggressiveness becomes more costly when males provision young less. I found no evidence of disassortative mating, although pairs differing more in aggressiveness laid more and larger eggs. When male provisioning was reduced, offspring were no worse in quality, but nestling mortality increased. Aggressive behavior was only associated with a fitness cost in control nests. Therefore, males may mitigate the cost of aggression for their female partners indirectly, not by compensating for poor parenting by aggressive females, but instead by females investing more heavily in reproduction when mated to a male that is more different from her own phenotype. To the extent this differential allocation outweighs the cost of aggressiveness, male phenotype may play a key role in understanding the selective pressures shaping the evolution of aggressive behavior in females. *Key words*: assortative mating, differential allocation, female aggression, parental care, trade-off, tree swallow. [*Behav Ecol* 21:161–168 (2010)]

Since David Lack (1966) first hypothesized that individuals face a trade-off between reproduction and survival, understanding how life-history trade-offs constrain the evolution of behavior has been a major focus in behavioral ecology (Stearns 1992; Roff et al. 2002). Recent interest in behavioral syndromes brings into focus the question of how selection on a particular behavior in one context may limit the evolution of that or correlated behaviors in another context (Sih et al. 2004). One particularly well-studied trade-off is between parental effort and mating effort (Trivers 1972; Magrath and Komdeur 2003), where individuals have limited energy to distribute between parental care on the one hand and attracting mates or repelling rivals on the other. For example, an individual that invests less in parental care may be more likely to gain additional mating opportunities (Møller and Birkhead 1993; Balshine-Earn and Earn 1998). Similarly, an individual may invest in parental care at the cost of territorial or nest defense behavior (Tuttle 2003; Duckworth 2006). These trade-offs may lead to differences in fitness if, for example, more aggressive parents do not care sufficiently for their young (Duckworth 2006) and if reduced care lowers reproductive success (Maynard Smith 1977; Wolf et al. 1988; Schwagmeyer and Mock 2008).

Differences in sex roles traditionally have placed males and females at opposite ends of the trade-off between parental and mating effort. Males are thought to increase reproductive success by investing in repelling rivals and attracting mates, whereas females are thought to increase reproductive success instead by investing in mate choice or parental care (Bateman

1948; Trivers 1972). At the same time, there is increasing evidence that female–female competition does occur in many systems (Clutton-Brock 2007, 2009), indicating not only that females may benefit from this dimension of increased mating effort but also that females can balance the competing demands of parental effort and female–female competition.

In systems where both males and females are likely to face a trade-off between mating effort and parental effort, a key question emerges: To what extent does an individual's mate influence the resolution of this trade-off? Investigators have rarely examined this question in spite of a wealth of research on the trade-off between parental and mating effort in biparental systems (e.g., Wingfield et al. 1987; Ketterson et al. 1992; Duckworth et al. 2003; Duckworth 2006). The white-throated sparrow (*Zonotrichia albicollis*) is a notable exception, where tan morphs (more parental) and white morphs (more aggressive) mate disassortatively, thus reducing or eliminating the cost of aggression (Knapton and Falls 1983; Kopachena and Falls 1993; Tuttle 2003). Previous work has addressed how several ecological factors (e.g., food availability: Dunn and Hannon 1992; operational sex ratio: Magrath and Elgar 1997) and phenotypic or life-history characters (e.g., ornamentation: Johnsen et al. 1998; age: Wetton et al. 1995) may influence trade-offs among mating effort and parental effort (Magrath and Komdeur 2003). However, to my knowledge, no study has asked experimentally whether males mitigate the cost of aggression for their female partners.

In tree swallows (*Tachycineta bicolor*), both sexes provide parental care, and both sexes are highly aggressive toward conspecific and heterospecific intruders (Robertson et al. 1992), which can usurp nesting cavities or kill offspring (Leffelaar and Robertson 1985; Chek and Robertson 1991). Rosvall (2008) showed that females may experience direct selection to be aggressive in the context of intrasexual competition, as more aggressive females are more likely to obtain a nesting cavity. However, offspring of more aggressive females are smaller on day 12 posthatch (Rosvall KA, unpublished data).

Address correspondence to K.A. Rosvall, who is now at Department of Biology, Indiana University, 1001 E 3rd Street, Jordan Hall, Room 142, Bloomington, IN 47405, USA. E-mail: krosvall@indiana.edu.

Received 24 February 2009; revised 23 July 2009; accepted 10 September 2009.

Although the resulting evolutionary consequences may vary (vom Saal et al. 1990; Mazuc et al. 2003; Grootuis et al. 2005), this finding likely represents a fitness cost of female aggression because smaller pre fledging mass in birds tends to correspond to lower survival or recruitment (Tinbergen and Boerlijst 1990; Magrath 1991; McCarty 2001; Schwagmeyer and Mock 2008), lower fecundity (Alatalo and Lundberg 1986; Haywood and Perrins 1992), smaller adult body size (Richner 1992), or reduced expression of sexually selected traits (Nowicki, Searcy, and Peters, 2002). The mechanisms by which more aggressive females have lower quality offspring remain complex; however, a trade-off between female aggression and provisioning may partly account for this finding because more aggressive females provision relatively less at some sites (Rosvall KA, unpublished data).

Regardless of the precise mechanism by which more aggressive females have smaller offspring, males may be able to mitigate this cost by influencing the relationship between female aggressiveness and the number or quality of her offspring. First, males may directly increase offspring mass through provisioning, thus minimizing the cost of female aggression. Second, if males influence female allocation strategies (Sheldon 2000), males may indirectly offset the cost of aggression through other currencies of reproductive success. For example, a female may invest more in a reproductive bout (e.g., by laying more eggs) in anticipation of the level of care when mated to a male with whom she may achieve a greater division of labor (e.g., a highly aggressive female paired to an unaggressive male). If this scenario is true, 2 predictions should hold: 1) males and females should mate disassortatively by aggressiveness and 2) reduced male parental care should prove more costly to more aggressive females. To test these 2 predictions, I first determined whether males and females mate disassortatively by their aggressiveness and whether pair dissimilarity in aggressiveness correlates with clutch size, brood size, or egg mass. Second, using offspring mass as a proxy for offspring quality, I asked whether female aggressiveness becomes more costly when males are experimentally manipulated to play a reduced role in provisioning, with the prediction that the offspring of more aggressive females should be differentially affected by a reduction of male parental care (i.e., the negative relationship between female aggression and offspring quality should become stronger). Together, these 2 studies address the extent to which an individual's partner may influence selection on female aggressiveness in the context of intrasexual competition.

## MATERIALS AND METHODS

This study was conducted in 2006 and 2007 using a population of tree swallows breeding at nestboxes near Linesville, PA (41°40'N, 80°26'W), United States. The population consists of approximately 80–90 pairs of tree swallows at the Linesville State Fish Hatchery and Pennsylvania State Gamelands #214. Although there are various differences among the 2 main sites, they are effectively one population, as both breeders and juveniles commonly disperse among sites (Rosvall KA, personal observation). Preliminary analyses indicated no site differences in the studies described here, and so I do not further address site differences in this paper. Since 2004, nearly all breeding females and nestlings, along with most males in this population, have been captured and marked with a US Fish and Wildlife metal band. To distinguish among individuals, males and females were also marked with one plastic color band (red for females, blue for males) and unique color combinations of nontoxic acrylic paint on the wings and rump (Dunn et al. 1994).

## Do pairs sort by aggressiveness?

In 2006 and 2007, I assayed the aggressiveness of males and females defending nestboxes ( $n = 21$  pairs in 2006,  $n = 32$  pairs in 2007) with a 5-min simulated intrusion using a live, caged tree swallow as a decoy (Rosvall 2008). To frame the assay in the context of intrasexual aggression, I used a subadult (i.e., 1-year-old) female decoy for all female trials and a male decoy in all male trials. This design maximized the likelihood that focal birds would quickly identify the sex of the decoy, as subadult females have brown plumage that is distinct from the iridescent blue–green plumage of all males and older females (Hussell 1983). Previous work has shown that a female's response to a subadult intruder is highly repeatable ( $r = 0.79$ ) within a breeding season and independent of the identity of the decoy (Rosvall 2008). Thus, I did not control for the identity of the decoy. Data from 10 females showed that female aggression is the same when the male was present than when males were temporarily removed (Wilcoxon sign-rank test:  $z = 0$ ,  $P = 1.00$ ,  $n = 10$ ; Spearman rank correlation:  $r_s = 0.91$ ,  $P = 0.0002$ ,  $n = 10$ ). Accordingly, I did not control for the presence or behavior of an individual's mate during its aggression trial. I did not perform analogous validations with the male aggression assay because repeatable responses by males to simulated intrusion are more common throughout the songbird literature (e.g., Nowicki, Searcy, Krueger, and Hughes 2002; McGlothlin et al. 2007), and I have no reason to believe that males and females would differ in repeatability of aggression in this system. All aggression trials were performed between 0600 and 1200 h prior to the day the female laid her first egg. Decoys were captured from at least 1 km away and were returned to their site of capture immediately after trials concluded. Aggression scores were calculated as the total number of 5-s intervals during which the focal female responded by diving at or perching on the decoy's cage (i.e., aggression scores ranged from 0 to 60 intervals). I used the absolute value of difference in aggression scores (hereafter, "aggression difference scores") as an estimate of the dissimilarity of aggressiveness among males and females in a breeding pair. For informational purposes, I also report the actual difference in aggression score, calculated by subtracting male aggression score from female aggression score.

To determine whether pairs that are more different in aggressiveness experience fitness benefits, I compared aggression difference scores with 3 reproductive parameters. I measured the number of eggs laid (clutch size) and the number of young hatched (brood size). Additionally, in 2007 only, I measured average egg mass on the day of clutch completion as an estimate of each female's reproductive investment. Sample sizes for reproductive parameters vary from the number of male–female pairs originally assayed for aggression ( $n = 53$ ) because I excluded nests in which either partial broods (in 2006) or complete clutches (in 2007) were cross-fostered for another study (not described here). For this same reason, I was unable to test for a relationship between aggression difference score and offspring mass (i.e., offspring quality).

## Is aggressive behavior more costly with reduced male care?

In 2007, I experimentally manipulated the male's ability to contribute to provisioning by wing clipping (Whittingham et al. 1994; Winkler and Allen 1995). To control for any effect of hatch date or site, pairs were assigned to either control or experimental (clipped) group on their hatch date by alternating treatment groups and sites. Tree swallows are single brooded (Robertson et al. 1992), and all broods used in this study were the first and only brood for each pair. Males were captured using nestbox traps while feeding young by day 4 of

the nestling period, where hatch day is denoted as day 1 (average day of capture = 2.4, range: 2–4 days). For experimental males ( $n = 15$ ), I used scissors to cut all even-numbered primaries at their base. Control males ( $n = 15$ ) were handled in the same way as experimental males, but without clipping feathers, and there was no difference in handling time between control and experimental males (unpaired  $t$ -test:  $t = -1.14$ ,  $P = 0.26$ ,  $X_{\text{clip}} = 9.2 \pm 0.4$  min,  $X_{\text{control}} = 8.5 \pm 0.5$  min). All males also had one drop of blood drawn from the brachial vein and 5–10 small body feathers plucked from their rump for another study.

### Effects of treatment

Observations of parental feeding were conducted between 1100 and 1700 h on either day 8 or 9 posthatch. Each feeding watch consisted of 60 min of observation, beginning with the first female visit to the nestbox. All feeding watches were performed from inside a vehicle that served as a blind, parked at least 10 m from the focal nestbox. To examine the role of each parent in provisioning young, I measured the number of feeds per hour by each parent and the ratio of male feeds to female feeds (# male feeds/# female feeds). All females also were assayed for aggression during the nestling period (average day of trial = day 6.7 posthatch, range = 4–11 days).

To examine the fitness effects of clipping, I compared 2 measures of female reproductive success between treatment groups. First, I used nestling mass on day 12 of the nestling period, averaged per nest, as a proxy for offspring quality. Although this measure of offspring quality does not distinguish among the possible factors that could influence mass (e.g., larger body size, faster growth, and higher fat reserves), it does provide a convenient proxy for quality because offspring with larger mass prior to fledging tend to experience higher reproductive success or survival in several avian taxa (see references in the Introduction), including tree swallows (McCarty 2001). Next, I measured nest mortality as the number of eggs per clutch that did not eventually result in a fledged offspring. Together, these 2 measures give an estimate of both quality and quantity of offspring.

### Statistical methods

Statistical tests were conducted using JMP 7.0 (SAS Institute Inc.). Results are reported as mean  $\pm$  standard error (SE), and all tests are 2-tailed. In the first study, to examine the effect of aggression difference score on clutch size and brood size, I used a least squares model with restricted maximum likelihood (ReML). Year was entered as a random effect and difference score as a fixed effect. To explore annual differences, I analyzed these same relationships within each year using Spearman rank correlations. I analyzed the relationship between aggression difference score and egg mass using a general linear model (GLM). In the second study, I used a forward stepwise logistic model to examine the effect of clipping (to enter,  $P < 0.250$ ; to leave,  $P > 0.10$ ). In the original model, I included 3 measures of feeding (female feeds, male feeds, and ratio of male-to-female feeds) along with 2 measures of reproductive success (offspring mass and mortality). The purpose of this logistical model was 2-fold: 1) to ask whether wing clipping influenced provisioning patterns and 2) to determine the effect of the manipulation on reproductive success. To test whether the relationship between female aggression and offspring mass varied among treatment groups, I used a GLM on offspring mass on day 12 to test for an interaction between female aggression and treatment group. Aggression scores were square root transformed to achieve normality. To examine the nature of the effect further, I examined the

correlation between female aggression and average nestling mass on day 12 separately for each treatment group.

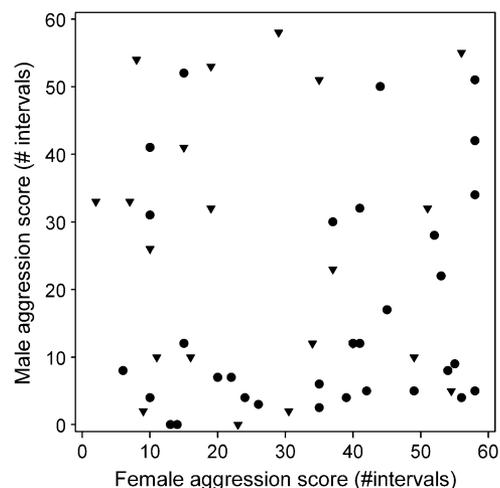
## RESULTS

### Reproductive correlates of disassortative mating

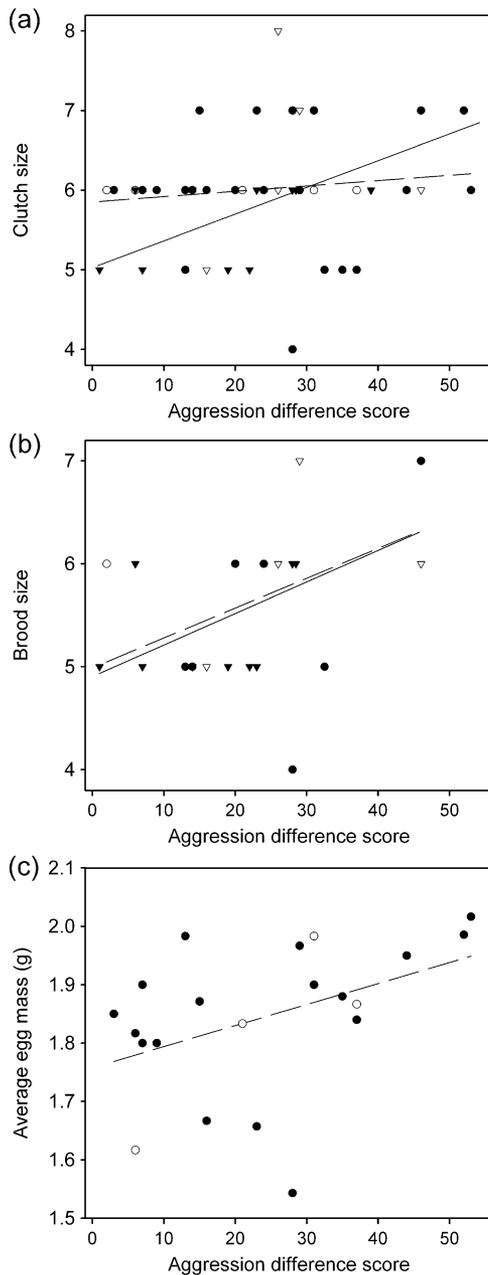
There was no tendency for assortative or disassortatively mating by aggressiveness (Spearman rank correlation,  $n = 53$  pairs,  $r_s = 0.045$ ,  $P = 0.75$ ; Figure 1). There was no significant relationship between aggression difference score and clutch size (ReML of clutch size, with year as a random effect:  $R^2_{\text{adj}} = 0.041$ ,  $F = 2.78$ ,  $P = 0.10$ ,  $n = 48$ ; Figure 2a), but there was a significant positive relationship between aggression difference score and brood size (ReML of brood size, with year as a random effect:  $R^2_{\text{adj}} = 0.20$ ,  $n = 25$ ;  $F = 8.50$ ,  $P = 0.0078$ ; Figure 2b). Analyzing the 2 years separately, only the 2006 data show a correlation between these 2 reproductive parameters and aggression difference score (clutch, 2006:  $r_s = 0.59$ ,  $n = 16$ ,  $P = 0.016$ ; brood, 2006:  $r_s = 0.68$ ,  $n = 15$ ,  $P = 0.0055$ ; clutch, 2007:  $r_s = 0.13$ ,  $n = 32$ ,  $P = 0.46$ ; brood, 2007:  $r_s = 0.36$ ,  $n = 10$ ,  $P = 0.31$ ). Females mated to males that were more different in aggressiveness laid eggs with a significantly larger mass (GLM of average egg mass:  $\chi^2 = 4.29$ ,  $n = 21$ ,  $P = 0.038$ ; Figure 2c. None of these relationships were significant when using the actual difference in aggressiveness between females and males, as opposed to the absolute value of that difference (see supplementary material).

### Effect of male handicapping

Control and experimental nests significantly differed in aspects of behavior and reproductive success. The original model included 3 measures of feeding (female feeds, male feeds, and ratio of male-to-female feeds) along with 2 reproductive parameters (offspring mass and offspring mortality). After forward stepwise logistic regression, the final model indicated that the ratio of male-to-female feeds was significantly lower in the clipped group and nestling mortality was significantly higher in the clipped group; female feeds, male feeds, and offspring mass did not differ significantly among treatments (Table 1, Figure 3). Clipped nests did not differ from control nests in average offspring mass on day 12 (Figure 3e). Clipped nests experienced significantly higher mortality, with clipped nests losing greater than 0.6 more offspring than



**Figure 1**  
The relationship between male aggression and female aggression scores. Circles denote 2007, whereas triangles denote 2006.



**Figure 2**

The relationship between aggression difference scores and (a) clutch size, (b) brood size, and (c) average egg mass. Triangles and solid lines represent data from 2006, whereas circles and dashed lines denote 2007. Pair difference score was calculated as the absolute value of the difference in aggression scores of females and their mates. Filled symbols represent pairs in which the female was more aggressive than her mate, and open symbols represent pairs in which the male was more aggressive than the female.

control nests (Figure 3d). Only 5 of 15 experimental nests did not experience any mortality, whereas 12 of 15 control nests experienced no mortality (Pearson Chi-square:  $\chi^2 = 6.65$ ,  $df = 1$ ,  $P = 0.0099$ ).

As shown in Figure 4, whether or not the male's wings are clipped impacted the relationship between female aggression and offspring mass. A GLM of female aggression and treatment on offspring mass indicated a nearly significant interaction of aggression and treatment (GLM of offspring mass:  $\chi^2 = 4.27$ ,  $P = 0.23$ , aggression  $\times$  treatment:

**Table 1**

**Differences between treatment groups**

Source	df	Wald statistic	<i>P</i>
Original model			
Female feeds	1	0.23	0.64
Male feeds	1	2.81	0.093
Ratio of male: female feeds	1	4.29	0.038
Average nestling mass	1	0.10	0.75
Mortality	1	5.27	0.022
Final model			
Ratio of male: female feeds	1	4.20	0.040
Mortality	1	5.23	0.022

A forward stepwise logistic model was used to determine which variables best captured the differences between control and experimental nests. The original model included 3 measures of feeding and 2 measures of reproductive success. The final model ( $R^2 = 0.24$ ,  $P = 0.0071$ ) indicated that offspring mortality was significantly higher and that the ratio of male-to-female feeds was significantly lower in the experimental treatment group, meaning that clipped males provisioned relatively less and those nests experienced higher mortality.

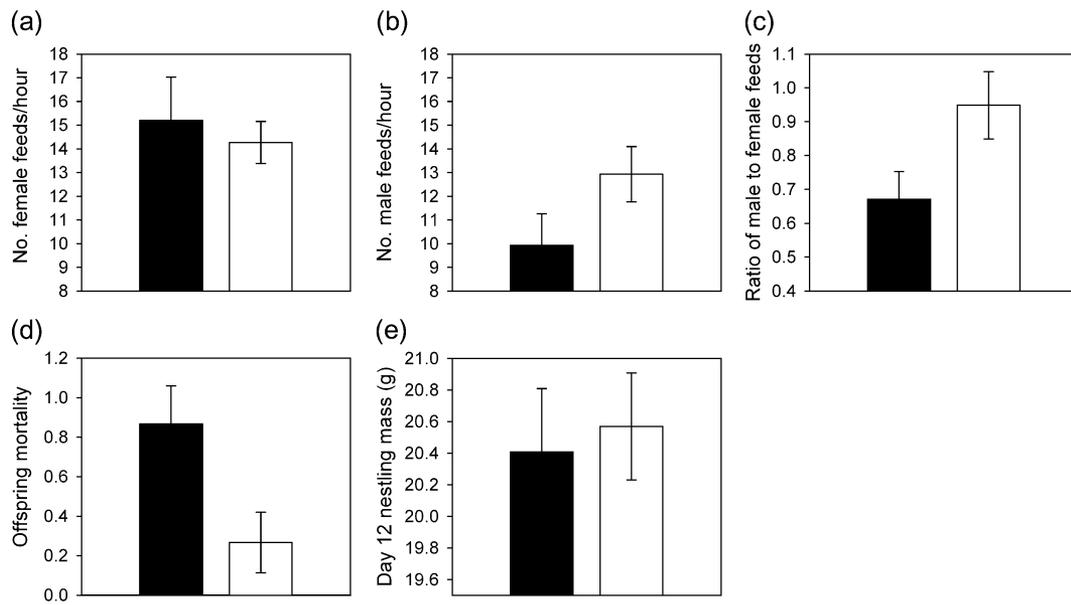
$\chi^2 = 3.37$ ,  $P = 0.067$ ), suggesting that female aggressiveness has some effect on the extent to which females are able to compensate for male handicapping. Analyzed separately, only control nests showed a significant negative relationship between female aggression and offspring mass (Figure 4; Spearman rank correlation, clipped:  $r_s = 0.061$ ,  $n = 15$ ,  $P = 0.83$ ; control:  $r_s = -0.58$ ,  $n = 15$ ,  $P = 0.023$ ). Female aggressiveness did not map onto nest mortality across treatments (Wilcoxon sign-rank test:  $Z = 0.23$ ,  $P = 0.80$ ) or within treatments (clipped:  $Z = -0.059$ ,  $P = 0.95$ ; control:  $Z = -0.14$ ,  $P = 0.89$ ).

## DISCUSSION

Although individuals did not mate assortatively by aggressiveness (Figure 1), pairs that were more different in aggressiveness had larger broods (Figure 2b), and those females invested more in the reproductive bout (Figure 2c). They did not, however, have larger clutches (Figure 2a). None of these relationships were significant looking at the actual difference in pair aggression score, indicating that the relative similarity in aggressiveness predicts aspects of reproductive success, independent of which sex was more aggressive. When males were experimentally forced to play a reduced role in provisioning, offspring were no worse in quality, but nests experienced greater offspring mortality (Table 1, Figure 3). Unexpectedly, aggressive females did not suffer greater costs when their males were handicapped; in fact, the cost of aggression was not evident in experimental nests (Figure 4). Taken together, these results suggest that males may mitigate the cost of aggression for their female partners, although not necessarily through provisioning. Instead, females may invest more heavily in reproduction by laying more or larger eggs when mated to a male that is more different from her own phenotype. If differential investment via larger or more eggs outweighs the cost of aggressive behavior on offspring quality, male phenotype may play a key role in understanding the selective pressures shaping the evolution of aggressive behavior in females.

### A benefit to disassortative mating?

In pairs that differ more in aggressiveness, there is some evidence that females invest more in their reproductive bout. Females belonging to pairs with high aggression difference

**Figure 3**

Open bars indicate control nests, and closed bars indicate experimental nests. These figures are visual representations of the key findings from Table 1, showing mean  $\pm$  SE for (a) the number of female feeds per hour, (b) the number of male feeds per hour, (c) the ratio of male-to-female feeding visits, where values  $>1$  indicate that the male provisioned more, and values  $<1$  indicate that the female provisioned more, (d) offspring mortality, measured as the number of eggs that did not ultimately translate into a fledged offspring, and (e) average brood mass on day 12 posthatch. See Table 1 for statistical results.

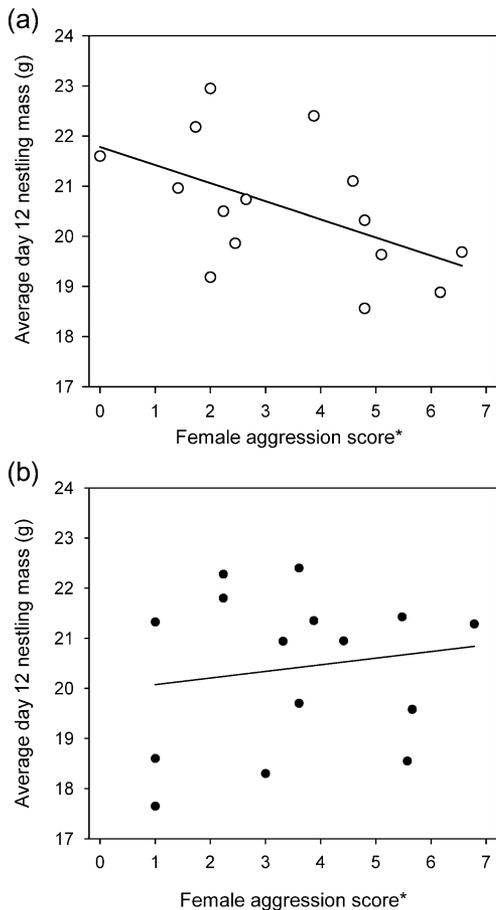
scores laid larger eggs and had larger broods, although they did not always have larger clutches. Because larger eggs tend to yield larger, better quality offspring (Williams 1994; Styrsky et al. 1999; Whittingham et al. 2007), the potential positive effect of laying larger eggs could diminish the negative association between female aggressiveness and offspring quality, thus mitigating the cost of female aggression. Similarly, if aggressive females opportunistically lay more eggs when mated to less aggressive males, the cost aggressive females bear in terms of offspring quality may be outweighed by their gain in offspring quantity.

Although there is a significant relationship between aggression difference score and 2 reproductive parameters, this study does not test a causal link between these variables. On the one hand, differential allocation may have occurred, with females increasing reproductive investment based on the quality of their mating opportunity (Burley 1986; Sheldon 2000) by laying more or larger eggs when mated to a male with which they would achieve a greater division of labor of parental and aggressive behaviors. On the other hand, laying more or larger eggs may have increased the value of the reproductive bout, prompting females to respond more aggressively to intruders (Trivers 1972; Montgomerie and Weatherhead 1988), although this would only apply to cases where females were much more aggressive than their mates (i.e., filled points on the far right side of Figure 2). Neither of these views, however, is consistent with the puzzling result that clutch size did not correlate significantly with aggression difference score. Recall that many of the nests for which I assayed aggression were used in another experiment that prevented me from obtaining an unmanipulated measure of brood size. As a result, nests for which I have an unmanipulated measure of brood size are mostly from 2006 ( $n = 15$  in 2006,  $n = 10$  in 2007), whereas those for which I have an unmanipulated measure of clutch size are primarily from 2007 ( $n = 16$  in 2006,  $n = 32$  in 2007). Thus, differences in the results between brood and clutch size are confounded with differences between years.

If pairs that differ more in aggressiveness have larger broods or larger eggs, as my results indicate, why would pairs not mate disassortatively even though doing so could be advantageous? If female mate choice is constrained by limited access to suitable nesting cavities (Holroyd 1975), females may not have the opportunity to select a social mate based on his aggressiveness. In addition, differences between years in the relationships between aggression difference score and reproductive parameters suggest the potential for variation in the benefits of disassortative mating. Analyzed separately, only the 2006 data show a significant positive relationship between aggression difference scores and brood and clutch sizes. In light of this potential temporal variation, it may be unsurprising that pairs do not mate disassortatively, even if this behavior may be adaptive at times.

### Effects of male handicapping

Male handicapping had a significant effect on a male's relative role in provisioning young, but were females able to compensate for this reduced role of their mates? Control and experimental females did not differ significantly in their average number of feeds per hour, indicating that females did not increase their parental effort to compensate for the reduction in male care. Experimental nests, however, experienced reduced hatching success. This finding matches previous work in tree swallows suggesting that females do not compensate fully for a reduction in male parental care and that these effects extend to reproductive success (Whittingham et al. 1994). Experimental nests suffered higher mortality during the nestling period, losing on average 0.6 more offspring per nest than control nests. Mortality occurred at all stages, including unhatched eggs and nestlings dying both early and late in the nestling period. This variation makes it difficult to interpret precisely how experimental nests had increased mortality. Although the quantity of offspring was reduced in experimental nests, the surviving offspring did not suffer in quality, at least



**Figure 4**  
Female aggressiveness is associated with a fitness cost in control nests (a) but not in experimental nests (b). Spearman rank correlation: experimental:  $r_s = 0.061$ ,  $n = 15$ ,  $P = 0.83$ ; control:  $r_s = -0.58$ ,  $n = 15$ ,  $P = 0.023$ . Filled circles indicate experimental nests, whereas open circles indicate control nests. \*Aggression scores are square root transformed.

as measured in terms of mass. Experimental and control broods did not differ in average day 12 nestling mass, indicating that experimental females appear to be able to compensate for their male's reduced help just enough avoid a loss in the quality of their offspring.

I originally predicted that the cost of female aggression, measured as lower quality offspring, would intensify with reduced male parental care. If true, the relationship between female aggression and offspring quality should be more severe (i.e., have a steeper slope) in the experimental group than in the control group. Contrary to this prediction, I found no detectable relationship between female aggression and offspring mass in the experimental group, indicating that a reduction in male assistance is not more costly for more aggressive females. Furthermore, more aggressive females were no more likely to experience nestling mortality. Control females, however, experienced a cost associated with their aggressiveness, in that their offspring were smaller prior to fledging, a finding consistent with a multiyear study of the cost of female aggression in this population (Rosvall KA, unpublished data).

There are several possible explanations for the unanticipated finding that female aggression was not associated with a fitness cost when male care was reduced. For example, if the negative relationship between female aggression and offspring mass is typically driven by the smallest offspring, clipped

nests might not show this relationship due to mortality of the runt. If correct, analyzing offspring mass without runts in the control group should eliminate the negative relationship between offspring mass and female aggression, but it does not (Spearman rank correlation, control:  $r_s = -0.60$ ,  $n = 15$ ,  $P = 0.019$ ). Thus, finding no cost of aggression in the experimental group cannot be solely attributed to the loss of the runt.

If clipping males impacted the level of aggression expressed by females, it is also possible that aggression scores measured in the clipped group may not reflect a female's true level of aggression, because female aggression assays occurred after clipping males. Although the most direct test of whether or not male clipping affected female aggression was not performed here (i.e., a paired comparison of female aggression scores before and after male clipping), 3 lines of evidence suggest that female aggression is not a plastic trait and is therefore unlikely to change after the manipulation of males. First, if handicapping males systematically alters female aggression scores measured approximately 4 days later, control and experimental females should exhibit different levels of aggression, but they do not (Wilcoxon sign-rank test:  $Z = -0.19$ ,  $n = 15$  per group,  $P = 0.85$ ). Second, aggression scores in female tree swallows have been shown to be highly repeatable within a breeding season (Rosvall 2008). Third, short-term male absence during a trial does not influence a female's aggression score (see Materials and Methods). It remains unknown, however, if a few days of reduced male parental care caused females to alter their phenotype and respond less to the behavioral assay.

Finally, if the cost of aggression is flexible, females in the experimental group may have been able to overcome this cost with slight changes in parental investment. If females responded to the male's reduced role in provisioning by delivering larger prey items, I would not have detected this level of compensation with my focal observations. Furthermore, females may optimize clutch size (Lack 1947), leaving 12 of 15 females in the clipped group (i.e., those experiencing some nestling mortality) with fewer mouths to feed than anticipated. A reduction in male help, paired with one less offspring or an adjustment in prey choice, may have allowed females to overcome the typical cost of aggressive behavior. Whatever the reason for not finding a cost of aggression in the clipped treatment group, it is clear that the cost of aggressive behavior did not become stronger when males played a reduced role in provisioning. The prediction that males may mitigate the cost of aggression, in terms of offspring quality, was not supported.

## CONCLUSIONS

If one parent faces a trade-off between parental effort and aggressive nest defense, it should benefit that parent to mate with a partner that could mitigate the cost of being aggressive. I found evidence suggesting that female tree swallows adjust their investment in a reproductive bout based on the relative aggressiveness of their mates. Male provisioning of offspring is key to increased reproductive success, but male provisioning does not appear to lessen the cost of female aggressive behavior. Reevaluating the cost of female aggression may be particularly relevant in light of more recent research demonstrating that female animals, like their male counterparts, are likely to experience selection to compete aggressively among themselves for access to males or resources (Slagsvold and Lifjeld 1994; Sandell 1998; Palombit et al. 2001; Clutton-Brock 2007, 2009; Rosvall 2008). Moreover, it may be important to consider the role of an individual's mate in the relative cost-benefit ratio of behaviors that repel rivals, especially because

the majority of work on this topic has been done in biparental systems (Magrath and Komdeur 2003).

## SUPPLEMENTARY MATERIAL

Supplementary material can be found at <http://www.behco.oxfordjournals.org/>.

## FUNDING

National Science Foundation Dissertation Improvement Grant (IBN#0710118); Graduate Women in Science; University of Pittsburgh Pymatuning Lab of Ecology McKinley Award; and American Ornithologists' Union.

This work would not have been possible without the extraordinary field assistance of Corinne Campbell. I am grateful especially to S. Nowicki, R.C. Anderson, and 2 anonymous reviewers for extensive comments on earlier versions of the manuscript, as well as to E.P. Derryberry, M. Hughes, I.A. Liu, R.F. Lachlan, S. Peters, and the Behavior, Population and Community Ecology group at Duke for helpful discussion. I also thank the Pennsylvania Game Commission, Linesville State Fish Hatchery and Pymatuning Laboratory of Ecology for logistical support. All aspects of this research were conducted in accordance with the laws of the United States and the Institutional Animal Care and Use Committees at both Duke University (A062-04-02, A050-07-02) and University of Pittsburgh (0404837A-2). This is publication no. 235 from the Pymatuning Laboratory of Ecology.

## REFERENCES

- Alatalo RV, Lundberg A. 1986. Heritability and selection on tarsus length in the pied flycatcher (*Ficedula hypoleuca*). *Evolution*. 40: 574–583.
- Balshine-Earn S, Earn DJD. 1998. On the evolutionary pathway of parental care in mouth-brooding cichlid fish. *Proc R Soc Lond Ser B-Biol Sci*. 265:2217–2222.
- Bateman AJ. 1948. Intrasexual selection in *Drosophila*. *Heredity*. 2:349–368.
- Burley N. 1986. Sexual selection for aesthetic traits in species with biparental care. *Am Nat*. 127:415–445.
- Chek AA, Robertson RJ. 1991. Infanticide in female tree swallows—a role for sexual selection. *Condor*. 93:454–457.
- Clutton-Brock T. 2007. Sexual selection in males and females. *Science*. 318:1882–1885.
- Clutton-Brock T. 2009. Sexual selection in females. *Anim Behav*. 77:3–11.
- Duckworth RA. 2006. Behavioral correlations across breeding contexts provide a mechanism for a cost of aggression. *Behav Ecol*. 17: 1011–1019.
- Duckworth RA, Badyaev AV, Parlow AF. 2003. Elaborately ornamented males avoid costly parental care in the house finch (*Carpodacus mexicanus*): a proximate perspective. *Behav Ecol Sociobiol*. 55:176–183.
- Dunn PO, Hannon SJ. 1992. Effects of food abundance and male parental care on reproductive success and monogamy in tree swallows. *Auk*. 109:488–499.
- Dunn PO, Whittingham LA, Lifjeld JT, Robertson RJ, Boag PT. 1994. Effects of breeding density, synchrony, and experience on extrapair paternity in tree swallows. *Behav Ecol*. 5:123–129.
- Groothuis TGG, Muller W, von Engelhardt N, Carere C, Eising C. 2005. Maternal hormones as a tool to adjust offspring phenotype in avian species. *Neurosci Biobehav Rev*. 29:329–352.
- Haywood S, Perrins CM. 1992. Is clutch size in birds affected by environmental conditions during growth. *Proc R Soc Lond Ser B-Biol Sci*. 249:195–197.
- Holroyd GL. 1975. Nest site availability as a factor limiting population size of swallows. *Can Field Nat*. 89:60–64.
- Hussell DJT. 1983. Age and plumage color in female tree swallows. *J Field Ornithol*. 54:312–318.
- Johnsen A, Lifjeld JT, Rohde PA, Primmer CR, Ellegren H. 1998. Sexual conflict over fertilizations: female bluethroats escape male paternity guards. *Behav Ecol Sociobiol*. 43:401–408.
- Ketterson ED, Nolan V, Wolf L, Ziegenfus C. 1992. Testosterone and avian life histories—effects of experimentally elevated testosterone on behavior and correlates of fitness in the dark-eyed junco (*Junco hyemalis*). *Am Nat*. 140:980–999.
- Knapton RW, Falls JB. 1983. Differences in parental contribution among pair types in the polymorphic white-throated sparrow. *Can J Zool*. 61:1288–1292.
- Kopachena JG, Falls JB. 1993. Aggressive performance as a behavioral correlate of plumage polymorphism in the white-throated sparrow (*Zonotrichia albicollis*). *Behaviour*. 124:249–266.
- Lack DL. 1947. The significance of clutch size. *Ibis*. 89:302–352.
- Lack DL. 1966. Population studies of birds. London: Oxford University Press.
- Leffelaar D, Robertson RJ. 1985. Nest usurpation and female competition for breeding opportunities by tree swallows. *Wilson Bull*. 97:221–224.
- Magrath MJL, Elgar MA. 1997. Paternal care declines with increased opportunity for extra-pair matings in fairy martins. *Proc R Soc Lond Ser B-Biol Sci*. 264:1731–1736.
- Magrath MJL, Komdeur J. 2003. Is male care compromised by additional mating opportunity? *Trends Ecol Evol*. 18:424–430.
- Magrath RD. 1991. Nestling weight and juvenile survival in the black-bird, *Turdus merula*. *J Anim Ecol*. 60:335–351.
- Maynard Smith J. 1977. Parental Investment - Prospective Analysis. *Anim Behav*. 25:1–9.
- Mazur J, Bonneaud C, Chastel O, Sorci G. 2003. Social environment affects female and egg testosterone levels in the house sparrow (*Passer domesticus*). *Ecol Lett*. 6:1084–1090.
- McCarty JP. 2001. Variation in growth of nestling tree swallows across multiple temporal and spatial scales. *Auk*. 118:176–190.
- McGlothlin JW, Jawor JM, Ketterson ED. 2007. Natural variation in a testosterone-mediated trade-off between mating effort and parental effort. *Am Nat*. 170:864–875.
- Møller AP, Birkhead TR. 1993. Certainty of paternity covaries with paternal care in birds. *Behav Ecol Sociobiol*. 33:261–268.
- Montgomerie RD, Weatherhead PJ. 1988. Risks and rewards of nest defense by parent birds. *Q Rev Biol*. 63:167–187.
- Nowicki S, Searcy WA, Krueger T, Hughes M. 2002. Individual variation in response to simulated territorial challenge among territory-holding song sparrows. *J Avian Biol*. 33:253–259.
- Nowicki S, Searcy WA, Peters S. 2002. Brain development, song learning and mate choice in birds: a review and experimental test of the “nutritional stress hypothesis”. *J Compar Physiol A*. 188:1003–1014.
- Palombit RA, Cheney DL, Seyfarth RM. 2001. Female–female competition for male ‘friends’ in wild chacma baboons, *Papio cynocephalus ursinus*. *Anim Behav*. 61:1159–1171.
- Richner H. 1992. The effect of extra food on fitness in breeding carrion crows. *Ecology*. 73:330–335.
- Robertson RJ, Stutchbury BJ, Cohen RR. 1992. Tree swallow (*Tachycineta bicolor*). The birds of North America. No. 11. Philadelphia (PA): Academy of Natural Sciences, and Washington (DC): American Ornithologists' Union.
- Roff DA, Mostow S, Fairbairn DJ. 2002. The evolution of trade-offs: testing predictions on response to selection and environmental variation. *Evolution*. 56:84–95.
- Rosvall KA. 2008. Sexual selection on aggressiveness in females: evidence from an experimental test with tree swallows. *Anim Behav*. 75:1603–1610.
- Sandell MI. 1998. Female aggression and the maintenance of monogamy: female behaviour predicts male mating status in European starlings. *Proc R Soc Lond Ser B Biol Sci*. 265:1307–1311.
- Schwagmeyer PL, Mock DW. 2008. Parental provisioning and offspring fitness: size matters. *Anim Behav*. 75:291–298.
- Sheldon BC. 2000. Differential allocation: tests, mechanisms and implications. *Trends Ecol Evol*. 15:397–402.
- Sih A, Bell AM, Johnson JC, Ziemba RE. 2004. Behavioral syndromes: an integrative overview. *Q Rev Biol*. 79:241–277.
- Slagsvold T, Lifjeld JT. 1994. Polygyny in birds—the role of competition between females for male parental care. *Am Nat*. 143: 59–94.
- Stearns SC. 1992. The evolution of life histories. Oxford: Oxford University Press.

- Styrsky JD, Eckerle MP, Thompson CF. 1999. Fitness-related consequences of egg mass in nestling house wrens. *Proc R Soc Lond Ser B-Biol Sci.* 266:1253–1258.
- Tinbergen JM, Boerlijst MC. 1990. Nestling weight and survival in individual great tits (*Parus major*). *J Anim Ecol.* 59:1113–1127.
- Trivers RL. 1972. Parental investment and sexual selection. In: Cambell B, editor. *Sexual selection and the descent of man, 1871–1971*. London: Heinemann. p. 136–179.
- Tuttle EM. 2003. Alternative reproductive strategies in the white-throated sparrow: behavioral and genetic evidence. *Behav Ecol.* 14: 425–432.
- vom Saal FS, Quadagno DM, Even MD, Keisler LW, Keisler DH Khan S. 1990. Paradoxical effects of maternal stress on fetal steroids and postnatal reproductive traits in female mice from different intrauterine positions. *Biol Reprod.* 43:751–761.
- Wetton JH, Burke T, Parkin DT, Cairns E. 1995. Single-locus DNA-fingerprinting reveals that male reproductive success increases with age through extra-pair paternity in the house sparrow (*Passer domesticus*). *Proc R Soc Lond Ser B Biol Sci.* 260:91–98.
- Whittingham LA, Dunn PO, Liffield JT. 2007. Egg mass influences nestling quality in tree swallows, but there is no differential allocation in relation to laying order or sex. *Condor.* 109:585–594.
- Whittingham LA, Dunn PO, Robertson RJ. 1994. Female response to reduced male parental care in birds—an experiment in tree swallows. *Ethology.* 96:260–269.
- Williams TD. 1994. Intraspecific variation in egg size and egg composition in birds—effects on offspring fitness. *Biol Rev Cambr Phil Soc.* 69:35–59.
- Wingfield JC, Ball GF, Dufty AM, Hegner RE, Ramenofsky M. 1987. Testosterone and aggression in birds. *Am Sci.* 75:602–608.
- Winkler DW, Allen PE. 1995. Effects of handicapping on female condition and reproduction in tree swallows (*Tachycineta bicolor*). *Auk.* 112:737–747.
- Wolf L, Ketterson ED, Nolan V. 1988. Paternal influence on growth and survival of dark-eyed junco young—do parental males benefit. *Anim Behav.* 36:1601–1618.