

# Costs and Benefits of Competitive Traits in Females: Aggression, Maternal Care and Reproductive Success

Kristal E. Cain<sup>1,2,3\*</sup>, Ellen D. Ketterson<sup>1,2</sup>

**1** Department of Biology, Indiana University, Bloomington, Indiana, United States of America, **2** Center for the Integrative Study of Animal Behavior, Bloomington, Indiana, United States of America, **3** Research School of Biology, Australian National University, Acton, Australia

## Abstract

Recent research has shown that female expression of competitive traits can be advantageous, providing greater access to limited reproductive resources. In males increased competitive trait expression often comes at a cost, e.g. trading off with parental effort. However, it is currently unclear whether, and to what extent, females also face such tradeoffs, whether the costs associated with that tradeoff overwhelm the potential benefits of resource acquisition, and how environmental factors might alter those relationships. To address this gap, we examine the relationships between aggression, maternal effort, offspring quality and reproductive success in a common songbird, the dark-eyed junco (*Junco hyemalis*), over two breeding seasons. We found that compared to less aggressive females, more aggressive females spent less time brooding nestlings, but fed nestlings more frequently. In the year with better breeding conditions, more aggressive females produced smaller eggs and lighter hatchlings, but in the year with poorer breeding conditions they produced larger eggs and achieved greater nest success. There was no relationship between aggression and nestling mass after hatch day in either year. These findings suggest that though females appear to tradeoff competitive ability with some forms of maternal care, the costs may be less than previously thought. Further, the observed year effects suggest that costs and benefits vary according to environmental variables, which may help to account for variation in the level of trait expression.

**Citation:** Cain KE, Ketterson ED (2013) Costs and Benefits of Competitive Traits in Females: Aggression, Maternal Care and Reproductive Success. PLoS ONE 8(10): e77816. doi:10.1371/journal.pone.0077816

**Editor:** Dustin Rubenstein, Columbia University, United States of America

**Received:** May 16, 2013; **Accepted:** September 4, 2013; **Published:** October 30, 2013

**Copyright:** © 2013 Cain, Ketterson. This is an open-access article distributed under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

**Funding:** Research was supported by National Science Foundation (NSF) grants to EK (BSC 05-19211 and IOS 08-20055) and an NSF Doctoral Dissertation Improvement Grant to KC (09-10036). KC was also supported by NSF Graduate Research Fellowship ([www.nsfgrfp.org](http://www.nsfgrfp.org)). The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

**Competing Interests:** The authors have declared that no competing interests exist.

\* E-mail: [kristalcain@gmail.com](mailto:kristalcain@gmail.com)

## Introduction

Intense competition for limited reproductive resources (mates, territories, etc.) can favor the expression of traits that improve access to these resources, i.e. competitive traits such as ornaments, armaments, or intense same-sex aggression [1–5]. However, investment in such traits is often costly. Energy invested in the development or expression of competitive traits is energy no longer available for growth, self-maintenance, or the production and care of offspring. Further, increased trait expression often reduces survival [4,6]. For males, these costs are generally balanced by improved access to females, leading to increased reproductive success [4]. Our understanding of why females express competitive traits, however, is still limited [1–3,7,8].

Theory argues that female reproductive success is generally limited by the production and care of offspring, rather than mate number [5,9–11]. Furthermore, because energy invested in the development or expression of competitive traits is no longer available for egg production or offspring care, females should face greater costs than males for competitive trait expression, and experience less benefit [6]. As a consequence, female expression of competitive traits has often been explained as a costly, non-functional by-product of selection on males, reviewed in [1,3,12]. However, female reproductive success can also be limited by access to limited, sex-specific reproductive resources (paternal care, nest sites, etc.), rather than solely by ability to produce eggs

or care for offspring [1,3,8,12–15]. Recent evidence indicates that females also use competitive traits to improve access to resources and that trait expression is often positively related to reproductive success [1,3,8,12–14,16]. Together, these findings suggest that the benefits females accrue from expressing competitive traits may be greater than previously assumed. However, it is currently unclear whether our assumptions about the costs of female trait expression have been similarly inexact.

For species investing in parental care, one of the most important potential costs of competitive trait expression is a negative effect on the amount of time and energy available for offspring production and care [6,17,18]. This tradeoff has been well studied in males of many avian species with paternal care [18–23]. Because females are often essential caregivers, these costs may be even more substantial for females [6,10,14]. Alternatively, because female frequently compete for access to reproductive resources that may have a positive effect on offspring production and care, the relationship between parental care and competitive trait expression in female may be more complex than what is commonly seen in males. However, few studies have directly examined the tradeoff between competitive traits and maternal care [24]. Consequently, it is currently unclear whether females face a similar tradeoff, i.e. a negative relationship between competitive trait expression and investment in offspring. Such data are essential if we are to develop a solid understanding of why females express competitive traits; it

is the interplay of costs and benefits that determine the net strength and direction of selection [25].

The dark-eyed junco (*Junco hyemalis*) is a common songbird that is a perennial model for understanding the evolution of morphological, physiological and behavioral traits, e.g. [26–30]. Here, we examine the relationship between maternal behavior (brooding and provisioning) and intra-sexual aggression, an important and ubiquitous competitive trait in females that can be costly in terms of time, energy, and risk of injury [8,14,16,31,32]. We then quantify the fitness consequences of aggression and maternal behavior; directly, by quantifying reproductive success (nest success), and indirectly, by examining egg and nestling mass, proxies for offspring quality [33]. These measures are examined across two breeding seasons that differed in terms of breeding conditions (temperature, precipitation and predation rates). Collectively, these data allow us to examine the potential costs and benefits of competitive trait expression, and how ecology might alter those relationships.

## Methods

### Ethics Statement

This research adhered to the Association for the Study of Animal Behavior/Animal Behavior Society Guidelines for the Use of Animals in Research, the legal requirements of the United States of America (USFWS special use permit number MB093279-2, USGS banding permit number 20261), and The Virginia Department of Game and Fish (#041506). The protocol was approved by the University of Virginia and Indiana University Institutional Animal Care and Use Committees (protocol # 06-242 for both). Research was conducted on the grounds of the Mountain Lake Biological Station, with permission from the station director, in the Jefferson National Forest with permission from The US Department of Agriculture, Forest Service, and on private property with the permission of the landowners. This research did not involve endangered or threatened species.

### Study Species, Site and General Methods

Dark-eyed juncos (*J. h. carolinensis*) are a mildly dimorphic, socially monogamous songbird with biparental care; females alone build the nest, incubate, and brood nestlings, while males assist in feeding and defense [34]. This subspecies of junco are seasonal, partial migrants; males arrive first and establish general use territories ( $1.316 \pm 0.525$  ha) that are maintained through the breeding season [34]. Little is known about the role of females in the acquisition and maintenance of territories, however females use non-overlapping home ranges that change in size according to breeding stage (fertile period,  $2.44 \pm 0.992$  ha [35]; nestling period,  $0.833 \text{ ha} \pm 0.156$  ha [36]). This study took place on and around Mountain Lake Biological Station, in Giles Co., Virginia ( $37^{\circ}22'N$ ,  $80^{\circ}32'W$ ), from April 15–August 10, 2009–2010. Details regarding the study site, species and general practices are available elsewhere [37,38]. In brief, all resident individuals were captured, banded with serially numbered metal bands and a unique combination of color bands, and aged using a combination of mark-recapture data, and plumage and eye coloration [34]. Once breeding commenced, we searched daily for the nests of all females on the study site. Once a nest was found it was marked, the social pair identified, and the nest monitored daily until egg-laying was complete, then every three days until hatching. As part of a separate experiment, within 24 h of clutch completion, we collected the third-laid egg from each female. If egg order was unknown, e.g. because the nest was found after laying commenced, we selected the largest egg, as the 3rd egg is often largest

[34]. Eggs were weighed on a digital scale. After hatching, the nest was monitored every three days until the nest fledged or failed. Nestlings were weighed and measured (nearest 0.1 g) in the afternoon of days 0 (hatch day), 3, 6, and the morning of day 12 (fledging), using the smallest Pesola scale possible (5 g, 10 g or 50 g).

### Aggression Towards an Intruder

Intrasexual aggression was measured in 2009 ( $N=17$ ) and 2010 ( $N=14$ ) by recording behavioral response to a caged conspecific female bird (lure) between days 3–9 of incubation May 15 to June 30; females incubate eggs for 12 days and nests are built throughout the season (May–July). One female was assayed in both years. This behavioral assay we used for intrasexual aggression is described in detail elsewhere [31]. Briefly, during the incubation period we placed a caged same-sex conspecific  $\sim 1$  m from the nest and covered the cage with a camouflaged piece of cloth. When the female returned to within 5 m of the nest we removed the cloth and observed the female's response from  $\sim 15$  m using binoculars. We recorded the amount of time spent within 0.25 m, 0.25–1 m, 1–5 m, outside of 5 m, sitting on the nest, and the number of attacks towards the lure (swoops at the lure without contact and actual contacts with the lure's cage) during a 10 min period.

Females generally responded in one of three ways: attacking persistently throughout the trial, alternating between attacking and sitting on their nest (which was  $\sim 1$  m from the intruder), or apparently avoiding interaction by staying  $>5$  m away. Time spent attacking and time spent on the nest were not related (Spearman's, both years,  $\rho < 0.20$ ,  $P > 0.35$ ). To capture this potentially important variation in response style, i.e. differences in tendency to attack, remain in area and occasionally attack, or leave the area entirely, we calculated two distinct aggression scores. We used the amount of time spent within 0.25 m of the lure to gauge overt aggression (time-attacking). Time-attacking was a strong predictor of overtly aggressive behaviors (Spearman's correlation, time-attacking and dives+hits summed  $\rho_{15} = 0.8702$ ,  $P < 0.0001$ ). We used the total amount of time a female spent within a 1 m radius (time sitting on nest, time attacking and time 0.25–1 m away from nest) to estimate female persistence in the face of a sustained intruder (time-present). Individual females with high time-attacking scores spent most of the trial in direct interaction with the simulated intruder, while those with high time-present scores alternated between attacking and incubating but remained in the immediate area, females that were low in both scores avoided interacting with the intruder. These low scoring females generally left the area and spent the majority of the trial out of sight or more than 5 m away from the simulated intruder. All females eventually returned to incubating, no nests were abandoned due to the trial. To improve normality, variables were square root-transformed. Because there were a number of females that spent zero time within 0.25 m, no transformation could achieve normality; however, linear regressions are generally robust to violations of normality [39]. Date of trial, number of eggs, year, day of incubation, and lure identity had no effect on female response (all  $P > 0.30$ ), and all were excluded from further analysis.

### Maternal Behavior

Maternal behavior was estimated by quantifying brooding and provisioning behavior at day 3 post-hatching. Because nest failure is common, sample size was limited (2009,  $N=13$ ; 2010,  $N=17$ ). Day 3 was chosen because females are still actively warming young, and chicks are large enough to need frequent feedings [34]. The behavioral assay for parental care is described elsewhere [40].

Briefly, we placed a camera 2–4 m from the nest and recorded for 4 h, within 0900–1700. A single observer later analyzed recordings to quantify the number of feeding trips per minute and the length of each brooding bout. For each female we calculated the average length of a brood bout (mean brood bout), excluding the final bout if the female was still on the nest at the end of the observation period. We recorded ambient temperature at 1400 (mid-point for most recordings) using a Campbell CR10 logger located on the study site. There was a negative relationship between average brood length and provisioning rate (per nestling) ( $R^2 = 0.297$ ,  $F_{1,25} = 10.14$ ,  $P = 0.0040$ ).

### Statistical Analysis

To examine the relationship between both measures of aggression and maternal behavior, we set the behavioral measure of interest (brooding or provisioning) as the dependent variable and used forward step-wise regression (0.25 to enter, 0.10 to leave) to select informative variables, only final models are reported. The initial full model included age, date of the year, year, ambient temperature, number of nestlings, and measure of aggression. To test for year-specific relationships, we also included a year by aggression interaction term. If the interaction term was significant, we examined relationships independently by year. We used the same approach to examine the relationship between aggression and egg mass; the initial model for egg mass included age, date the egg was collected, measure of aggression, year, and year by aggression interaction. To determine how aggression was related to mean nestling mass at hatch day, day 3, 6, and at fledging we used the same approach; the initial complete model included age, year, date, ambient temperature, number of nestlings, year, and a year by behavior interaction term. Females with more than one nest were included only once, using data from the nesting attempt closest in time to when the behavioral measures were taken. Excluding the one female that was measured in both years had no qualitative effect on the results; all significant effects remained.

To analyze the effect of aggression on nest fate we coded females as successful if any nesting attempt in a given year produced fledglings, or failed if all attempts were unsuccessful. We then used logistic regression to determine whether behavior was predictive of nest success. For visualization of the relationships in Figure 1, we calculated individual leverage effect pairs from leverage plots. Leverage pairs are derived from the actual residuals from the best-fit line and the residual error without the effect in the model; the result shows the relationships between the two variables after controlling for the other variables in the final model, similar to a partial correlation.

## Results

### Aggression and Maternal Behavior

Measures of aggression toward a same-sex intruder were significantly related to measures of parental behavior, but in opposite directions. Time-attacking and time-present were both negatively related to mean brood bout (Figure 1, Table 1), (time-attacking: final model Adj.  $R^2 = 0.54$ ,  $F_{3,15} = 4.39$ ,  $P = 0.0291$ , time-attacking  $P = 0.0313$ ), (time-present: final model Adj.  $R^2 = 0.40$ ,  $F_{2,15} = 3.91$ ,  $P = 0.0183$ ; time-present  $P = 0.0299$ ). In contrast, both measures of aggression were positively related to provisioning rate (Figure 1, Table 1), (time-attacking: final model Adj.  $R^2 = 0.71$ ,  $F_{3,14} = 11.43$ ,  $P = 0.0014$ ; time-attacking  $P = 0.0159$ ), (time-present: final model Adj.  $R^2 = 0.66$ ,  $F_{3,14} = 9.31$ ,  $P = 0.0030$ ; time-present  $P = 0.0103$ ). Year was not a significant predictor of either aggression or parental behavior,

nor was there a significant year by behavior interaction (all  $P > 0.30$ ).

### Aggression and Egg Mass

There were no direct relationships between egg mass and aggression (all  $P > 0.25$ ); however, there were significant year by aggression interactions. Controlling for the date the egg was collected, in 2009 there was a positive relationship between time-present and egg mass, but in 2010 the relationship was negative (Table 1, Figure 2), (final model Adj.  $R^2 = 0.37$ ,  $P = 0.0179$ ; time-present  $P = 0.21$ ; time-present  $\times$  year  $P = 0.0043$ ). Examining the relationship between time-present and egg mass separately by year reveals that the relationship was significant in 2009 ( $R^2 = 0.33$ ,  $P = 0.0131$ ) but not in 2010 ( $R^2 = 0.13$ ,  $P = 0.2463$ ). There was no statistically detectable relationship between time-attacking and egg mass ( $P > 0.40$ ); however, the data followed a similar pattern, no relationship in 2009 and a negative trend in 2010 (Figure 2), (2009:  $P > 0.50$ ; 2010:  $R^2 = 0.23$ ,  $P = 0.1179$ ).

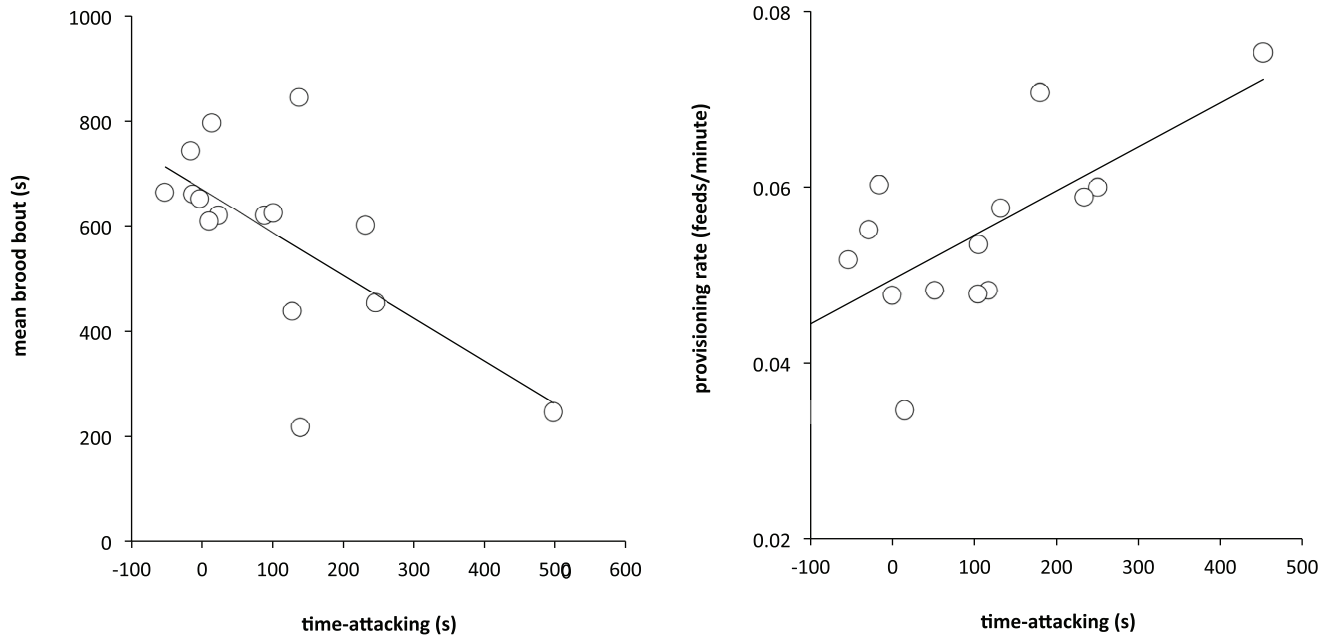
### Aggression, Maternal Behavior and Measures of Reproductive Success

Neither aggression nor mass at hatching differed by year, and when the years were pooled, neither measure of aggression was related to hatchling mass (all  $P > 0.25$ ). However, there were significant year by aggression interactions for both measures (time-attacking: final model Adj.  $R^2 = 0.24$ ,  $P = 0.0168$ ; year by time-attacking interaction  $P = 0.0072$ ,  $N = 30$ ), (time-present: final model Adj.  $R^2 = 0.21$ ,  $P = 0.1059$ ; year by time-present interaction  $P = 0.0072$ ,  $N = 30$ ). Examining the years separately revealed that in 2009 there was no relationship between time-attacking and mass at hatching (Figure 2), (Adj.  $R^2 = 0.09$ ,  $P = 0.1524$ ,  $N = 15$ ); in 2010 there was a pronounced negative relationship between time-attacking and mass at hatching (Figure 2), (Adj.  $R^2 = 0.30$ ,  $P = 0.0198$ ,  $N = 15$ ). Similarly, there was no relationship between time-present and hatchling mass in 2009 (Adj.  $R^2 = 0.06$ ,  $P = 0.3828$ ,  $N = 15$ ), and a negative trend in 2010 (Adj.  $R^2 = 0.23$ ,  $P = 0.0703$ ,  $N = 15$ ). Average nestling mass at hatching was not related to mean brood bout or provisioning rate in either year ( $P > 0.40$ ). Mass on any day after hatching (3, 6 or fledging) was unrelated to time-attacking, time-present, mean brood bout, or provisioning rate (all  $P > 0.25$ ).

In 2009, there were 106 nesting attempts with eggs or young in the entire study population, 26 were successful (~25%); 5 of 17 focal females produced at least one successful nest (29%), 12 did not, indicating that the focal females were representative. Time-present was positively related to probability of producing a successful nest (Figure 3), ( $X^2_{1,17} = 6.54$ ,  $P = 0.0106$ ); time-attacking was positively, but not significantly, related to nest success ( $X^2_{1,17} = 1.80$ ,  $P = 0.1806$ ). In 2010, there were 81 nesting attempts with eggs or young, 37 were successful (~46%); 12 of 14 focal females produced a successful nest (86%). Consequently, we did not have sufficient numbers of unsuccessful females to determine whether there was a relationship between aggression, maternal care and nest success in 2010.

## Discussion

We found that the relationships between aggression and parental behavior were mixed, depending upon the type of parental care (summarized in Table 2). Aggressive females brooded nestlings less, but fed nestlings more frequently. The consequences of being aggressive varied according to year. In one year (2010), egg and hatchling mass were negatively related to aggression, and almost all females had a successful nest, suggesting



**Figure 1. Parental behavior and aggression.** Scatter plots relating parental behavior (left: brooding behavior; right: provisioning behavior) to one measure of aggression (time-attacking). Points in the scatter plots are leverage pairs, i.e. the relationship between the variables after controlling for other factors in the model (see Methods and Table 1), akin to partial correlation. Relationships with time-present show similar patterns. doi:10.1371/journal.pone.0077816.g001

important costs with no measurable benefit. However, in the other year (2009), aggression was positively related to egg mass, unrelated to hatchling mass, and positively related to nest success. There was no detectable relationship between either measure of aggression and nestling mass at after hatching. This suggests that aggression provides a large but inconsistent benefit.

**Competitive Ability/Maternal Effort Tradeoff**

In support of the idea that females, like males, face tradeoffs between competitive ability and parental care, we found a negative relationship between brooding and both aggression measures. This suggests that females may be limited in their ability to invest in all behaviors and thus face tradeoffs in how they allocate time and

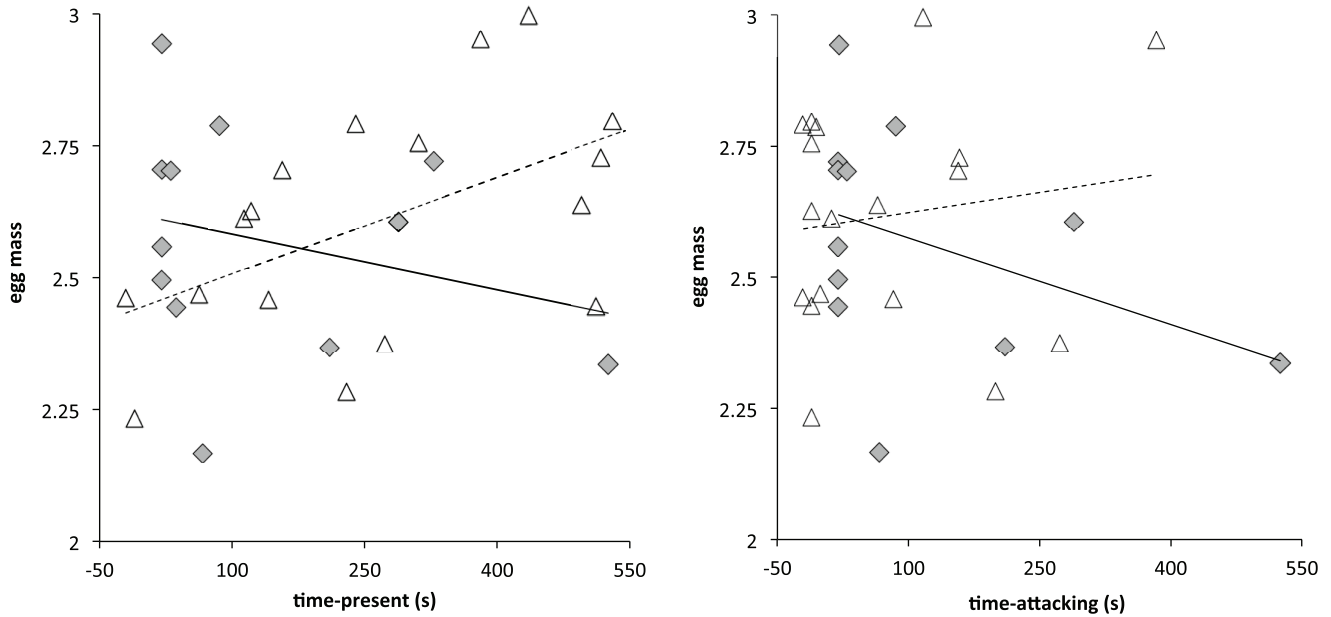
effort. In juncos, females alone brood [34] and longer brooding bouts may be more effective at warming developing young, which would allow chicks to devote more energy to growth and less to thermoregulation [33,40–43], suggesting an important potential costs for competitive trait expression. Because the relationships between brooding and aggression have rarely been examined it is difficult to say whether this is a general pattern or an isolated finding.

The relationship between provisioning rate and aggression has been examined more often. In males, competitive traits often function to improve access to mates but often produce a tradeoff, resulting in reduced investment in offspring care [18,20,22,23]. Because females often use competitive traits such as aggression to

**Table 1. Final models of the relationships between measures of parental behavior and measures of aggression.**

Measure of maternal effort	Final model results	Trait/Control variable	<i>b</i> ( <i>P</i> )
mean brood bout	Adj. $R^2 = 0.54$	<b>time-attacking</b>	<b>-14.49 (0.031)</b>
	$F_{3, 15} = 4.39$	date	0.823 (0.089)
	$P = 0.029$	# of nestlings	-67.54 (0.249)
provisioning rate	Adj. $R^2 = 0.71$	<b>time-attacking</b>	<b>0.0009 (0.016)</b>
	$F_{3, 14} = 11.43$	date	-0.001 (0.0018)
	$P = 0.001$	# of nestlings	0.007 (0.0350)
mean brood bout	Adj. $R^2 = 0.40$	<b>time-present</b>	<b>-12.41 (0.030)</b>
	$F_{2, 15} = 5.69$	date	8.51 (0.072)
	$P = 0.018$		
provisioning rate	Adj. $R^2 = 0.66$	<b>time-present</b>	<b>0.001 (0.010)</b>
	$F_{3, 14} = 9.31$	date	-0.002 (0.0001)
	$P = 0.003$	temperature	0.002 (0.010)

Models are multiple regressions. There were no significant year effects, or year by behavior interactions in these models. doi:10.1371/journal.pone.0077816.t001



**Figure 2. Offspring quality and aggression, by year.** Scatter plots illustrating the relationship between aggression measures and one measure of offspring quality (egg mass), according to year. Time-present showed a positive relationship with egg mass in 2009, and a negative, but not significant, relationship in 2010. Conversely, amount of time a female spent attacking was not related to egg mass in 2009 (open triangles and dashed line), but was negatively related to egg mass in 2010 (grey diamonds and solid line). The pattern is similar to the relationships between aggression measures and nestling mass at hatching. Overlapping points are jittered slightly for visual clarity and x-axis begins at  $-50$  s to permit viewing of females that did not respond. Raw data presented for visualization; see text and Table 2 for full analysis. doi:10.1371/journal.pone.0077816.g002

improve access to resources, rather than to acquire multiple mates, as males are thought to do, competitive ability may improve female ability to invest in offspring. If so, the tradeoff between competitive trait expression and parental care may not always be present [24], and the relationship between aggression and provisioning among females would be less consistent than among males. In support of this possibility, in white-throated sparrow females (*Zonotrichia albicollis*), the more aggressive white-striped morph female provisions less frequently than the less aggressive tan morph female [44], similar to the pattern generally seen in males. However, in tree swallows (*Tachycineta bicolor*), this relationship varies according to population, negative at one study site and a positive trend at the other study site, suggesting that trade-offs may be driven by ecological variables rather than time limitations [45]. Similarly, in female northern cardinals, more

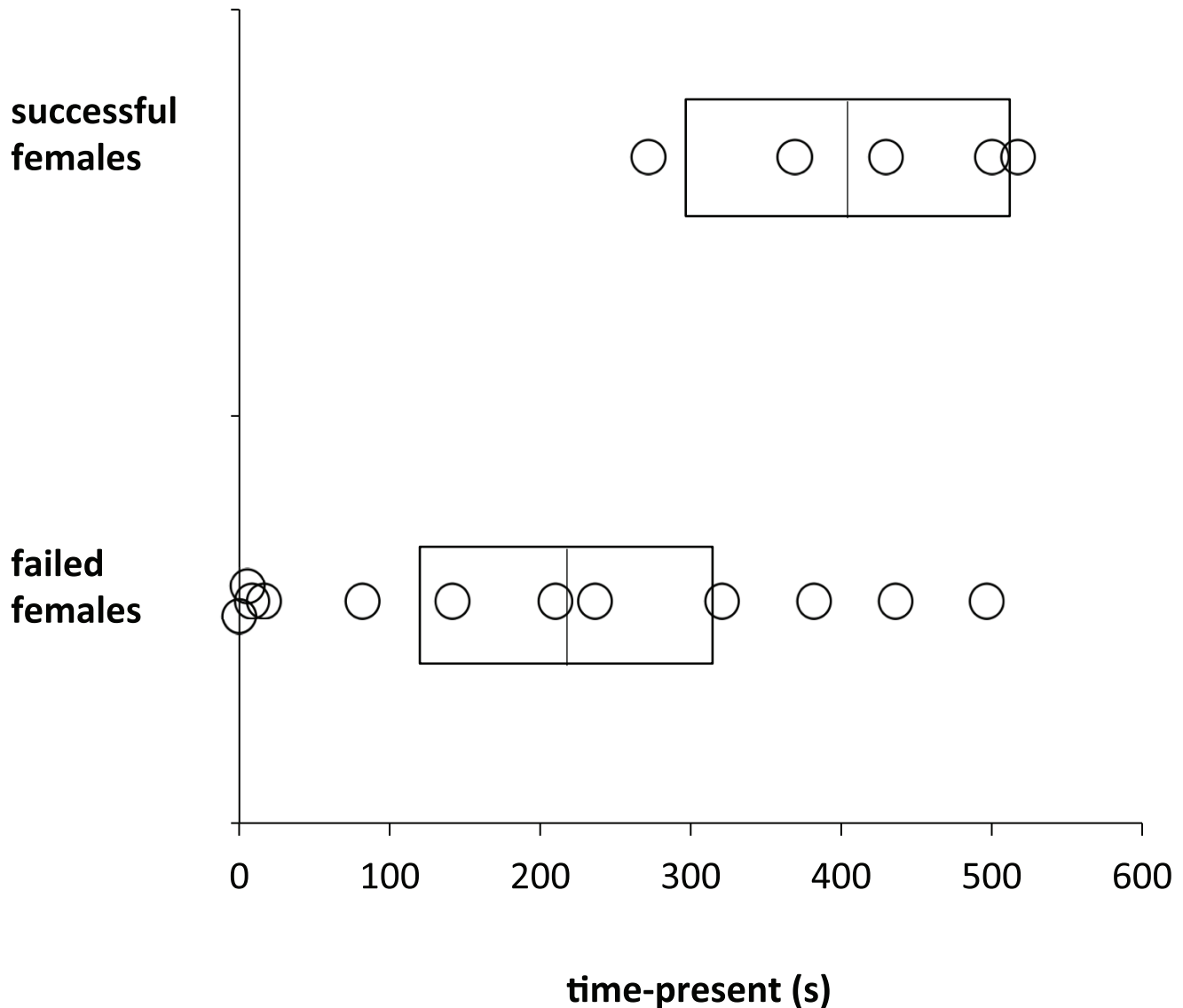
exaggerated facemasks are positively associated with both intrasexual aggression and provisioning rate [46].

We also found that provisioning and brooding were negatively related, which is perhaps not surprising given that females cannot do both simultaneously. Consequently, rather than indicating a cost per se, the negative relationships seen between brooding and aggression, and between brooding and provisioning, may instead be indicative of different behavioral strategies, i.e. some females engaged in a more passive style (low aggression & high brooding) while others engaged in a more active style (high aggression & high provisioning). Finally, it is important to note that male juncos assist in offspring care, and may influence focal female care and nestling growth. Previous experimental work in juncos found positive covariation in male and female provisioning rates, and found that both sexes compensate for reduced care from the mate [47–49].

**Table 2.** Summary of the cost and benefits of competitive trait expression by year.

Measure of aggression	Potential cost or benefit	Direction of relationship	
		2009 (tough year)	2010 (moderate year)
time-attacking	egg mass	0	0
	hatchling mass	0	—
	nest success	+^	n.a.
time-present	egg mass	+	—^
	hatchling mass	0	—^
	nest success	+	n.a.

A plus (+) denotes a positive relationship or a benefit from competitive ability, a minus (–) denotes a negative relationship or cost, a null (0) indicates that no detectable relationship was found. Relationships that were not significant but showed a trend are marked with a caret (^). doi:10.1371/journal.pone.0077816.t002



**Figure 3. Nest success and aggression in one year.** Illustration of aggression score (time-present) in relation to nest fate in 2009. Successful females produced at least one successful nest; failed females had no nest success for the entire season. Time-attacking showed a similar relationship, but was not significant. doi:10.1371/journal.pone.0077816.g003

However the nature of the relationship in un-manipulated junco pairs remains to be determined.

#### Year Effect on Functional Consequences

The functional consequences of competitive trait expression varied in strength and direction depending on year (see Table 2). This pronounced effect of year on the direction of the relationships suggests that changes in biotic or abiotic variables can alter the costs and benefits associated with competitive phenotypes. The two years differed in weather and predation rates, 2009 was cooler and wetter, with a much higher predation rate relative to 2010. In the tougher year (2009), the relationship between aggression and proxies for offspring quality (egg and nestling mass) were either positive or nonexistent, and aggression was positively related to nest success. In the easier year (2010), aggressive females appeared to pay a cost in terms of smaller eggs and nestlings, and most females experienced some nest success. This suggests that females benefit from a more aggressive behavioral type in tough years, but

pay a cost when resources are more abundant. Alternatively, the pronounced year effect may also be attributable to the year differences in predation pressure. Previous work found that aggression towards conspecifics was positively related to aggression towards a simulated predator [31]. Thus, when predation pressure is high, females may benefit if they are better able to deter nest predators. Further research is necessary to determine whether the observed year effects were due to differences in food availability, predation pressure, both, or another variable we did not measure.

However, regardless of the ecological factor responsible, the annual variation in the functional consequences of aggression reported here adds to the growing body of work suggesting that fluctuating ecological variables can be an important force shaping the strength and direction of selection. For instance, in great tit females (*Parus major*), selection favors fast exploring females in years when food is limited, but slow exploring females when food is more freely available [50]. Similar annual variation has also been

reported in Galapagos finches, which experience fluctuating natural selection on beak dimensions [51], and in male lark buntings (*Calamospiza melanocorys*), which experience substantial variation in the annual strength and direction of sexual selection [52].

### Aggression and Egg Mass

In the easier year (2010) we found that aggressive females produced smaller eggs, suggesting either a cost, or that females engage in different parenting strategies. Egg size can have important consequences for developing offspring, suggesting this might be a substantial cost; egg size is positively related to a variety of offspring traits including morphology, survival and growth rate [53]. However, although larger eggs are likely to improve individual offspring survival, investing in offspring quantity, rather than offspring quality, may optimize maternal reproductive success. Larger hatchlings may attract more predators [54] and smaller eggs may permit shorter intra-clutch intervals [55]. This may be important factor for species like the junco, which experience heavy nest predation [31,55–56]. Consequently, caution is warranted when interpreting reduced egg size as a cost, rather than as a strategy.

### Aggression and Nestling Mass

We also found a negative relationship between aggression and hatchling mass in 2009, likely driven by the tendency for more aggressive females to lay smaller eggs that year [53,57]. We did not measure incubation behavior, but it is likely positively related to brooding, circulating prolactin levels modulate both [58]. If more aggressive females incubate relatively less, as we have shown that they brood less, then nestlings of more aggressive females might also have slower development rates [40–43].

However, by 3 days post-hatching, this pattern was no longer detectable, suggesting growth was enhanced in the early nestling period in chicks of aggressive mothers, or suppressed in chicks of less aggressive mothers. The apparent difference in chick growth rates is likely driven by a complex combination of factors, but two possibilities are suggested by other research in this species. First, more aggressive females may have brooded less, but they also provisioned more, and provisioning rate and total food provided are positively correlated in the junco [49]. Thus chicks of aggressive mothers may not be forced to allocate resources to growth *or* thermoregulation, but have sufficient energy for both. A second possibility is that more aggressive females may deposit relatively more testosterone in the yolks of their eggs [57]. More aggressive female juncos produce more testosterone in response to a physiological challenge (injection of gonadotropin releasing hormone or GnRH challenge) [2], and testosterone production ability is positively related to yolk testosterone [59–61]. Increased developmental exposure to testosterone can accelerate chick growth and begging [62–66]. However, both high levels of testosterone and compensatory growth can have negative long-term consequences [67–70], and thus low hatching mass may still be an important cost.

### Aggression and Nest Success

Though maternal care and egg investment can both have important effects on offspring growth and quality, these efforts come to nothing if offspring do not survive. For songbirds, nest success is a crucial component of reproductive success [71]. We found that in one of two years aggressive females had greater nest success, replicating an earlier finding [2]. This suggests that aggressive females experience a major benefit and that there may be strong selection for competitive trait expression in some years.

It is currently unclear why more aggressive female juncos have greater nest success in some years but not others. Females in other species have been shown to compete for limited reproductive resources such as access to nest sites [72,73], paternal care [32,74–76], mates [77–80], territories [81–85], dominance [86,87] or other resources important for reproductive success [88,89]. For juncos, the main cause of nest failure is predation by small mammals [34,56], so any female attribute that reduces the probability of predation should be strongly favored. More aggressive females may be better at acquiring a territory with fewer predators or better-protected nest sites, or they may simply be more effective at deterring predators when they approach the nest [2,31].

Research in other species has also shown that benefits can neutralize the costs of competitive trait expression. For instance, aggressive mothers produce nestlings with lower mass in tree swallows [45], but aggression positively predicts nest site acquisition [73]; aggressive, dominant female baboons (*Papio cynocephalus*) have higher miscarriage rates and reduced fertility, but also experience shorter birth intervals and improved infant survival [90]. Female white-throated sparrows of the white-striped morph are more aggressive and provision less than tan morphs, but experience similar overall fitness [20]. In dung beetles, females with large horns for their body size had higher reproductive success when resources were limited [89], and showed no detectable fecundity cost [91], suggesting that the level of investment in competitive traits may be due to female quality rather than a tradeoff.

Overall, our finding of relatively minor costs, coupled with major benefits, suggests that our understanding to date of what makes a ‘good’ mother may be too simplistic. If we had measured only brooding behavior, we might have been inclined to label low brooding females poor quality mothers; however our findings suggest that these females are high quality mothers in other measures, i.e. provide more food or increased chance of survival. In fact, one might hypothesize that less aggressive, less competitive females have reduced access to important limited resources, but offset this loss by investing more in maternal care (spend more time brooding or make larger eggs).

Finally, there are many other potential costs and benefits that this study did not measure, e.g. survival, offspring recruitment, attractiveness to males. Female expression of competitive traits may increase access to important resources in the non-breeding season [3,79,88,92–96], which could strengthen the observed benefits of aggression. However, competitive traits can also have negative effects on survival [8,14,16]. Further, while female-female fights may be less frequent, they are also appear to be less ritualized and more likely to result in injury or death, possibly due to differences in the payoff of success and costs of failure [97,98]. Consequently, a more complete estimate of fitness is necessary before we can conclude whether, and to what extent, social selection is favoring the expression of competitive traits in females (Cain & Rosvall unpublished) [3,96].

### Conclusions

Our findings suggest that although females pay a cost for expressing competitive traits, here intrasexual aggression, these costs may be outweighed by benefits, at least in some years. These results add to the growing body of work from a wide-variety of taxa supporting the hypothesis that female competitive traits often function in manner analogous to male competitive traits, i.e. they improve reproductive success via access to limited resources,

whether those resources are mates, or some other reproductive resources (Cain & Rosvall unpublished) [1–3,8,13–16,91].

## Acknowledgments

The authors thank S Wanamaker, A Dapper, M Forquer, and D Reichard for assistance with data collection; the Ketterson Lab and the United Junco Workers for the field assistance; KA Rosvall and DM O'Neal for helpful discussions; SL Hoobler for additional support; and Mountain Lake

Biological Station (E Brodie III, Director and E Nagy, Associate Director) and Mountain Lake Hotel for the facilities and permission to work on their property.

## Author Contributions

Conceived and designed the experiments: KC EK. Performed the experiments: KC. Analyzed the data: KC. Contributed reagents/materials/analysis tools: KC EK. Wrote the paper: KC EK.

## References

- West-Eberhard MJ (1983) Sexual selection, social competition, and speciation. *Q Rev Biol* 58: 155–183.
- Cain KE, Ketterson ED (2012) Competitive females are successful females; phenotype, mechanism and selection in a common songbird. *Behav Ecol Sociobiol* 66: 241–252. doi:10.1007/s00265-011-1272-5.
- Tobias JA, Montgomerie RD, Lyon BE (2012) The evolution of female ornaments and weaponry: social selection, sexual selection and ecological competition. *Phil Trans Roy Soc B* 367: 2274–2293. doi:10.1098/rstb.2011.0280.
- Andersson M (1994) *Sexual Selection*. Princeton: Princeton University Press.
- Shuster SM, Wade MJ (2003) *Mating Systems and Strategies: (Monographs in Behavior and Ecology)*. Princeton: Princeton University Press.
- Fitzpatrick S, Berglund A, Rosenqvist G (1995) Ornaments or offspring: costs to reproductive success restrict sexual selection processes. *Biol J Linn Soc* 55: 251–260.
- Rubenstein DR, Lovette IJ (2009) Reproductive skew and selection on female ornamentation in social species. *Nature* 462: 786–789. doi:10.1038/nature08614.
- Rosvall KA (2011) Intrasexual competition in females: evidence for sexual selection? *Behav Ecol* 22: 1131–1140. doi:10.1093/beheco/arr106.
- Bateman AJ (1948) Intra-sexual selection in *Drosophila*. *Heredity* 2: 349–368.
- Trivers R (1972) Parental Investment and Sexual Selection. In: Campbell B, editor. *Sexual selection and the descent of man 1871–1971*. Chicago: Aldine. 136–179.
- Williams GC (1996) *Adaptation and natural selection: a critique of some current evolutionary thought*. Princeton: Princeton University Press.
- Amundsen TT (2000) Why are female birds ornamented? *Trends Ecol Evol* 15: 149–155.
- Clutton-Brock TH (2009) Sexual selection in females. *Anim Behav* 77: 3–11. doi:10.1016/j.anbehav.2008.08.026.
- Stockley P, Bro-Jørgensen J (2011) Female competition and its evolutionary consequences in mammals. *Biol Rev* 86: 341–366. doi:10.1111/j.1469-185X.2010.00149.x.
- LeBas NR (2006) Female finery is not for males. *Trends Ecol Evol* 21: 170–173. doi:10.1016/j.tree.2006.01.007.
- Clutton-Brock TH, Huchard E (2013) Social competition and its consequences in female mammals. *J Zool* 289: 151–171. doi:10.1111/jzo.12023.
- Magrath MJL, Komdeur J (2003) Is male care compromised by additional mating opportunity? *Trends Ecol Evol* 18: 424–430. doi:10.1016/S0169-5347(03)00124-1.
- 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. doi:10.1086/522838.
- Badyaev AV, Hill GE (2002) Paternal care as a conditional strategy: distinct reproductive tactics associated with elaboration of plumage ornamentation in the house finch. *Behav Ecol* 13: 591–597.
- Tuttle EM (2003) Alternative reproductive strategies in the white-throated sparrow: behavioral and genetic evidence. *Behav Ecol* 14: 425–432.
- 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. doi:10.1007/s00265-003-0671-7.
- Duckworth RA (2006) Behavioral correlations across breeding contexts provide a mechanism for a cost of aggression. *Behav Ecol* 17: 1011–1019. doi:10.1093/beheco/arl035.
- Pryke SR, Griffith SC (2009) Socially mediated trade-offs between aggression and parental effort in competing color morphs. *Am Nat* 174: 455–464. doi:10.1086/605376.
- Stiver KA, Alonzo SH (2009) Parental and mating effort: Is there necessarily a trade-off? *Ethol* 115: 1101–1126. doi:10.1111/j.1439-0310.2009.01707.x.
- Johnstone RA (1997) The evolution of animal signals. In: Krebs JR, Davies NB, editors. *Behavioural Ecology*. Oxford: Blackwell. 155–178.
- Balph MH (1977) Winter social behaviour of dark-eyed juncos: communication, social organization, and ecological implications. *Anim Behav* 25: 859–884.
- Ketterson ED, Nolan Jr V (1999) Adaptation, exaptation, and constraint: a hormonal perspective. *Am Nat* 154: S4–S25.
- Mila B, McCormack JE, Castaneda G, Wayne RK, Smith TB (2007) Recent postglacial range expansion drives the rapid diversification of a songbird lineage in the genus *Junco*. *Proc Biol Sci* 274: 2653–2660. doi:10.1098/rspb.2007.0852.
- Holberton RL, Boswell T, Hunter MJ (2008) Circulating prolactin and corticosterone concentrations during the development of migratory condition in the Dark-eyed Junco, *Junco hyemalis*. *Gen Comp Endocrinol* 155: 641–649. doi:10.1016/j.ygcen.2007.11.001.
- Cain KE, Burns C, Ketterson ED (2013) Testosterone production, sexually dimorphic morphology, and digit ratio in the dark-eyed junco. *Behav Ecol* 24: 462–469. doi:10.1093/beheco/ars186.
- Cain KE, Rich MS, Ainsworth K, Ketterson ED (2011) Two sides of the same coin? Consistency in aggression to conspecifics and predators in a female songbird. *Ethol* 117: 786–795. doi:10.1111/j.1439-0310.2011.01932.x.
- Sandell MI (1998) Female aggression and the maintenance of monogamy: female behaviour predicts male mating status in European starlings. *Proc Biol Sci* 265: 1307–1311.
- Starck JM, Ricklefs RE (1998) *Avian Growth and Development*. Oxford University Press on Demand.
- Nolan Jr V, Ketterson ED, Cristol DA, Rogers CM, Clotfelter ED, et al. (2002) Dark-eyed Junco. Poole A, Gill F, editors Philadelphia: Cornell Lab of Ornithology.
- Neudorf DL, Ziolkowski DJ, Nolan Jr V, Ketterson ED (2002) Testosterone manipulation of male attractiveness has no detectable effect on female home-range size and behavior during the fertile period. *Ethol* 108: 713–726. doi:10.1046/j.1439-0310.2002.00806.x.
- Reichard DG, Ketterson ED (2012) Estimation of female home-range size during the nestling period of dark-eyed juncos. *Wilson J Ornithol* 124: 614–620. doi:10.1676/11-189.1.
- Reed WL, Clark ME, Parker PG, Raouf SA, Arguedas N, et al. (2006) Physiological effects on demography: a long-term experimental study of testosterone's effects on fitness. *Am Nat* 167: 667–683.
- McGlothlin JW, Whittaker DJ, Schrock SE, Gerlach NM, Jawor JM, et al. (2010) Natural selection on testosterone production in a wild songbird population. *Am Nat* 175: 687–701. doi:10.1086/652469.
- Box GE, Watson GS (1962) Robustness to non-normality of regression tests. *Biometrika* 49: 93–106.
- O'Neal DM, Reichard DG, Pavilis K, Ketterson ED (2008) Experimentally-elevated testosterone, female parental care, and reproductive success in a songbird, the Dark-eyed Junco (*Junco hyemalis*). *Horm Behav* 54: 571–578. doi:10.1016/j.yhbeh.2008.05.017.
- Martin TE, Schwabl H (2008) Variation in maternal effects and embryonic development rates among passerine species. *Phil Trans Roy Soc B* 363: 1663–1674. doi:10.1098/rstb.2007.0009.
- Ardia DR, Pérez JH, Clotfelter ED (2010) Experimental cooling during incubation leads to reduced innate immunity and body condition in nestling tree swallows. *Proc Biol Sci* 277: 1881–1888. doi:10.1098/rspb.2009.2138.
- Rosvall KA (2013) Life history trade-offs and behavioral sensitivity to testosterone: An experimental test when female aggression and maternal care co-occur. *PLoS ONE* 8: e54120. doi:10.1371/journal.pone.0054120.g004.
- Kopachena JG, Falls JB (1993) Re-evaluation of morph-specific variations in parental behavior of the white-throated sparrow. *Wilson Bull* 105: 48–59.
- Rosvall KA (2011) Cost of female intrasexual aggression in terms of offspring quality: A cross-fostering study. *Ethol* 117: 332–344. doi:10.1111/j.1439-0310.2011.01881.x.
- Jawor JM, Gray N, Beall SM, Breitwisch R (2004) Multiple ornaments correlate with aspects of condition and behaviour in female northern cardinals, *Cardinalis cardinalis*. *Anim. Behav.* 67: 875–882.
- Ketterson ED, Nolan Jr 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*: 980–999.
- Wolf L, Ketterson ED, Nolan Jr V (1990) Behavioural response of female dark-eyed juncos to the experimental removal of their mates: implications for the evolution of male parental care. *Anim Behav* 39: 125–134.
- Clotfelter ED, Ray Chandler C, Nolan Jr V, Ketterson ED (2007) The influence of exogenous testosterone on the dynamics of nestling provisioning in dark-eyed juncos. *Ethol* 113: 18–25. doi:10.1111/j.1439-0310.2006.01286.x.
- Dingemans NJ, Both C, Drent PJ, Tinbergen JM (2004) Fitness consequences of avian personalities in a fluctuating environment. *Proc Biol Sci* 271: 847–852. doi:10.1098/rspb.2004.2680.
- Grant PR, Grant BR (2002) Unpredictable evolution in a 30-year study of Darwin's finches. *Science* 296: 707–711. doi:10.1126/science.1070315.
- Chaine AS, Lyon BE (2008) Adaptive plasticity in female mate choice dampens sexual selection on male ornaments in the lark bunting. *Science* 319: 459–462.



53. Krist M (2010) Egg size and offspring quality: a meta-analysis in birds. *Biol Rev* 86: 692–716. doi:10.1111/j.1469-185X.2010.00166.x.
54. Briskie JV, Martin PR, Martin TE (1999) Nest predation and the evolution of nestling begging calls. *Proc Biol Sci* 266: 2153–2159.
55. Janzen FJ, Warner DA (2009) Parent-offspring conflict and selection on egg size in turtles. *J Evol Biol* 22: 2222–2230. doi:10.1111/j.1420-9101.2009.01838.x.
56. Clotfelter ED, Pedersen AB, Cranford JA, Ram N, Snajdr EA, et al. (2007) Acorn mast drives long-term dynamics of rodent and songbird populations. *Oecologia* 154: 493–503. doi:10.1007/s00442-007-0859-z.
57. Whittingham LA, Dunn PO, Lijfeld 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.
58. Vleck CM (1998) Hormonal control of incubation/brooding behavior: lessons from wild birds. *Proceedings of the WSPA 10th European Poultry Conference, Israel*: 163–169.
59. Cain KE, Ketterson ED (2013) Individual variation in testosterone and parental care in a female songbird; the dark-eyed junco (*Junco hyemalis*). *Hormones and Behavior* (in press).
60. Whittingham LA, Schwabl H (2002) Maternal testosterone in tree swallow eggs varies with female aggression. *Anim Behav* 63: 63–67. doi:10.1006/anbe.2001.1889.
61. Müller W, Groothuis TGG, Goerlich VC, Ems M (2011) GnRH - A missing link between testosterone concentrations in yolk and plasma and its intergenerational effects. *PLoS ONE* 6: e22675. doi:10.1371/journal.pone.0022675.t001.
62. Jawor JM, McGlothlin JW, Casto JM, Greives TJ, Snajdr EA, et al. (2007) Testosterone response to GnRH in a female songbird varies with stage of reproduction: implications for adult behaviour and maternal effects. *Funct Ecol* 21: 767–775. doi:10.1111/j.1365-2435.2007.01280.x.
63. Schwabl H (1993) Yolk is a source of maternal testosterone for developing birds. *Proc Natl Acad Sci USA* 90: 11446–11450.
64. Groothuis TGG, Müller W, Engelhardt von NK, Carere C, Eising C (2005) Maternal hormones as a tool to adjust offspring phenotype in avian species. *Neurosci Biobehav Rev* 29: 329–352. doi:10.1016/j.neubiorev.2004.12.002.
65. Gil D (2003) Golden eggs: maternal manipulation of offspring phenotype by egg androgen in birds. *Ardeola* 50: 281–294.
66. Schwabl H, Palacios MG, Martin TE (2007) Selection for rapid embryo development correlates with embryo exposure to maternal androgens among passerine birds. *Am Nat* 170: 196–206. doi:10.1086/519397.
67. Sockman KW, Schwabl H (2000) Yolk androgens reduce offspring survival. *Proc Biol Sci* 267: 1451–1456. doi:10.1098/rspb.2000.1163.
68. Navara KJ, Hill GE, Mendonca MT (2005) Variable effects of yolk androgens on growth, survival, and immunity in eastern bluebird nestlings. *Physiol Biochem Zool* 78: 570–578. doi:10.1086/430689.
69. Fisher MO, Nager RG, Monaghan P (2006) Compensatory growth impairs adult cognitive performance. *Plos Biol* 4: e251. doi:10.1371/journal.pbio.0040251.
70. Alonso-Alvarez C, Bertrand S, Faivre B, Sorci G (2007) Increased susceptibility to oxidative damage as a cost of accelerated somatic growth in zebra finches. *Funct Ecol* 21: 873–879. doi:10.1111/j.1365-2435.2007.01300.x.
71. Martin TE (1995) Avian life history evolution in relation to nest sites, nest predation, and food. *Ecol Monograph* 65: 101–127.
72. Heinsohn R, Legge S, Endler JA (2005) Extreme reversed sexual dichromatism in a bird without sex role reversal. *Science* 309: 617–619. doi:10.1126/science.1112774.
73. Rosvall KA (2008) Sexual selection on aggressiveness in females: evidence from an experimental test with tree swallows. *Anim Behav* 75: 1603–1610. doi:10.1016/j.anbehav.2007.09.038.
74. Yasukawa K, Searcy WA (1982) Aggression in female red-winged blackbirds: a strategy to ensure male parental investment. *Behav Ecol Sociobiol* 11: 13–17.
75. Slagsvold T (1993) Female-female aggression and monogamy in great tits *Parus major*. *Ornis Scandinavica* 24: 155–158.
76. Langmore NE, Cockrem JF, Candy EJ (2002) Competition for male reproductive investment elevates testosterone levels in female dunlocks, *Prunella modularis*. *Proc Biol Sci* 269: 2473–2478. doi:10.1098/rspb.2002.2167.
77. Amundsen TT, Forsgren EE, Hansen LTT (1997) On the function of female ornaments: male bluethroats prefer colourful females. *Proc Biol Sci* 264: 1579–1586.
78. Kraaijeveld K, Kraaijeveld-Smit FJL, Komdeur J (2007) The evolution of mutual ornamentation. *Anim Behav* 74: 657–677. doi:10.1016/j.anbehav.2006.12.027.
79. Griggio M, Valera F, Casas A, Pilastro A (2005) Males prefer ornamented females: a field experiment of male choice in the rock sparrow. *Anim Behav* 69: 1243–1250.
80. Weiss SL, Kennedy EA, Bernhard JA (2009) Female-specific ornamentation predicts offspring quality in the striped plateau lizard, *Sceloporus virgatus*. *Behav Ecol* 20: 1063–1071. doi:10.1093/beheco/arp098.
81. Cooney R, Cockburn A (1995) Territorial defence is the major function of female song in the superb fairy-wren, *Malurus cyaneus*. *Anim Behav* 49: 1635–1647. doi:10.1016/0003-3472(95)90086-1.
82. Heinsohn R (1997) Group territoriality in two populations of African lions. *Anim Behav* 53: 1143–1147.
83. Fedy BC, Stutchbury BJM (2005) Territory defence in tropical birds: are females as aggressive as males? *Behav Ecol Sociobiol* 58: 414–422.
84. Hall ML, Peters A (2008) Coordination between the sexes for territorial defence in a duetting fairy-wren. *Anim Behav* 76: 65–73. doi:10.1016/j.anbehav.2008.01.010.
85. Valcu M, Kempenaers B (2008) Causes and consequences of breeding dispersal and divorce in a blue tit, *Cyanistes caeruleus*, population. *Anim Behav* 75: 1949–1963. doi:10.1016/j.anbehav.2007.12.005.
86. Hofer H, East ML (2003) Behavioral processes and costs of co-existence in female spotted hyenas: a life history perspective. *Evol Ecol* 17: 315–331. doi:10.1023/A:1027352517231.
87. Hodge SJ, Manica A, Flower TP, Clutton-Brock TH (2008) Determinants of reproductive success in dominant female meerkats. *J Anim Ecol* 77: 92–102. doi:10.1111/j.1365-2656.2007.01318.x.
88. Pryke SR (2007) Fiery red heads: female dominance among head color morphs in the Gouldian finch. *Behav Ecol* 18: 621–627. doi:10.1093/beheco/arm020.
89. Watson NL, Simmons LW (2010) Reproductive competition promotes the evolution of female weaponry. *Proc Biol Sci* 277: 2035–2040. doi:10.1098/rspb.2009.2335.
90. Packer C, Collins DA, Sindimwo A, Goodall J (1995) Reproductive constraints on aggressive competition in female baboons. *Nature* 373: 60–63. doi:10.1038/373060a0.
91. Simmons LW, Emlen DJ (2008) No fecundity cost of female secondary sexual trait expression in the horned beetle *Onthophagus sagittarius*. *J Exp Biol* 21: 1227–1235. doi:10.1111/j.1420-9101.2008.01575.x.
92. Crowhurst CJ, Zanollo V, Griggio M, Robertson J, Kleindorfer S (2012) White flank spots signal feeding dominance in female diamond firetails, *Stagonopleura guttata*. *Ethol* 118: 63–75.
93. Marra PP (2000) The role of behavioral dominance in structuring patterns of habitat occupancy in a migrant bird during the nonbreeding season. *Behav Ecol* 11: 299–308.
94. Murphy TG, Rosenthal MF, Montgomerie RD, Tarvin KA (2009). Female American goldfinches use carotenoid-based bill coloration to signal status. *Behav Ecol* 20: 1348–1355.
95. Holberton RL, Able KP, Wingfield JC (1989) Status signalling in dark-eyed juncos, *Junco hyemalis*: plumage manipulations and hormonal correlates of dominance. *Anim Behav* 37: 681–689.
96. Rubenstein DR (2012) Sexual and social competition: broadening perspectives by defining female roles. *Phil Trans Roy Soc B* 367: 2248–2252. doi:10.1098/rstb.2011.0278.
97. Elias DO, Botero CA, Andrade MCB, Mason AC, Kasumovic MM (2010) High resource valuation fuels “desperado” fighting tactics in female jumping spiders. *Behav Ecol* 21: 868–875.
98. Arnott G, Elwood RW (2009) Gender differences in aggressive behaviour in convict cichlids. *Anim Behav* 78: 1221–1227.