

Behavioral correlations across breeding contexts provide a mechanism for a cost of aggression

Renée A. Duckworth

Biology Department, Duke University, Durham, NC 27708, USA

Identifying correlations among behaviors is important for understanding how selection shapes the phenotype. Correlated behaviors can indicate constraints on the evolution of behavioral plasticity or may reflect selection for functional integration among behaviors. Obligate cavity-nesting birds provide an opportunity to examine these correlations because males must defend limited nest cavities while also competing for mating opportunities and providing parental care. Here, I investigated the role of behavioral correlations in producing a counterintuitive relationship between nest defense and reproductive success in western bluebirds (*Sialia mexicana*) such that males that defended their nests most intensely had the lowest reproductive success, measured as the number of within and extrapair offspring that fledged. By experimentally measuring aggression across contexts, I show that this cost of nest defense was due to the correlated expression of aggression across the contexts of nest defense and male–male competition coupled with a trade-off between male–male aggression and parental care. In particular, more aggressive males provisioned their females less during incubation and this led to disrupted incubation patterns and fewer fledged offspring. However, aggressive males did not benefit from avoiding parental investment by gaining extrapair fertilizations, and thus, it is unclear how high levels of aggression are maintained in this population despite apparent costs. These results suggest that there are constraints to the evolution of plasticity in aggression and emphasize the importance of considering the integrated behavioral phenotype to understand how variation in behavior is linked to fitness. *Key words:* aggression, behavioral syndrome, fitness cost, parental care, *Sialia mexicana*. [*Behav Ecol* 17:1011–1019 (2006)]

A major objective of studies of animal behavior is to understand the adaptive significance of behavioral variation (Mayr 1974). Correlations among behaviors are important to consider because they can indicate either constraints to the independent evolution of behaviors or suites of behaviors favored by selection (Arnold 1992; Price and Langen 1992; Bell 2005). However, the evolutionary causes and consequences of trait correlations are rarely considered in studies of behavior (but see Arnold 1981; Riechert and Hedrick 1993; Sih et al. 2003) even though correlations among behaviors are common (Sih et al. 2004). Measuring behavioral correlations not only provides insight into the processes of behavioral evolution but also allows for a more sophisticated analysis of the targets of selection by shedding light on the functional relationship between variation in fitness and variation in behavior.

Behavioral syndromes are a special case of behavioral correlation and occur when the same behavior is correlated across different functional contexts (Stamps 2003; Sih et al. 2004). Examples of behavioral syndromes include positive correlations in aggression across the contexts of foraging and territory defense in funnel web spiders *Agelenopsis aperta* (Riechert and Hedrick 1993) and across the contexts of anti-predator response and territory defense in the stickleback *Gasterosteus aculeatus* (Huntingford 1976) as well as positive correlations in activity level across the contexts of foraging and anti-predator response in the streamside salamander *Ambystoma barbouri* (Sih et al. 2003). These examples demonstrate that the expression of behavior can be consistent across different situations and indicate a need to identify sources of

variation among individuals in order to understand adaptive variation in behavior (Boake 1989; Gordon 1991).

Aggressive behavior has been well studied due to its links to individual fitness in many different contexts. Animals often use aggressive behaviors to defend a resource (Stamps and Krishnan 1997; Garcia and Arroyo 2002), to compete for mates (Hill et al. 1999; Hagelin 2002), to fend off predators (Redondo and Carranza 1989), and during foraging (Riechert 1993). There are different costs and benefits of expressing aggression in each of these contexts, and it is often assumed that individuals will modulate their aggressive behavior depending on the situation (Andersson et al. 1980; Redondo 1989). However, as illustrated by the stickleback and funnel web spider examples above, plasticity in aggression might sometimes be limited, and this can lead to carryover effects such that behaviors are not expressed independently across contexts (Sih et al. 2003). Yet, the fitness consequences of these carryover effects are rarely examined.

The objective of this study was to identify the mechanism of a cost of aggressive nest defense behavior in western bluebirds (*Sialia mexicana*). First, I show that males that defend their nest sites most intensely from an interspecific competitor, the tree swallow (*Tachycineta bicolor*), have the lowest reproductive success. This result presents an apparent paradox because tree swallows pose a serious threat to both current and future reproductive attempts of western bluebirds (Gillis 1989; Brawn 1990), and therefore, a more vigorous nest defense is expected to result in higher, not lower, reproductive success. Second, I test the hypothesis that the effects of aggression during male–male competition best explain this cost. Studies of mating behavior in birds have found that males often face a trade-off between investing in mating effort and parental effort, and as a consequence high levels of conspecific aggression are often antagonistic to male investment in parental care (Wingfield et al. 1987; Ketterson et al. 1992; Stoehr and Hill 2000). Therefore, I wanted to determine whether the correlated expression of aggression across the contexts of nest defense and male–male competition might explain

Address correspondence to R.A. Duckworth, who is now at the Institute of Evolutionary Biology, School of Biological Sciences, King's Buildings, University of Edinburgh, Edinburgh EH9 3JT, UK. E-mail: rad3@duke.edu.

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the counterintuitive finding of a cost of nest defense. To test this idea, I first use simulated intrusions of competitors to experimentally measure correlations in aggression across contexts. Then, I examine the relationship between reproductive success and male aggression in each context to determine whether aggression during nest defense is directly or indirectly related to reproductive success. Finally, I examine the relationship between male aggression and both parental care and extrapair paternity to determine whether the cost of aggression reflects a trade-off between male competitive behavior and parental investment.

MATERIALS AND METHODS

Study system

Western bluebirds are obligate secondary cavity nesters (they depend on nest cavities to reproduce, but cannot excavate their own) and nest cavities are a limited resource (Brawn and Balda 1988; Holt and Martin 1997). This leads to intense competition over nest sites between western bluebirds and other cavity-nesting species (Guinan et al. 2000). In particular, tree swallows, which co-occur with western bluebirds across most of their range, are their most persistent competitor for nest sites (Robertson et al. 1992; Meek and Robertson 1994). Both male and female western bluebirds defend the nest cavity against tree swallows; however, males are generally more aggressive (Brawn 1990). Only the female incubates, but males provision the female during incubation and both sexes provision the offspring (Guinan et al. 2000). Males also guard females during their fertile period (Dickinson and Leonard 1996; see Figure 1), and intense aggressive encounters between males over females are common at this time (Guinan et al. 2000; RA Duckworth, personal observation). Although western bluebirds are socially monogamous, extrapair fertilizations are common (Dickinson and Akre 1998).

In Montana, the site of this study, western bluebirds arrive to the breeding grounds before tree swallows and are able to select their nest site without interference (RA Duckworth, personal observation). However, tree swallows return from migration at about the time western bluebirds initiate nest building (Robertson et al. 1992). Thus, from nest building and throughout the nesting cycle, tree swallows frequently intrude on occupied nest sites attempting to usurp the nest cavity (Stutchbury and Robertson 1985; Brawn 1990; Figure 1). Although male western bluebirds usually respond aggressively to these territorial intrusions (Gillis 1989; Meek and Robertson 1994), individuals vary in the intensity of their response (see Results).

General methods

The study site is located in the Lolo National Forest in western Montana (lat 46°55' N, long 114°5' W). See Duckworth (2006) for a detailed description of study site. Both western bluebirds and tree swallows routinely nest at the study site, and I have often observed competitive interactions between them. Western bluebirds at this location initiate 1 or 2 nesting attempts per season (Duckworth 2006).

I collected data for this study during 3 breeding seasons (2002–2004). Each year, I trapped resident western bluebirds either at feeding trays baited with mealworms or in their nest-box to mark them with a unique color band combination and collected a blood sample for paternity analysis. I visited nest-boxes at least twice weekly from April through July of each year to monitor the progress of nests, collect blood samples from nestlings, and determine pairing and nesting affiliations of breeding adults. Initiation date, clutch size, brood size, and the number of nestlings that fledged were recorded for each nest. Reproductive success was calculated for each male as the total number of within and extrapair offspring that successfully fledged during one breeding season.

Microsatellite genotyping and paternity analysis

For paternity analysis, I collected 20 μ l of blood from each individual by brachial venipuncture. For eggs and nestlings that died in the nest, I collected a tissue sample. A total of 314 individuals were genotyped for this analysis, and 42 adult males were used in the analysis of paternity status and aggressive behavior. All adults and offspring were genotyped at 4 polymorphic microsatellite loci: Cup 02 and Cup 04, developed for Swainson's thrush, *Catharus ustulatus* (Gibbs et al. 1999), and Ssi 8-19 and Ssi 9-32, developed for eastern bluebirds, *Sialia sialis* (Cosh 1996). After digestion with proteinase K, DNA was extracted from blood and tissue samples using a 5 M salt solution (Miller et al. 1988). Polymerase chain reaction (PCR) was carried out in 20- μ l reactions with the following final conditions: 2.5 mM Hotmaster *Taq* buffer with Mg^{+2} , a 0.2 mM mix of deoxynucleoside triphosphates, 0.5 μ M of each primer (forward primer labeled with fluorescent dye, Taqman Probes, Applied Biosystems, Foster City, CA) and 1.75 U of *Taq* polymerase (Hotmaster *Taq* polymerase, Brinkmann Instruments, Inc., Westbury, NY), and 50–200 ng of genomic DNA. For the primers Cup 04 and Ssi 8-19, PCR amplifications were performed under the following cycling conditions: an initial denaturing step of 94 °C for 2 min followed by 30 cycles of 94 °C for 20 s, 54 °C for 30 s, and 70 °C for 30 s. An annealing temperature of 58 °C was used for primers Cup 02 and Ssi 9-32. PCR product was analyzed

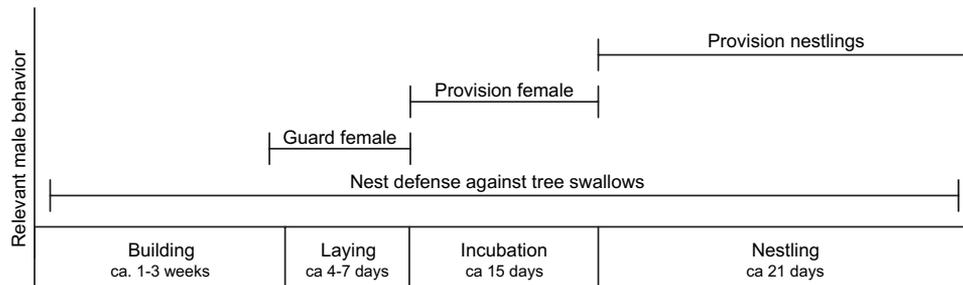


Figure 1

Summary of the nesting cycle of western bluebirds indicating how male behavior relates to each stage. The 2 contexts in which male aggression is important—nest defense and male–male competition—overlap during the laying stage when males guard females during their fertile period. Males defend the nest against tree swallow intrusions across all stages of the nesting cycle and provision females and nestlings during incubation and nestling stages, respectively.

using an ABI 3730 DNA Analyzer. Genotypes were analyzed by CERVUS v 2.0 (Marshall et al. 1998) to calculate expected and observed heterozygosities and to test for departure from Hardy–Weinberg equilibrium. Parentage was assessed for each nest by comparing genotypes of offspring and attending adults. Paternity for a putative father was excluded if one or more loci did not match. In each of the 3 years, the combined exclusion probability was >0.98.

Measuring nest defense

I measured male aggression toward tree swallows (hereafter referred to as nest defense) for 48 males during the early incubation stage (days 4–6). To measure nest defense, I presented bluebird pairs with a live tree swallow (captured on the day of the trial from a population located >30 km away) in a cubical wire cage placed on top of the nest-box. The caged bird (hereafter “model”) was concealed with a cloth cover which I did not remove until both members of the bluebird pair were visually located and within 100 m of the nest-box. Once the cloth was removed, I retreated to a blind ~15–30 m away to observe the bluebird pair’s response. All models were active during the trials, and their behavior did not differ noticeably among different trials. During the 2-min trial, I counted the number of times each pair member attacked the model, flew by it, or hovered near it (see Power and Doner 1980; Gowaty and Wagner 1988 for detailed description of these behaviors). Based on these behaviors, I assigned each male and female an aggressiveness score of 1–6 with 1 indicating a nonaggressive response and a 6 indicating the most aggressive response (see Table 1 for details on score assignment). This scoring system is similar to that used in other studies of nest defense (e.g., Hakkarainen et al. 1998).

For a subset of males in each year, I measured the nest defense response a second or third time during laying or incubation of the same or subsequent nest. These data were used to test for repeatability of aggressive behavior within the context of nest defense.

Measuring aggression across contexts

To determine whether male aggressive behavior was correlated across the contexts of nest defense and male–male competition, I conducted a series of behavioral trials similar to the nest defense trials (see above) on a subset of males in 2004 (N = 14). These trials were conducted during laying, when the female is fertile, and hence when male aggression toward a conspecific male should be maximized. I presented the focal male with either a live male western bluebird (to simulate a conspecific intrusion), a live tree swallow (to simulate a

heterospecific intrusion), or a live house finch *Carpodacus mexicanus* (as a control trial). All models were captured on the day of the trial from populations located 30–50 km away. A house finch was used as a control to measure the baseline aggressive response of western bluebirds to a bird that is common on the study site but does not compete with western bluebirds for either food or nest sites. Each male was tested with one of the models on 3 separate days, with the exception of 4 males who were not tested with the house finch because their nest failed before this trial could be completed. Males were tested on consecutive days whenever possible, but no more than 1 day separated each trial. The presentation order was randomized such that 7 males were presented with a bluebird first, 4 were presented with a tree swallow first, and 3 were presented with a house finch first. All males were tested when their females were present, and females’ responses toward the models were also recorded.

Measuring parental behavior

I observed the parental behavior of males during incubation and nestling stages either from a blind or by filming nests with a Samsung (SCD103) digital video recorder. Nest watches were conducted for 60 min once during days 10–14 of incubation and once during days 12–16 of the nestling stage for each nest initiated. Because nest success differed between pairs, the total observation time for each pair ranged from 60 to 240 min depending on the number of nests initiated and the success of each nest. During incubation, I recorded the number of times that males fed females both on and off the nest. During nestling watches, I recorded the number of times males visited the nest-box. Nestling feeding rates were calculated as the number of nest visits per nestling per hour.

In 2004, I monitored female incubation patterns by placing iButton (Dallas Semiconductor, Sunnyvale, CA) thermocouples directly under the eggs in each nest. These thermocouples were programmed to record temperature every 5 min for the duration of the incubation period allowing for detection of the presence/absence of the incubating female through the associated degree of temperature change of the incubated eggs. To record ambient temperature, I also taped 4 iButton thermocouples to the exterior bottom side of nest-boxes that were located in different sections of the study area. When ambient temperatures drop below 8 °C, as happens frequently in spring at the study site, female incubation patterns change dramatically and females vary in their ability to maintain consistent incubation temperatures (RA Duckworth, unpublished data). In order to determine whether male provisioning affected females’ ability to maintain incubation temperatures during these inclement weather periods, I calculated for each

Table 1
Assignment criteria for scoring aggressive behavior of male western bluebirds

Score	Behavior		Qualitative description
	Number of times flying or hovering within 0.5 m	Number of attacks	
1	0	0	No aggressive behaviors
2	1–5	0	Minimal response, moderately aggressive behaviors
3	>5	0	Moderate response, moderately aggressive behaviors
4	—	1–5	Moderate response, highly aggressive behaviors
5	—	6–9	High response, highly aggressive behaviors
6	—	>9	Very high response, many highly aggressive behaviors

These scores are based on quantitative (numbers of behaviors) and categorical (types of behaviors) data gathered during behavioral trials (see Methods for description of trials).

female the difference between mean incubation temperature on warm days (above 8 °C ambient) and the mean incubation temperature on cold days (8 °C or below) and related this to male provisioning behavior.

Ethical note

The birds used as models for the trials were placed in a wire cage where the distance between wires was too small for the focal birds to physically contact the model. Therefore, focal birds were never able to harm the models. Moreover, there were no signs of unusual stress in the models, and all resumed normal behavior on release. This study was conducted in compliance with Duke University Institutional Animal Care and Use Committee guidelines under permit A090-04-03.

Statistical analysis

All statistical analyses were performed using SAS (SAS Institute 1989). Because nest defense behavior was measured in multiple years for some males, I excluded observations so that each male is represented in the data set during only one year. I preferentially retained observations in years in which I had the most data on males. This allowed me to retain as large a sample as possible for analyses while maintaining independence of data. I calculated repeatability of each behavior as well as repeatability of the overall aggression score using the method of Lessells and Boag (1987) and the standard error (SE) of repeatability was calculated using the formulae from Becker (1984).

For the analysis of nest defense behavior and reproductive success, I applied a square root transformation to all aggression scores to normalize the data. For males measured multiple times in the same year, I used their mean aggression score in analyses. All variables were standardized to a mean of 0 and standard deviation of 1 before regression analyses.

There were no differences between years in reproductive success ($F_{2,47} = 1.15$, $P = 0.33$) or nest defense ($F_{2,48} = 0.32$, $P = 0.73$), and therefore, I pooled data for all 3 years. The failure of several nests during laying and incubation meant that I was only able to observe parental care for a subset of males for which I had measured aggressive behavior. Thus, sample sizes in analyses relating male aggressiveness to parental care vary accordingly. In addition, only nests that experienced both cold (8 °C or below) and warm (above 8 °C ambient) days during incubation were included in analyses of incubation temperatures.

To determine which type of aggressive behavior (during nest defense or during male–male competition) explained the most variance in reproductive success, I used multiple regression analysis, which included 2 explanatory variables: male aggression toward conspecifics and male nest defense behavior.

RESULTS

Variation in aggressive response

There was no difference in mean levels of male aggression toward the bluebird (mean \pm SE = 3.64 ± 0.45 , $N = 14$) and tree swallow (mean = 3.54 ± 0.46 , $N = 14$) models (paired t -test: $t = 0.28$, $P = 0.79$). However mean level of aggression toward the house finch model was consistently low (mean = 1.50 ± 0.31 , $N = 10$) and differed significantly from mean level of aggression toward bluebird and tree swallow models (ANOVA: $F_{2,38} = 7.00$, $P < 0.01$). The order of model presentation did not affect male aggressive behavior (nest defense: $F_{1,13} = 0.34$, $P = 0.57$; male–male aggression: $F_{1,13} = 0.68$, $P = 0.42$). The mean level of aggression by females was consistently low toward both finch (mean = 2.00 ± 0.47 , $N = 10$) and bluebird (mean = 1.33 ± 0.14 , $N = 14$) models and differed significantly from the level of aggression of males toward the bluebird model (paired t -test: $t = 4.17$, $P = 0.002$).

Male aggression was highly repeatable within the context of nest defense. The number of times a male flew by the model, hovered near it, and attacked it were repeatable within males, and thus, aggression scores based on these behaviors were also highly repeatable (Table 2). In addition, male nest defense behavior did not differ when measured across different breeding stages (paired t -test, laying versus incubation stage: $t = 0.32$, $P = 0.75$, $N = 11$).

Extrapair mating activity

Thirteen percent of nestlings (30/230) were extrapair offspring, and 27% of nests (14/51) contained nestlings that were sired by an extrapair male. I successfully assigned paternity to 28 of 30 extrapair offspring. In all cases of paternity assignment, there was only one male in the population with a genotype that completely matched the offspring's genotype. More aggressive males did not acquire more extrapair fertilizations compared with less aggressive males ($t = 0.23$, $P = 0.82$, $N = 42$), and males that lost paternity in their own nests did not differ in aggression from males that did not lose paternity in their own nests ($t = -1.56$, $P = 0.13$, $N = 42$; Figure 3).

Nest defense and reproductive success

In the context of nest defense, males that were more aggressive had lower reproductive success than less aggressive males ($F_{1,47} = 8.66$, $b_{ST} = -0.40$, $P = 0.005$; Figures 2A and 6). The relationship between male aggression and reproductive success was not a consequence of more aggressive males pairing with less fecund females as male aggressiveness did not vary in relation to the total number of eggs his female laid throughout the season ($F_{1,47} = 0.04$, $P = 0.85$). Nor was it a consequence of more aggressive males initiating breeding later as the date the first nest was initiated was not related to either

Table 2

Repeatability statistics for within-individual variation and mean, SE, and coefficient of variation (CV) in nest defense response measured as the aggressive response of male western bluebirds toward a tree swallow

Behavior	Repeatability within males ($N = 29$ males)				Descriptive statistics ($N = 48$ males)		
	r	SE	F	P	Mean	SE	CV
Flying by	0.43	0.15	2.53	<0.01	3.90	0.19	35.75
Hover	0.43	0.15	2.85	<0.005	3.27	0.61	130.05
Attack	0.72	0.09	6.44	<0.0001	1.20	0.24	137.70
Score (overall summary of aggression)	0.80	0.07	9.23	<0.0001	4.39	0.60	95.89

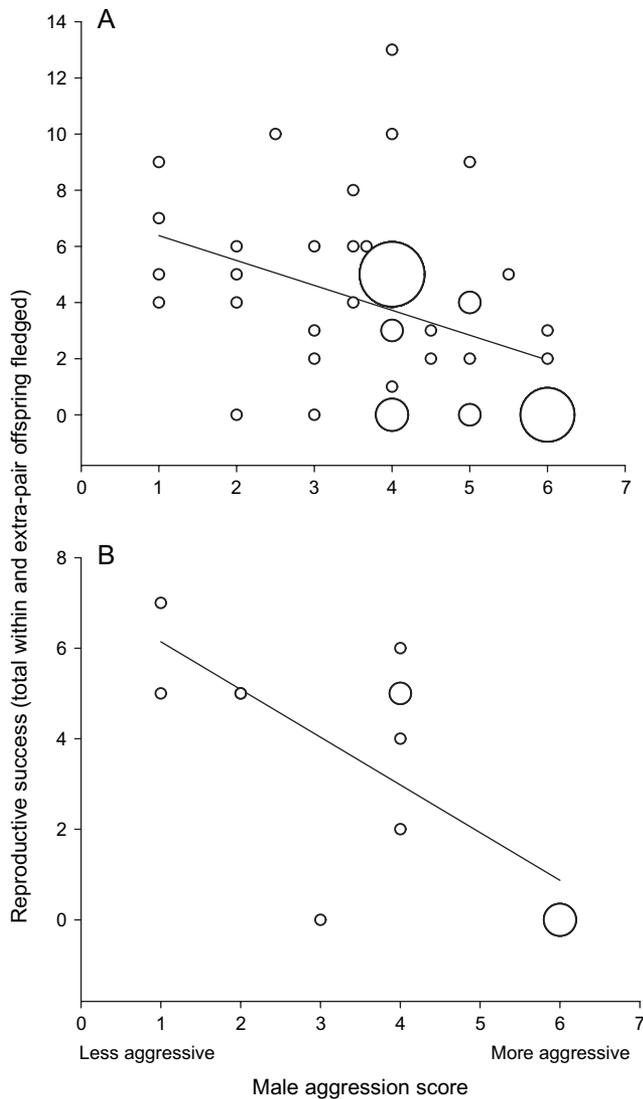


Figure 2 Negative relationship between aggression score and reproductive success of male western bluebirds (A) in the context of nest defense ($N = 48$) and (B) in the context of male–male competition ($N = 13$). Size of circles indicates number of individuals sampled with larger circles indicating more individuals.

reproductive success ($F_{1,47} = 0.78$, $b_{ST} = -0.13$, $P = 0.38$) or male behavior ($F_{1,47} = 1.16$, $b_{ST} = 0.16$, $P = 0.29$). Although male and female responses are correlated (Spearman $r = 0.48$, $P < 0.001$, $N = 48$), female nest defense response was unrelated to the reproductive success of her mate ($b_{ST} = 0.14$, $P = 0.42$) and did not affect the relationship between male nest defense and reproductive success because the relationship between male aggression and reproductive success persists when female aggression is statistically controlled for (male nest defense and reproductive success with female nest defense as a covariate: $b_{ST} = -0.42$, $P = 0.02$).

Aggression across contexts

Male aggression was positively correlated across the contexts of nest defense and male–male competition (Pearson $r = 0.63$, $P = 0.015$, $N = 14$; Figures 4 and 7). Male aggression in the context of male–male competition was also negatively related to reproductive success ($F_{1,12} = 11.36$, $b_{ST} = -0.71$,

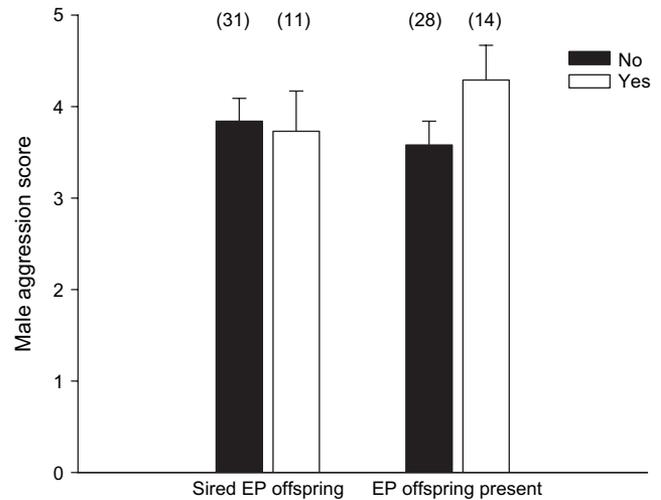


Figure 3 Aggression score (mean \pm SE) of male western bluebirds during nest defense in relation to whether males sired extrapair (EP) offspring in another male’s nest or had EP offspring present in their own nest. Numbers above bars indicate sample sizes.

$P < 0.01$, $N = 13$; Figures 2B and 7). In a multiple regression model including both types of aggressive behavior, aggression during nest defense explained very little variance in reproductive success, whereas aggression toward a conspecific male maintained high explanatory power (aggression during nest defense: $b_{ST} = -0.09$, $P = 0.77$; aggression during male–male competition: $b_{ST} = -0.66$, $P = 0.045$).

Male aggression and parental behavior

In the context of nest defense, male aggression was not significantly related to male feeding rates (incubation: $F_{1,26} = 0.94$, $b_{ST} = -0.19$, $P = 0.34$; nestling: $F_{1,25} = 1.62$, $b_{ST} = -0.25$, $P = 0.21$). Male aggression toward a conspecific male was negatively related to the rate at which males fed their females during incubation ($F_{1,8} = 19.31$, $b_{ST} = -0.86$, $P < 0.01$;

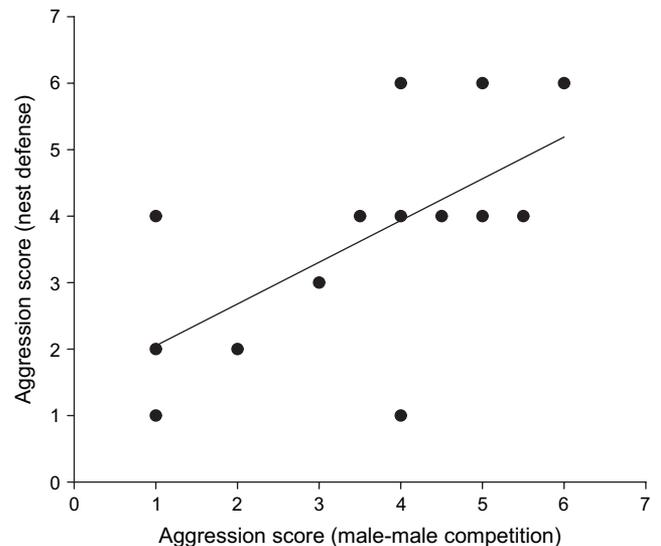


Figure 4 Positive correlation between aggression of western bluebird males toward conspecific males (male–male competition) and toward tree swallows (nest defense; $N = 14$).

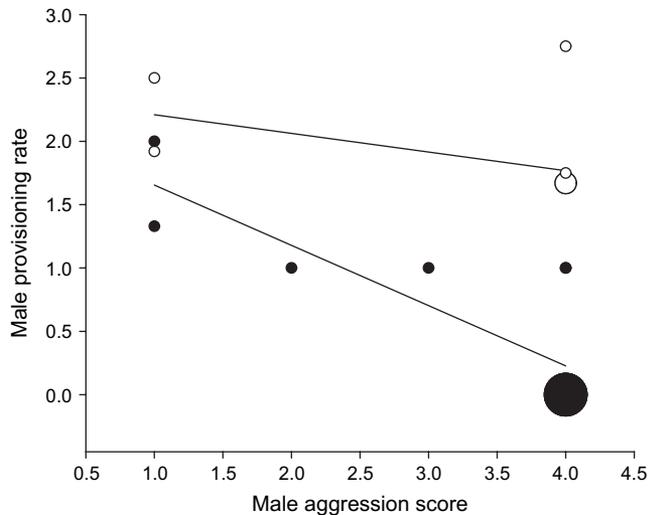


Figure 5

Relationship between aggression of male western bluebirds toward conspecific males and their provisioning rates during incubation (closed circles, $N = 9$) and nestling periods (open circles, $N = 7$). Provisioning rate during incubation is the number of times a male feeds his female on and off the nest per hour and provisioning rate during the nestling period is the number of times a male feeds per nestling per hour. Size of circles indicates number of individuals sampled with larger circles indicating more individuals.

Figures 5 and 7) and was negatively but not significantly related to nestling feeding rates ($F_{1,6} = 0.80$, $b_{ST} = -0.37$, $P = 0.41$; Figures 5 and 7). Male provisioning of the female during incubation had important consequences for the maintenance of incubation temperatures during inclement weather. In nests where males provisioned their incubating female very little, incubation temperatures dropped drastically compared with nests where females were provisioned more frequently ($F_{1,8} = 6.07$, $b_{ST} = -0.71$, $P < 0.05$, Figures 6A and 7). In turn, fewer offspring survived in nests in which incubation temperatures dropped drastically compared with nests with more stable incubation temperatures ($F_{1,10} = 7.32$, $b_{ST} = -0.67$, $P = 0.02$; Figures 6B and 7).

DISCUSSION

Behavioral correlations across contexts might indicate constraints to the evolution of adaptive plasticity in behavior (Riechert and Hedrick 1993) or might indicate a complex suite of functionally integrated behaviors (Cheverud 1982). Thus, identifying correlations among behaviors is important for understanding the role of selection in shaping the overall "behavioral phenotype" of an organism. In this study, identifying correlations among behaviors enabled a deeper understanding of the mechanisms linking aggression and reproductive success of male western bluebirds. Because tree swallows are an important threat to the success of western bluebirds' nests (Gillis 1989; Meek and Robertson 1994), it was expected that individuals defending their nests most intensely would have the highest reproductive success, yet the opposite relationship was found. Measuring aggressive behavior in a second context—the context of male–male competition—strongly suggests that this counterintuitive cost of nest defense was an indirect consequence of the correlation of aggression across the 2 contexts coupled with the strong negative effects of male–male aggression on reproductive success (Figure 7).

There are several lines of evidence that support an indirect link between nest defense and reproductive success. First, the

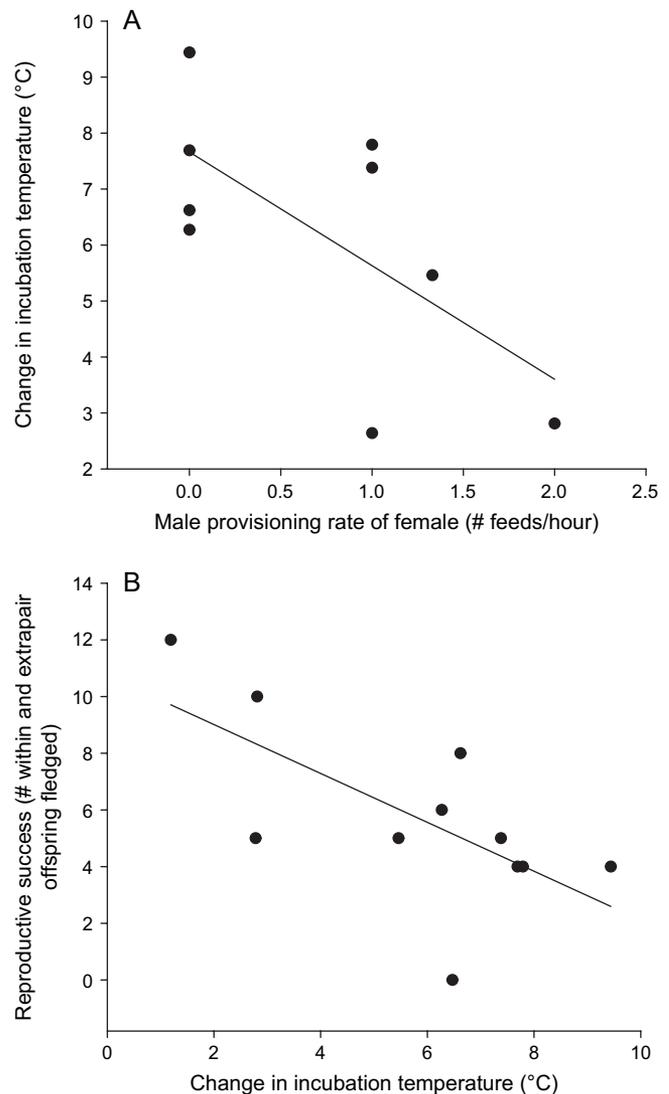


Figure 6

Relationship between the change in incubation temperature and (A) male provisioning rate and (B) reproductive success of western bluebirds. Change in incubation temperature is measured as the difference in mean temperature of the eggs on warm ($>8^{\circ}\text{C}$) versus cold days ($<8^{\circ}\text{C}$ or below).

costs of nest defense were specific to males, and this suggests that aggression in a uniquely male context—such as male–male competition over fertile females—is the true source of the cost of aggression. Second, aggression during male–male competition was highly correlated with nest defense (Figure 4), and, after statistically controlling for this correlation, it was evident that nest defense was only indirectly related to reproductive success through its relationship to male–male aggression (Figure 7). Finally, the negative relationship between aggression during male–male competition and parental care (Figure 5) provides a mechanism linking aggression and reproductive success. Specifically, males that were highly aggressive during male–male competition fed their incubating females very little compared with less aggressive males. A main source of variation in nest mortality in this population occurs when late spring snow and cold rainstorms cause some females to abandon their nests during incubation or early nestling stages and this produces extensive variation in hatching success and survival of young nestlings (RA Duckworth,

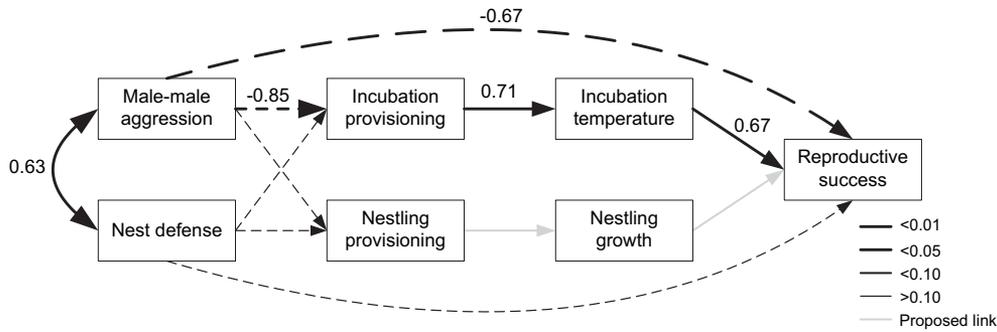


Figure 7

Summary of proposed and documented links between male aggression and reproductive success in the western bluebird. Male aggression during male–male competition is negatively related to reproductive success through its effects on male parental care, specifically in relation to male provisioning of his incubating female. Nest defense is only indirectly related to reproductive success through its correlation with male–male aggression. Double-headed arrows indicate correlations and single-headed arrows indicate least-square regressions. Numbers shown are regression or correlation coefficients for relationships in which $P < 0.10$. Dashed lines indicate negative relationships and solid lines indicate positive relationships.

unpublished data). Male provisioning during these periods appears to be vital (Figure 6A), most likely because it allows the female to meet energy demands during incubation and brooding of young nestlings (Lyon and Montgomerie 1985; Liffield and Slagsvold 1989; Halupka 1994). Consequently, in nests in which males provisioned females more, incubation temperatures changed little during cold days, whereas nests where males provisioned less experienced large drops in incubation temperatures and overall fledged fewer offspring (Figure 6A,B). These patterns provide the functional links between male aggression, parental behavior, and reproductive success enabling a deeper understanding of how the costs of aggression are generated in this system.

The measurement of aggression across different contexts resolves the counterintuitive finding of a negative relationship between nest defense and reproductive success; however it introduces a new paradox. Why do males that are more aggressive during male–male competition have lower reproductive success? At one level, we know the answer to this question—males that were more aggressive during male–male competition invested less in parental care which negatively impacted offspring survival. However, this proximate explanation does not resolve the ultimate question of why aggressive males forego investment in parental behavior despite the apparent costs. A trade-off between male aggressive behavior and investment in parental care has been well documented in avian species (Ketterson et al. 1992; Stoehr and Hill 2000; Tuttle 2002), and it is often assumed that aggressive males benefit by foregoing investment in parental care because it allows them to pursue additional mating opportunities and ultimately gain extrapair fertilizations. However, I found that highly aggressive males did not differ from less aggressive males in either gaining extrapair paternity or in losing paternity in their own nests. In fact, more aggressive males tended to lose paternity in their own nests more than less aggressive males. Therefore, the costs of aggression remain even when accounting for differences among males in extrapair mating activity.

A highly aggressive phenotype is common in this population (Table 2, Duckworth 2006) even though less aggressive males are favored. This suggests that either constraints prevent the evolution of the optimal expression of aggression or that there are fitness benefits to aggression that were not measured in this study. A possible example of such fitness benefits is that more aggressive males are better at acquiring nest cavities and territories (Duckworth 2006). Therefore, even though aggressive males fledged fewer offspring, some minimum level of aggression is likely necessary to acquire

a nest cavity and have an opportunity to breed. This may be particularly true given the intense intra- and interspecific competition for nest cavities in this species (Guinan et al. 2000). Although this benefit of aggression might explain the prevalence of highly aggressive males, the question remains as to why aggressive males do not invest in parental care. Ideally, male western bluebirds would exhibit flexibility in aggression such that they can turn it on when guarding their female or territory and turn it off when caring for offspring. Yet, aggression is remarkably consistent within males as indicated by its high repeatability during nest defense and by its correlated expression across multiple contexts—that of nest defense and male–male competition as well as across different breeding stages. It is well known that testosterone affects the expression of aggression across a wide variety of taxa and is also antagonistic to the expression of parental behaviors (Wingfield et al. 1987; Ketterson and Nolan 1999). Therefore, investigating the role of development, and in particular the role of hormonal variation, in producing different aggressive phenotypes might hold the key to understanding the seemingly maladaptive and inflexible expression of aggression in this species, particularly in relation to its antagonistic effects on parental care.

Recently, there has been an increased interest in behaviors that are context dependent in their expression (Qvarnström et al. 2000; Maddocks et al. 2001; Badyaev and Qvarnström 2003). The results of this study along with other recent studies (see Sih et al. 2004 for review) suggest that the context-independent expression of behavior is common and can also have important evolutionary implications, making it apparent that both consistency and plasticity in the expression of behaviors should be explored in order to understand the basis for variation among individuals (Gordon 1991).

More generally, the concept of phenotypic integration, which describes patterns of correlation between traits to understand their functional, developmental, and evolutionary relationships, has played a central role in addressing the relative importance of constraint versus selection in shaping morphologies (Cheverud 1982). The conceptual framework of phenotypic integration can aid our understanding of behavioral evolution as well by providing specific testable hypotheses about behavioral constraint and adaptation, a topic that remains central to the critique of the “adaptationist programme” (Gould and Lewontin 1979; Mayr 1983). Once a suite of correlated behaviors is identified, studies on the development, function, and fitness consequences of variation in these behaviors can address the alternative hypotheses of constraint and selection in producing the integrated behavioral

phenotype (Stamps 1991; Arnold 1992; Ketterson and Nolan 1999).

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