INTERSPECIFIC COMPETITION AFFECTS AVIAN PERSONALITY, ASSORTATIVE MATING, AND REPRODUCTIVE SUCCESS

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by
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Abstract

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Animal personality, or consistent and predictable behavioral responses of individuals, is thought to influence monogamous relationships by better allowing mates to coordinate territory defense and parental care behaviors. Aggressive territorial defense and boldness to potential predators are often important and ecologically relevant animal personality traits; however, the effects of heterogeneous social environments on the expression of assortative mating (mated pairs that behave similarly), personality, and behavioral syndromes (suites of correlated personality traits) are poorly understood. Eastern bluebirds (*Sialia sialis*) are secondary cavity nesting birds that are facing a changing social environment in the mountains of North Carolina. Tree swallows (*Tachycineta bicolor*) are expanding their range southward and have only been in the field site for less than 40 years. Tree swallows are highly aggressive birds that compete with bluebirds for limited nesting cavities. This new selection pressure may interfere with otherwise adaptive personality traits. This thesis aims to understand the multiple ways that interspecific competition with a highly active/aggressive species may shape individual behavior and affect reproductive

success in cavity nesting birds. Here, I examined how interspecific competition with tree swallows affects the propensity of paired male and female Eastern bluebirds to mate assortatively for behavior and how that may affect reproductive success. Furthermore, I also examined how interspecific competition may affect behavior, in general, in an attempt to understand how the environment plays a role in shaping animal personality and plasticity.

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Table of Contents

Foreword

Chapters 2 of this thesis has been published in *PLoS One* and chapter 3 has been submitted to *Behavioral Ecology* for review and thus are formatted according to their respective journal specifications.

Chapter 1

General Introduction/Terminology

This thesis will cover three different aspects of animal behavior as it pertains to consistency or flexibility of behavior: behavioral plasticity, animal personality, and assortative mating. Behavioral plasticity is behavioral flexibility that allows individuals to adapt their behavior to best deal with current environmental conditions and thus provides a selective advantage (Nussey et al. 2007). In the past, plasticity was thought to be the norm as it allows individuals to adjust their behavior accordingly and inflexibility was thought to be noise around a maximally adapted mean (Wilson 1998; Buss and Greiling 1999; Dall et al. 2004). However, behavioral ecologists realized that the inflexibility of individuals was actually biologically important and sparked the current enthusiasm about animal personality. Animal personality traits are defined as consistent individual differences in behavior across different contexts and time (Wilson et al. 1994; Gosling et al. 1999). This phenomenon has also been described as coping styles, temperament, axes, predispositions, profiles, or constructs (Gosling 2001; Sih et al. 2004; Groothuis and Carere 2005; Réale et al. 2007) and has been investigated across taxa including insects, fish, reptiles, birds, and mammals (Gosling et al. 1999). Furthermore, multiple personality traits may be correlated and that correlation is sometimes consistent across spatial and temporal contexts (Sih et al. 2004). This relationship between personality traits has been termed "behavioral syndromes" and constitutes the complete personality of an individual (Sih et al. 2004). Boldness to predators and exploratory

behavior are perhaps the most commonly used behaviors to quantify animal personality, but other behaviors such as aggression and activity level are often used to describe personality traits as well (Gosling et al. 1999).

Many studies have shown adaptive benefits of animal personality (Wilson 1998; Buss and Greiling 1999; Dall et al. 2004) as well as benefits of assortative mating for personality (Schuett et al. 2011; Harris and Siefferman 2014). Assortative mating can be defined in two different ways. Assortative mating suggests that individuals choose their mates based on particular traits (such as behavior) and, therefore, display similarities in those particular traits within the mated pair (Burley 1983). The term has also been referred to as simply the pattern of similarity in behavior across the populations and does not suggest that individuals choose their mates based on any predisposition (Burley 1983; Gimelfarb 1988; Jawor et al. 2003) and individuals may, in fact, may change their behavior to match the behavior of their mate (Harris & Siefferman 2014), which complicates the measurement of consistent personality traits.

Assortative mating for personality has been identified in many species, including great tits (Groothuis and Carere 2005), zebra finches, *Taeniopygia guttata* (Schuett et al. 2011), Stellar's jays, *Cyanocitta stelleri* (Gabriel and Black 2012), bridge spiders, *Larinioides sclopetarius* (Kralj-Fiser et al. 2013), dumpling squids, *Euprymna tasmanica* (Sinn et al. 2006), convict cichlids, *Cichlasom nigrofasciatum* (Budaev et al. 1999), and humans (Schuett et al. 2010). Furthermore, assortative mating may also have implications for reproductive success (Both et al. 2005; Harris and Siefferman 2014). The causal nature of assortative mating in a population is problematic because it is difficult to know the behavior of individuals prior to mating (Schuett et al. 2010) and this

leads to difficulty in understanding the role of personality in mate choice. Research in animal personality is becoming more and more complex as we begin to understand all of the variables that may play a role in shaping individual behavior and we now seem to have come full circle. As plasticity once dominated behavioral research and then behavioral consistency (personality), now researchers are gathering a body of evidence to suggest that there is an intricate interplay between personality and plasticity within species, populations, and even within individuals (Dingemanse et al. 2009; Betini and Norris 2012; Dingemanse et al. 2012; Mathot et al. 2012) and that the environment may shape patterns of assortative mating as well as individual behavior.

Recently, studies focusing on complexity of the relationships between animal personality and plasticity are being published at a high rate, and these studies are exposing the difficulties in understanding animal personality as it relates to environmental conditions (Archard and Bratihwaite 2010) and individual plasticity (Dingemanse et al. 2009; Betini and Norris 2012; Dingemanse et al. 2012; Mathot et al. 2012). For example, individual great tits (*Parus major*) exhibit consistent feeding behavior when measured multiple times within static environments (either high or low risk of predation), yet when individuals experience both risk environments their behavior is not consistent across contexts (Quinn et al. 2012). One example of variable environmental conditions that is extremely understudied is the social environment and, in particular, interspecific competition. Interspecific competition is defined as competition between two species for similar resources (Schoener 1983) and may also be termed heterospecific competition. Interspecific competition has implications for community and population structure (Webster et al. 2009), character displacement (Webster et al. 2009),

settlement patterns (Murray 1971), invasiveness or susceptibility to invasions (Carere and Gherardi 2013), and may have an effect on repeatability of behavior (discussed in Chapter 3), correlations between behaviors (discussed in Chapter 3), and reproductive success as well (discussed in Chapter 2).

The way that the social environment interacts with personality and plasticity is not well known and the effects of interspecific competition have been studied even less. Furthermore, there have been no studies to my knowledge that have sought to understand how interspecific competition plays a role in personality and plasticity except one study by Webster et al. (2009) that found that personality type affects the outcome of interspecific competition for food or habitat use. However, no studies have examined how interspecific competition affects individual personality and plasticity.

Chapter 2

Interspecific Competition Influences Fitness Benefits of Assortative Mating for Territorial Aggression in Eastern Bluebirds (*Sialia Sialis*)[1]

Abstract

Territorial aggression influences fitness and, in monogamous pairs, the behavior of both individuals could impact reproductive success. Moreover, territorial aggression is particularly important in the context of interspecific competition. Tree swallows and eastern bluebirds are highly aggressive, secondary cavity-nesting birds that compete for limited nesting sites. We studied eastern bluebirds at a field site in the southern Appalachian Mountains that has been recently colonized (< 40yr) by tree swallows undergoing a natural range expansion. The field site is composed of distinct areas where bluebirds compete regularly with tree swallows and areas where there is little interaction between the two species. Once birds had settled, we measured how interspecific competition affects the relationship between assortative mating (paired individuals that behave similarly) and reproductive success in eastern bluebirds. We found a strong tendency toward assortative mating throughout the field site. In areas of high interspecific competition, pairs that behaved the most similarly and displayed either extremely aggressive or extremely non-aggressive phenotypes experienced higher reproductive success. Our data suggest that interspecific competition with tree swallows

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may select for bluebirds that express similar behavior to that of their mate. Furthermore, animal personality may be an important factor influencing the outcome of interactions between native and aggressive, invasive species.

Introduction

Quantifying consistent individual differences in behavior across different spatial and temporal contexts [1, 2] may be important to understanding how ecological and evolutionary forces shape populations, communities, and ecosystems [3]. To explore ecological processes, the contribution of individuals to the overall function of populations within an integrated ecosystem must be considered [4]. Individual behavior dictates how individuals interact with their environment, and in turn, affects how other individuals or species respond to their environment. Moreover, interspecific competition has implications for community and population structure [5], character displacement [5], settlement patterns [6], and invasiveness or susceptibility to invasions [7], while individual behavior influences reproductive output and survivorship [8-12].

Boldness to predators, exploratory behavior, and territorial aggression, are a few traits used to quantify individual differences in behavior. However, the "shy-bold continuum" [1, 13] and exploratory behavior [9, 14-18] are well studied, while territorial aggression as a repeatable trait is discussed less often in the literature [but see 19-23]. Indeed, aggression – defined as behavior directed toward individuals that are intended to or have the capacity to harm or intimidate an individual [24] – is ecologically important due to its inherent risk of injury [21] and/or death [10]. Yet the implications of aggression for reproductive success can vary with species, local environment, and life-

history tradeoffs [22, 25-29]. Few studies have examined relationships between interspecific competition and the expression of consistent individual behavior. One exception is Webster et al.'s [5] study of two species of sticklebacks (*Gasterosteus sp.*), which demonstrated that individual boldness affects the outcome of interspecific competition for resources. Instead, most research has focused on the effects of individual behavior on the outcome of intraspecific contests. For example, Rosvall [20] and Cain & Ketterson [30] found that more aggressive individuals are more competitive and have higher reproductive success.

Monogamous birds generally defend breeding territories and aggression is an important component to territorial defense. For obligate secondary cavity-nesting birds (i.e. those that do not excavate their own nesting cavities), nest sites are limited [31], especially in human-altered landscapes [32]. As a consequence of competition for nesting cavities, both males and females of many secondary cavity-nesters are extremely aggressive [33-35]. Moreover, biparental care is the norm and parents often experience tradeoffs between territorial aggression and parental care. Individuals that devote a great deal of time and energy to parental effort may do so at the cost of territory and nest defense [19, 36], and thus may allow intruders to usurp nesting cavities [37]. Yet, extremely aggressive nest defense behavior can lead to insufficient parental care [19]. It stands to reason that, in species with biparental care of young, the behavior of both parents can influence reproductive success [reviewed in 38]. When choosing mates, individuals may mate assortatively or disassortatively for behavioral traits. In disassortative pairs, members may exhibit a sort of division-of-labor that leads to increased performance or rear young that exhibit an intermediate behavioral phenotype

that leads to high survivorship [8]. In assortative pairs, members may cooperate more efficiently and thus experience mutual reproductive benefits [38]. For example, great tit (*Parus major*) pairs that display similar and extreme exploratory behavior produce the highest-quality offspring [9]. Currently, the definition of assortative mating is unclear. The term assortative mating implies that paired mates choose their partners based on particular traits [39]. However, because researchers rarely measure behavioral traits prior to pairing, assortative mating is often defined as similar behavior among mated pairs [9, 12]. Here, to simplify wording, we refer to assortative mating as the pattern of mated pairs in a population [39-41].

Eastern bluebirds (*Sialia sialis*) are a secondary cavity-nesting species that exhibits repeatable aggressive behaviors in the face of simulated territorial intrusions (STIs) and there is a large amount of variation in territorial aggression within populations [23]. Eastern bluebirds have a wide geographic range that covers nearly all of the eastern United States from central Ontario south to central Texas [33]. Throughout this range, bluebird populations face very different environmental constraints and challenges. For example, bluebirds that breed in northern regions compete with tree swallows (*Tachycineta bicolor*) for nest cavities while bluebirds breeding in more southern locations do not [33, 34]. Indeed our field site is a mosaic of distinct areas where bluebirds compete with tree swallows for nesting cavities and areas with little interaction between the two species. Eastern bluebirds and tree swallows act aggressively toward one another [33, 34, 37] and the result of competition between the two species is often eviction of the bluebird pair from the nest-box [37, Harris, pers. obs.]. In this system it seems that as the breeding season continues, interspecific competition from tree swallows

has a larger effect on breeding bluebirds than does intraspecific competition. Intraspecific competition certainly has a large effect on settlement in bluebirds [42], but once bluebirds have established nesting territories aggressive interactions are rare [Harris pers. obs.]. For example, at our field site once bluebirds have begun nesting, we have not documented nest usurpation by other bluebirds, but 15% of bluebird nests were usurped by tree swallows. Swallows occur in high densities, are aerial foragers that generally forage within 300 m of their nest, unmated 'floaters' are common and this species readily mobs other species [34].

Here we examine whether interspecific competition with tree swallows influences the relationship between territorial aggression and reproductive success in eastern bluebirds. First, we explore whether individuals within bluebird pairs are mated assortatively for territorial aggression (mated males and females demonstrate similar responses to simulated territorial intrusions). Second, we quantify how interspecific competition influences the relationship between assortative mating for territorial aggression and reproductive success.

Methods

Ethics Statement

This study was carried out in strict accordance with the recommendations in the guide for the Care and Use of Animals for Research, Teaching, or Demonstration provided by Appalachian State University through the Institutional Animal Care and Use Committee (IACUC). The methods were approved by IACUC at Appalachian State University (permit number: 12-09). All animals were handled in such a way to reduce

stress and avoid physical harm. Research was conducted under North Carolina State and U.S. Fish and Wildlife permits. All adults were released in their home territory and nestlings returned to their nest-boxes. We had permission from all landowners.

General Field Methods

We studied eastern bluebirds breeding in Watauga County, NC during the 2012 breeding season. We monitored egg laying, hatching, and fledging success of eastern bluebirds and tree swallows. In all bluebird nests, we measured mass (± 0.1g) of nestlings at age 14 days (hatch day = day 1). From the time they hatch until they are about 11 days old, nestlings increase rapidly in mass, but by age 13 days, the mass of nestlings begins to asymptote [43] and nestlings fledge between age 15 and 21 days [33]. Hence, the mass of nestlings 14 days after hatching is an accurate estimate of fledgling mass. Nestling mass is an important measure of reproductive success in birds because, in many species, nestling condition is positively related to the probability of becoming a recruit in the following breeding season [44]. Therefore, we used the number of fledglings and the mass of nestlings at age 14 days as two proxies of reproductive success. We captured breeding bluebirds and fitted them with an aluminum, numbered USGS band and three plastic colored leg bands to facilitate subsequent identification.

Determining the Distribution of Interspecific Competition

The field site included five distinct spatial clusters of nest-boxes, hereafter referred to as ‘zones’. We defined zones as areas where nest-boxes were < 0.50 km apart (mean = 0.15 km) while zones were > 1 km apart (mean = 1.32 km). We created a map

of the field site in Google Earth [45] and placed 300m radius buffers around each bluebird nest to calculate the local density of tree swallow nests within each buffer during the 2012 breeding season. From this, we calculated the mean density of tree swallow nests per zone [46]. Tree swallows normally forage within 300 m of their nest-box so a 300 m radius buffer from a bluebird nest should encompass the area where interspecific interactions are likely to occur [47].

Aggression Trials

We conducted simulated territorial intrusions (STIs) to measure territorial defense aggression at each eastern bluebird nest (n = 63). STIs were conducted during late incubation (day 10-14) for all birds and again during nestling rearing for a subset of parents (n = 17 pairs). We used live caged male and female bluebirds as stimulus models due to their availability at the beginning of the field season. Western bluebirds do not differ in their reaction to bluebirds or tree swallows, so we feel the use of a conspecific model represents a comparable territorial intrusion for a general measure of territorial aggression [19]. The models were captured > 30 km from the field site. We simultaneously placed one male and one female captive bluebird in separate cages 1 m from the focal pair's nest-box and broadcasted bluebird vocalizations ('chatter'). We quantified aggressive behavior separately for male and female bluebirds. Before beginning the trial we visually searched the territory to confirm that the breeding pair was in the area. Once a focal bird responded (male or female chattered or moved toward the intruders), we observed behavior for 10 minutes. Although bluebirds rarely dove or physically attacked the model, most landed on the intruder's cage. We calculated

aggression as the latency time (seconds) from the start of the trial until each focal bird landed on the cage of the same-sex conspecific intruder. The time it takes an individual to respond to an STI likely has ecological importance so the total time from the start of the trial until landing on the cage was used. The longest trial conducted lasted 23 minutes because it took the focal pair 13 minutes to respond to the intrusion. Thus, if a bird did not land within 10 minutes after responding, they were given a score of 1400 seconds.

Statistical Methods

All statistical tests were performed using SPSS v.20 statistics software [48]. For the subset of birds that experienced STIs twice, we examined repeatability of aggressive response using intraclass correlations [49]. We also used intraclass correlations to determine whether mated pairs behaved similarly.

To elucidate differences in the amount of interspecific competition between the zones we used a univariate analysis of variance (ANOVA) with tree swallow density as the dependent variable and zone as the fixed factor. To test the effect of parental behavior and of interspecific competition on nestling quality and reproductive output, we used two general linear mixed models (GLMM). In each model, nest ID was the random factor, male and female behavior were covariates, and the level of interspecific competition (high and low) was the fixed factor. Furthermore, because nestling sex, brood size and hatch date could influence reproductive output, these variables were also included in the original models. We used a stepwise backward procedure for simplification of the mixed models and tested interactions between the fixed factors and covariates. We also used a GLMM to investigate the difference in nestling mass between high and low competition

sites. Also, to determine the effect of parental behavior on reproductive output we used a univariate analysis of covariance (ANCOVA). The ANCOVA included number of nestlings fledged as the dependent variable, male and female behavior as the covariates, and hatch date and competition level as fixed factors.

Results

Distribution of Interspecific Competition

The average (± SD) tree swallow densities, measured in nests/territory (n/t – 300m radius buffer) were as follows: zone 1 = 4.16 n/t ± 1.74; zone 2 = 1.72 n/t ± 0.88; zone 3 = 1.25 n/t ± 0.97; zone 4 = 6.71 n/t ± 1.51; zone 5 = 4.00 n/t ± 2.00. The overall ANOVA revealed a significant effect of zone on tree swallow density ($df = 4$, $F = 29.46$, $p < 0.001$) and Fisher's LSD post-hoc tests revealed that zones 2 and 3 had significantly lower tree swallow densities compared to zones 1, 4, and 5 (all $p \leq 0.001$). Zone 4 had significantly higher density than any of the other 4 zones (all $p < 0.001$), but we categorized zones 1, 4, and 5 together as 'high competition' sites because densities were all significantly higher than zones 2 and 3. Therefore, zones 2 and 3 were categorized as 'low competition' sites.

Repeatability

Female eastern bluebirds exhibited significantly repeatable aggression ($df = 15$, *intraclass correlation* = 0.69, $p = 0.02$). However, male aggression was not significantly repeatable ($df = 16$, *intraclass correlation* = 0.159, $p = 0.37$).

Assortative Mating for Territorial Aggression

There was a significant positive relationship between the aggression of paired males and females ($df = 62$, *intraclass correlation* = 0.69, $p < 0.001$). Moreover, individuals within a pair behaved similarly (assortative mating) in both low ($df = 25$, *intraclass correlation* = 0.69, $p < 0.001$) and high competition sites ($df = 22$, *intraclass correlation* = 0.54, $p = 0.001$).

Effect of Assortative Mating on Number of Fledglings

Competition, male, or female aggression did not influence the number of nestlings fledged (*male aggression:* $df = 1$, $F = 0.13$, $p = 0.72$; *female aggression:* $df = 1$, $F = 1.24$, $p = 0.28$; *competition:* $df = 1$, $F = 0.65$, $p = 0.80$). Further, we found no significant interactions between any independent variables (all $p > 0.3$).

Effect of Assortative Mating on Fledgling Size

Brood size ($df = 23.25$, $F = 0.35$, $p = 0.71$), nestling sex ($df = 90.34$, $F = 0.32$, $p = 0.57$), and hatch date ($df = 22.19$, $F = 0.23$, $p = 0.64$) did not contribute significantly to the model of fledgling mass and were therefore excluded from further analyses. We found a significant interaction between competition level*male aggression*female aggression on nestling mass ($df = 33.41$, $F = 15.37$, $p < 0.001$). Because of this interaction, we split the dataset by high and low competition sites. In areas of low interspecific competition, we found no significant interaction between male and female aggression on nestling mass ($df = 14.56$, $F < 0.01$, $p = 0.94$). Further, neither male nor female aggression significantly affected nestling mass (Male aggression: $df = 14.69$, $F =$

0.11, $p = 0.75$; Female aggression: $df = 13.60$, $F = 0.11$, $p = 0.92$). However, in areas of high interspecific competition, we found a significant interaction between male and female aggression on nestling mass ($df = 13.91$, $F = 41.22$, $p < 0.001$).

Because of the significant interaction between male and female behavior on nestling mass in the high competition dataset, we categorized male aggression into three groups: 1) most aggressive third of males, 2) middle third of males, and 3) least aggressive third of males [8]. We then ran separate models for each category of male behavior. Pairs that were mated assortatively on the extremes for aggression produced the heaviest nestlings (Fig. 1). When mated to highly aggressive males, female aggression was significantly positively related to nestling quality ($df = 6.63$, $F = 8.30$, $p = 0.03$; Fig. 1a). When mated to males that were categorized as mid-level aggressive, female aggression did not significantly affect nestling quality ($df = 3.50$, $F = 4.25$, $p = 0.12$; Fig. 1b). However, when mated to low-aggression males, female aggression was significantly negatively related to nestling quality ($df = 3.94$, $F = 10.51$, $p = 0.03$; Fig. 1c). These data demonstrate that in high competition areas of the field site, pairs that show similar and the most extreme levels of aggression rear the heaviest offspring.

Overall, bluebird pairs in areas of low interspecific competition reared heavier nestlings compared to bluebird pairs that nested in areas of high interspecific competition ($df = 133$, $t = 2.71$, $p = 0.008$).

Discussion

Eastern bluebirds and tree swallows compete fiercely for nesting sites in some areas of our field site while, in other areas, competition is rare. Bluebird nestlings appear to suffer from competitive interactions with tree swallows because, at high-competition sites, nestlings are smaller at fledging age. When facing competition with tree swallows, pair similarity in aggression appears to strongly influence pair reproductive success; pairs that displayed similar and extreme responses to STIs fledged heavier offspring (see also Fig. 2 for a schematic overview). However, the total number of offspring fledged was not affected by parental behavior. This may be because we found little variation in brood sizes; 92% of pairs had broods of 3, 4, or 5 nestlings. Moreover, 'brood reduction', or the death of some nestlings within a brood, was rare (9.3% of broods). We also found evidence of assortative mating in all areas of the field site. It may be that the fitness benefits for assortative mating in the face of strong competition leads to the persistence of assortative behavior throughout the population.

Our data show fitness benefits for assortative pairs in high competition environments. This may be especially important in cavity-nesting species where defending a nesting cavity is extremely important and both sexes participate in nest defense. Great tit parents with similar personality types also produce higher quality young [9]. This relationship may occur because, when two highly aggressive birds mate, they are able to defend higher quality territories [9]; indeed, aggressive individuals have been shown to be more successful at securing high-quality nesting sites in a number of avian species [20, 50-53]. At the other end of the spectrum, pairs of great tits comprised of two non-aggressive individuals forage more efficiently even in lower quality habitats

[14]. Our data, however, differ from those of Both et al. [9] in that the advantage of assortative mating was only obvious when bluebirds experienced high levels of interspecific competition with tree swallows. Because we conducted this study on populations using artificial nest boxes, our results are likely conservative. In populations where breeding birds occupy natural nesting cavities, interspecific competition is more intense than in box nesting populations [54]. Our study may provide insight into how assortative mating became widespread in bluebirds and similar trends may be expected to occur in other cavity nesting species as well.

An alternative explanation for the relationship between assortative mating and offspring quality is that parents with similar personalities may be better at coordinating parental care duties. Coordination of parental care behavior is important for success in birds that exhibit biparental care [55]. Spoon et al. [56] found that pairs of cockatiels (*Nymphicus hollandicus*) that behaved similarly coordinated incubation more efficiently leading to higher reproductive success. If bluebird pairs that behave similarly are better able to coordinate nestling provisioning, this may be particularly adaptive in a high competition environment where parents might need to invest more energy into defending the territory. Indeed, Meek and Robertson [57] found that in locations where male bluebirds spent more time defending the nest against tree swallows, they were less diligent in guarding their fertile mates. Trade-offs in energy investment may have a similar effect on parental provisioning rates. Perhaps when tree swallows harass bluebirds, a coordinated aggressive response by bluebird pairs allows them to spend less time defending the nest and more time provisioning young. A study of how competition

influences the coordination of parental care and, in turn, how parental coordination influences offspring fitness would be helpful.

Many species mate assortatively for personality traits including great tits [58], zebra finches, *Taeniopygia guttata* [12], Stellar's jays, *Cyanocitta stelleri* [59], bridge spiders, *Larinioides sclopetarius* [60], dumpling squids, *Euprymna tasmanica* [61], convict cichlids, *Cichlasom nigrofasciatum* [62], and humans [reviewed in 38], while white-throated sparrows, *Zonotrichia albicollis,* tend to mate disassortatively for aggression [63]. It may be that assortative mating for personality plays a role in sexual selection; however, it is difficult to know if the behavior of the individual changes after mating or if behavior is consistent and personality is an important criteria for mate choice. In this study, we measured territorial aggression, which may be a component of personality, but individuals in a pair that behave similarly may be simply responding to one another. In a captive setting where paired males and females were tested separately for boldness and exploratory behaviors (and where territorial aggression is not possible to measure), paired individuals did not display similar exploratory behaviors (Morris & Siefferman unpub. data). However, our study seeks to understand the consequences of individual behavior in an ecological setting. The way individuals behave in the presence of mates accurately reflects their behavior in natural conditions during the breeding season.

In this study, we demonstrated that female eastern bluebirds exhibit consistent territorial aggression while males do not. This sex difference in the consistency of aggressive response is similar to findings in an Oklahoma population of bluebirds [23]. These data suggest that if individuals are adjusting their behavior to match that of their

mate, males might be adjusting more than females. However, this explanation is speculative because we do not know the behavior of the bluebirds before mate selection occurs. Nonetheless, there is widespread evidence for the benefits of assortative behavior suggesting it is an important component of fitness in many species [38].

One important limitation of our dataset, however, is that our proxy of fitness is limited to what can be measured at fledging (number and size of offspring). We do not yet understand how assortative mating for territorial aggression or how an individual's level of aggression influences survivorship during the adult or juvenile stages. In other species, the benefits of particular personality traits lead to tradeoffs between survival and reproductive success [1, 10]. Ultimately, such trade-offs may maintain behavioral variation within a population.

The results we documented at the front of a natural range expansion demonstrate how new selection pressure can influence the fitness consequences of assortative mating. Tree swallows are extending their range southward [64] and have been in the NC study area < 40 years [65] and from the perspective of bluebirds, are a highly aggressive invasive species. Invasive species are often more aggressive than native species [66, 67] and that could determine the success of invasions. One recent example is the endangered gouldian finch, *Erythrura gouldiae*, which is being out-competed by the more aggressive long-tailed finch, *Poephila acuticauda* [66]. As more invasive species are being introduced throughout the world, it is important to understand how aggression and other components of personality are affected and/or affect the outcome of competitive interactions. Animal personality has been largely overlooked in invasive species research, to date, despite its

importance [7]. Our data shed light on how interspecific competition with aggressive invasive species exerts selection pressure on a less-aggressive, resident species and have far-reaching application toward understanding how behavior affects the vulnerability of species to invasions.

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Figures

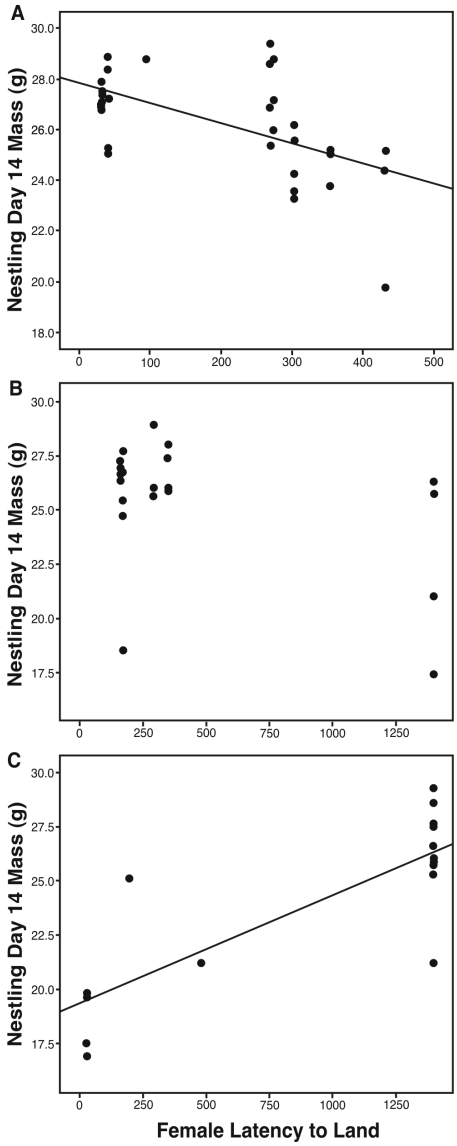

Figure 1. Effect of pair similarity on nestling quality (day 14 mass) in high competition sites. The graphs are split into groups for a) the most aggressive 3rd of males, b) the middle 3rd of males, and c) the least aggressive 3rd of males. Aggression in measured as the latency to land on a simulated territorial intruder's cage.

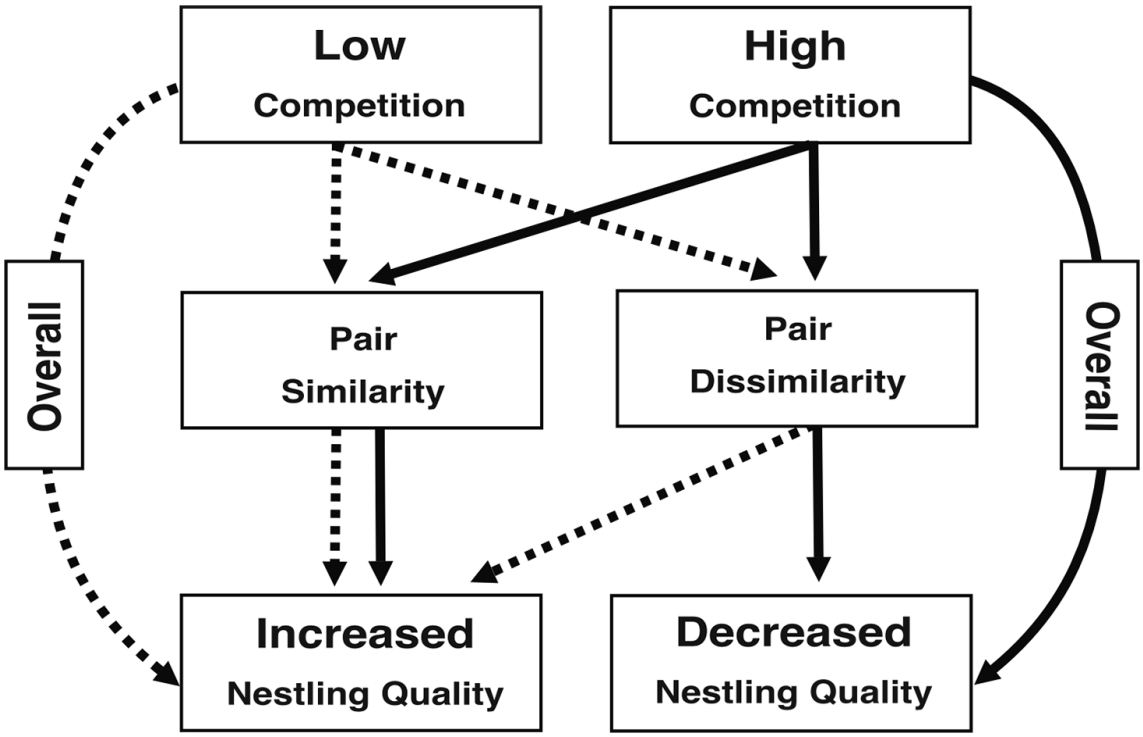

Figure 2. Overview of the effect of assortative mating on nestling quality. Solid lines represent high competition and dashed lines represent low competition environments. In either environment, pairs can either behave similarly or not. Our results suggest that nestling quality is higher in low compared to high competition sites, regardless of the degree of assortative mating. Pair similarity does not have a large effect on nestling quality in low competition sites, but in high competition sites, pair similarity significantly affects nestling quality. Pair similarity in high competition sites increases nestling quality and, conversely, pair dissimilarity decreases nestling quality.

Chapter 3

Interspecific competition influences behavioral flexibility in a cavity nesting bird

Abstract

Behavioral ecologists have become captivated with the concept of animal personalities (consistent individual differences in behavior across spatial and temporal contexts) and behavioral syndromes (suites of correlated personality traits). Personalities and behavioral syndromes have demonstrated adaptive value, yet the methods used to measure personality traits vary drastically from study to study. Most studies of animal personality have been conducted in controlled laboratory settings during the non-breeding season; however, field-based measures of behavior during the breeding season may better indicate how the environment shapes the expression of personality or plasticity. Here, we examined the repeatability of territorial aggression and boldness to predators and investigate correlations between these behaviors in heterogeneous environments. The field site consists of a mosaic of patches where eastern bluebirds compete with tree swallows and areas of little interaction between the two species. Our data reveal sex specific repeatability of territorial aggression and behavioral correlations in areas of low interspecific competition, suggesting that selection pressures differ because of divergent life-history strategies in male and female eastern bluebirds. We also found that intense interspecific competition reduces the consistency of territorial aggression and leads to a breakdown in behavioral correlations among traits, suggesting

that environmental heterogeneity reveals behavioral flexibility. *Key words*: Eastern bluebird, tree swallow, heterospecific competition, heterogeneous environment, stochastic environment, environmental predictability, plasticity, personality, behavioral syndrome, temperament.

Introduction

Animal personality, or consistent individual differences in behavior across spatial and temporal contexts, is currently a fertile topic in behavioral ecology. Recently, a plethora of studies have focused on how individuals exhibit personalities and on describing suites of correlated behaviors ("behavioral syndromes") within populations (reviewed in Sih and Bell 2008). Investigations of the evolution and expression of animal personalities and behavioral syndromes are often conducted in controlled laboratory conditions to reduce the likelihood that the environment influences behavior (Archard and Bratihwaite 2010). However, G.E. Hutchinson (1965) taught the biological community that the evolutionary play occurs within the ecological theater; therefore controlling the environment may lead to results that are not indicative of real-world behavior.

In many cases, behavior is controlled by gene x environment interactions, thus both personality and plasticity can be products of evolutionary processes (Sih et al. 2004; Carere et al. 2005; Dingemanse et al. 2009; Reddon 2011). However, environmental variables likely influence the expression of personality or plasticity and the relationship between the two traits (Bell 2005; Sih and Bell 2008; Evans et al. 2010; Scales et al. 2011; Quinn et al. 2012). Therefore, environmental variation may shape individual

behaviors over evolutionary (Sih et al. 2004; Nussey et al. 2007; Smith and Blumstein 2008; Wolf and Weissing 2012) and immediate time scales (Dolby and Grubb 2000; Archard and Braithwaite 2010; Couchoux and Crestwell 2011), and the environmental conditions over both time scales may affect the overall expression of personality or plasticity (Mathot et al. 2012).

Consistent behavior reported in studies conducted under controlled environmental conditions may be the result of static and predictable environmental conditions. For example, individual great tits (*Parus major*) exhibit consistent feeding behavior when measured multiple times within static environments (either high or low risk of predation); however, when individuals experience both risk environments their behavior is not consistent across contexts (Quinn et al. 2012). Thus, although studies of captive animals allow for accurate measures of information such as the genetic basis of animal personality, field-based studies may be more appropriate for understanding the flexibility of personality and the conditions under which personality traits influence fitness (Archard and Braithwaite 2010).

Field-based studies of animal personality are increasing in number and are important because they allow researchers to quantify how personality traits and behavioral syndromes are expressed (or not expressed) under natural conditions (Archard and Braithwaite 2010). There is evidence for fitness benefits of both consistent behavior (Dingemanse and Reale 2005; Smith and Blumstein 2008; Schuett et al. 2010) and flexibility in behavior across environmental contexts (Nussey et al. 2007; Betini and Norris 2012); however, there may be complex interactions between personality and plasticity such that both behavioral strategies contribute to the behavioral phenotype of

an individual (Dingemanse et al. 2009; Betini and Norris 2012). For example, when male tree swallows are exposed to different environmental conditions, more aggressive individuals are better able to adjust their behavior, and yet behavioral flexibility has a greater impact on fitness among the less aggressive males (Betini and Norris 2012).

Many studies have avoided measuring personality and behavioral syndromes during the breeding season, perhaps because the behavior of the focal animal could be influenced by the behavior of their social mate (Benskin et al. 2002; Malloy et al. 2005). Moreover, the interaction of the behavior of both individuals within a pair can influence fitness, especially in species that exhibit biparental care. In such mating systems, it seems logical that the coordination of behavior among parents would be important; indeed, positive assortative mating for behavior can lead to higher reproductive success (Verbeek et al. 1994; Budaev et al. 1999; Both et al. 2005; Sinn et al. 2006; Spoon et al. 2006; Harris and Siefferman 2014).

Despite the fact that pair similarity in behavior can contribute to reproductive success, little research has focused on differences between the sexes in personality and plasticity. Studies focusing on sex differences in personality have uncovered differences in behavioral repeatability in different social contexts (Aragon 2010; Schuett and Dall 2009; Piyapong et al. 2009) and across ontogeny (Hedrick and Kortet 2011). These studies suggest that the sex-based behavioral differences are likely linked to differences in life-histories of males and females, but this has not been empirically tested. Even fewer studies have examined how the expression of behavioral syndromes differs between the sexes. Despite genetic correlations between behavioral traits, van Oers (2005) found that the expression of behavioral syndromes changed with environmental

context and that the sexes differed in how those behavioral syndromes changed.

Variation in interspecific competition for limited resources is one example of social environmental heterogeneity that could influence the expression of animal personality, yet it has rarely been explored. Instead, most research has focused on relationships between personality and the outcome of intraspecific contests (Rosvall 2008; Cain and Ketterson 2012). An exception is the Webster et al. (2009) study of two species of sticklebacks (*Gasterosteus sp.*), which demonstrated that personality type affects the outcome of interspecific competition for resources or habitat use. How interspecific competition influences the expression of behavioral syndromes remains unknown.

Here, we investigate how interspecific competition between eastern bluebirds (*Sialia sialis*) and tree swallows (*Tachycineta bicolor*) influences both 1) the expression of consistency in aggression and 2) correlations between aggression and boldness in male and female eastern bluebirds. Tree swallows have been in this study site < 40 years. The field site contains areas where bluebirds compete with tree swallows and areas with little interaction between the two species. First, we quantify how interspecific competition influences the consistency of territorial aggression within individuals. Second, we test whether interspecific competition is related to the expression of correlations between territorial aggression and boldness to predators. Finally, we investigate how interspecific competition influences the overall expression aggression and boldness of eastern bluebirds.

Methods

Study Species

We studied box-breeding birds in Watauga County, NC from April-August 2012. We monitored egg laying, hatching, and fledging success of eastern bluebirds and tree swallows. Eastern bluebirds are secondary cavity nesting birds that exhibit repeatable personality traits (Burtka and Grindstaff 2013) in some parts of their range. They have a wide geographic range that covers nearly all of the eastern United States from Ontario to Texas (Gowaty and Plissner 1998). Throughout this range, bluebird populations face very different environmental constraints and challenges. For example, bluebirds that breed in the northern part of their range compete with tree swallows for nest cavities, while bluebirds breeding in more southern locations do not (Robertson et al. 1992; Lee 1993; Gowaty and Plissner 1998). For secondary cavity nesting birds, breeding cavities are limited (Newton 1994), especially in human-altered landscapes (Wiebe 2011). As a consequence of competition for limited breeding sites, both males and females of many secondary cavity nesters like eastern bluebirds and tree swallows are extremely aggressive (Robertson et al. 1992; Gowaty and Plissner 1998). In this system it seems that as the breeding season continues, interspecific competition from tree swallows has a larger effect on breeding bluebirds than does intraspecific competition. Intraspecific competition certainly has a large effect on settlement in bluebirds (Siefferman and Hill 2005), but once bluebirds have established nesting territories aggressive interactions are rare (Harris and Siefferman 2014). For example, at our field site once bluebirds have begun nesting, we have not documented nest usurpation by other bluebirds, but 15% of

bluebird nests were usurped by tree swallows. In swallow populations, unmated 'floaters' are common. Furthermore, swallows occur in high densities, are aerial foragers that generally forage within 300 m of their nest, and readily mob other species (Robertson et al. 1992).

Determining the Distribution of Interspecific Competition

The field site included five distinct spatial clusters of nest-boxes, hereafter referred to as 'zones.' We defined zones as areas where nest-boxes were < 0.50 km apart (mean = 0.15 km). All zones were separated by at least 1 km (mean difference between zones = 1.32 km). We identified 300 m-radius buffers around each nest (Google Earth; Source: Meat Camp, NC) to calculate the local density of tree swallows that could interact with each bluebird nest and then calculated the mean density per zone (Bentz et al. 2013). Tree swallows normally forage within 300 m of their nest-box so a 300 m radius buffer from a bluebird nest should encompass the area where interspecific interactions are likely to occur (McCarty and Winkler 1999). Furthermore, bluebirds and tree swallows compete fiercely for the limited nesting sites and we have documented agonistic interactions between bluebirds and tree swallows (Harris pers. obs.); therefore, higher densities of tree swallows in direct proximity to bluebirds nests likely leads to a higher occurrence of agonistic interactions between the two species.

Territorial Aggression

We conducted simulated territorial intrusions (STIs) to measure territorial defense aggression at each eastern bluebird nest (n = 52 breeding pairs) during late incubation (day 10-14) and again during nestling rearing for a subset of parents (n = 17 pairs; high competition n = 7 pairs; low competition n = 9 pairs). We used live caged male and female bluebirds as stimulus models due to their availability at the beginning of the field season. Western bluebirds do not differ in their reaction to bluebirds or tree swallows (Duckworth 2006), so the use of a conspecific model likely represents a comparable territorial intrusion for a general measure of territorial aggression. The model birds were captured > 30 km from the field site. We simultaneously placed one male and one female captive bluebird in separate cages 1 m from the focal pair's nest-box and broadcasted bluebird vocalizations ('chatter'). We quantified aggressive behavior separately for male and female bluebirds. Before beginning the trial we visually searched the territory to confirm that the breeding pair was in the area. Once a focal bird responded (male or female chattered or moved toward the intruders), we observed behavior for 10 minutes. Although bluebirds rarely dove or physically attacked the model, most landed on the intruder's cage. We calculated aggression as the latency time (seconds) from the start of the trial until each focal bird landed on the cage of the same-sex conspecific intruder. The time it takes an individual to respond to an STI likely has ecological importance. Consequently, the total time from the start of the trial until landing on the cage was used for the measure of aggression. The longest trial conducted lasted 23 minutes because it took the focal pair 13 minutes to respond to the intrusion. Thus, if a bird did not land within 10 minutes after responding, they were given a score of 1400 seconds.

Defense Against Potential Nest Predators

We conducted trials at a subset of bluebird nests (n = 25 pairs; high competition n = 10 pairs; low competition n = 15 pairs) to measure boldness of the parents to potential predators. For these trials an American crow (*Corvus brachyrhynchos*) model was suspended above the nest while we broadcasted sounds of the crow as well as nestling begging. American crows are a common predator of small birds (Verbeek and Caffrey 2002), so this model is appropriate to understand how parents react to a potential threat to the nest. Before each trial we scanned the area to ensure the presence of the focal bluebird pair. Once the focal pair responded (moved toward or made aggressive gestures) to the model, we recorded behavior for 10 minutes. The measure that we use in this study is the latency for the focal pair to approach the model crow (within 5 meters). Behavior was recorded separately for males and females. The longest trial conducted lasted 25 minutes because it took the focal pair 15 minutes to respond to the intrusion. If a bird did not land in 10 min after response, they were given a score of 1500 seconds because this was the maximum length of any trial conducted.

Statistical Analyses

All statistical analyses were performed using SPSS v.20 (IBM Corp. 2011). To test the repeatability of aggressive behavior we performed a reliability analysis (Lessels and Boag 1987) using two STI's conducted at each nest (we only measured boldness one time). To elucidate differences in the amount of interspecific competition between the zones we used a univariate analysis of variance (ANOVA) with tree swallow density as

the dependent variable and zone as the fixed factor. To test whether behavioral syndromes were present we used a univariate analysis of covariance (ANCOVA) followed by Pearson's correlations for territorial aggression and boldness to predators. In the ANCOVA, the dependent variable was boldness, the fixed factors were sex and level of interspecific competition (high vs. low), and the covariate was the first aggression trial. We tested interactions between the covariate and fixed factors. We used the first measure of aggression (instead of mean aggression) because we only sampled a subset of pairs a second time and there were very few nests where we had two measures of aggression as well as a measure of boldness (n = 7 pairs; n = 6 pairs in low competition; n = 1 pair in high competition). Aggression and boldness were not normally distributed and transformations did not affect the normality of the data; therefore, we employed Mann-Whitney U tests to look for differences in boldness and aggression in areas of high and low competition.

Results

Distribution of Interspecific Competition

The average (± SD) tree swallow densities, measured in nests/territory (n/t – 300m radius buffer) were as follows: zone 1 = 4.16 n/t ± 1.74; zone 2 = 1.72 n/t ± 0.88; zone 3 = 1.25 n/t ± 0.97; zone 4 = 6.71 n/t ± 1.51; zone 5 = 4.00 n/t ± 2.00. The overall ANOVA revealed a significant effect of zone on tree swallow density ($F_{4,73}$ = 29.46, P < 0.001) and Fisher's LSD post-hoc tests revealed that zones 2 and 3 had significantly lower tree swallow densities than did zones 1, 4, and 5 (all $P \leq 0.001$). Zone 4 had

significantly higher density than any of the other 4 zones (all $P < 0.001$), but we categorized zones 1, 4, and 5 together as 'high competition' sites because densities were all significantly higher than zones 2 and 3. Therefore, zones 2 and 3 were categorized as 'low competition' sites.

Repeatability of Behavior

Male eastern bluebirds did not show repeatable aggression across our population ($df = 16$, intraclass correlation = 0.16, $F = 1.19$, $P = 0.37$) and they were not repeatable in high- ($df = 6$, intraclass correlation = -0.15, $F = 0.87$, $P = 0.56$) or low-competition sites ($df = 8$, intraclass correlation = 0.109, $F = 1.12$, $P = 0.44$). Female eastern bluebirds demonstrated repeatable aggression across the population ($df = 15$, intraclass correlation = 0.69, $F = 3.17$, $P = 0.02$). However, females were not repeatable in aggression in high-competition sites ($df = 6$, intraclass correlation = 0.66, $F = 2.95$, $P = 0.11$) but were repeatable in low-competition sites ($df = 8$, intraclass correlation = 0.75, $F = 4.04$, $P = 0.03$).

Behavioral Syndromes

The initial ANCOVA revealed a significant effect of the interaction between competition level and aggression on boldness ($F_{1,15} = 4.12$, $P = 0.05$). To explore the interaction, we split the dataset by high- and low-interspecific competition and found a significant interaction between sex and aggression in low-competition areas ($F_{1,11} = 10.97$, $P = 0.003$). Because of the interaction in low-competition areas, we then further divided the dataset by sex and ran correlations to determine the presence/absence of

behavioral syndromes. Although we found no significant correlation between male boldness and aggression in areas of high competition ($n = 9$, $r = 0.38$, $P = 0.32$), aggression and boldness were significantly positively related in areas of low competition ($n = 14$, $r = 0.59$, $P = 0.03$). There was no correlation between boldness and aggression in females in areas of high ($n = 10$, $r = -0.10$, $P = 0.80$) or low competition ($n = 14$, $r = 0.42$, $P = 0.14$). Mean aggression and mean boldness did not differ between areas of high and low competition in males (Aggression: $n = 52$, $U = 316.50$, $P = 0.69$, Fig 2a; Boldness: $n = 25$, $U = 85.00$, $P = 0.61$) or females (Aggression: $n = 52$, $U = 349.50$, $P = 0.83$, Fig 2b; Boldness: $n = 25$, $U = 109.00$, $P = 0.06$).

Discussion

Our study site includes locations where eastern bluebirds and tree swallows compete for nesting sites and areas of low interspecific competition. The density of interspecific competitors (tree swallows) appears to influence the behavior of individual bluebirds. In areas of low interspecific competition, female eastern bluebirds exhibited consistent levels of aggressive behavior, but female aggression was not repeatable in high competition areas. Males, on the other hand, did not exhibit repeatable territorial aggression in either area, but aggression and boldness were significantly positively correlated in low, but not high, competition areas. These results suggest that the expression of aggressive and bold behaviors differ between male and female eastern bluebirds and that the environment influences the expression of behavioral traits. Our data suggest that personality traits (i.e., repeatable behaviors and behavioral syndromes) as expressed by wild breeding animals may be more readily apparent in more consistent

environmental conditions. The repeatability of behavioral responses and correlations among behavioral traits that are generally used to represent animal personality are only apparent when bluebirds do not coexist with high densities of tree swallows.

In high competition sites, tree swallows appear to create an environment that induces variation in behavior among individual bluebirds. Other studies have shown similar effects (changes in the expression of behavioral syndromes) when comparing personality measures in populations of animals breeding in different environments (Evans et al. 2010; Scales et al. 2012; Bókony et al. 2013; Royauté et al. 2014). However, because our field site is a mosaic of areas of high and low interspecific competition, we can assume that the breakdown of consistent behaviors and the correlation between aggression and boldness is likely due to flexibility in the expression of traits in response to the environment rather than differential selection pressures associated with different populations (i.e., genetic changes). Snekser et al. (2009) suggest that correlations between two flexible behaviors (behavioral syndromes) are likely a result of environmental conditions rather than genetic linkages. Indeed, behavioral syndromes are not always genetically based and the degree to which behavioral syndromes have a genetic basis may vary between populations of the same species (Bell 2005).

Dingemanse et al. (2004) suggest that the environment plays a role in selection for personality types and/or flexibility versus consistency in behavior. The new (< 40 yrs), stressful environment associated with intense interspecific competition seems to be a strong force shaping the behavioral phenotype of bluebirds in our population. In rapidly changing or variable environments, behavioral plasticity should be advantageous and

therefore behaviors that correlate well in stable environments may not be correlated in less stable environments because either one or both behaviors are flexible and respond to environmental change (Snekser et al. 2009).

In this study, male bluebirds exhibited significant and positive correlations between aggression and boldness in areas of low, but not high, competition areas. Tree swallows are highly aggressive interspecific competitors and, periodically, invade eastern bluebird territories (Harris pers. obs.). Therefore, swallows may cause male bluebirds to exhibit aggressive behavior that is artificially heightened directly after a territorial intrusion, similar to how testosterone levels increase dramatically after aggressive interactions (Winglfield et al. 1987). High competition areas at the field site therefore represent a stressful social environment in which the social environment is both temporally and spatially heterogeneous that likely makes it difficult for bluebirds to predict when territorial intrusions will occur, the level and intensity of the intrusion, and from where they may come. In the presence of high densities of tree swallows, we might also expect to find that bluebirds tend to respond to our behavioral assays more aggressively or with increased boldness, but our data do not support this. On the other hand, it may be that our behavioral assays really only show us snapshots of male behavior. For example, we may have tested some males immediately after a swallow territorial intrusion and tested others after longer periods without an intrusion. Indeed, variation in male aggression was higher in areas of high competition compared to areas of low competition (Figure 2). If high competition areas represent heterogeneity or unpredictability of the social environment and environmental stochasticity leads to changes in sampling behavior (Mathot et al. 2012), then we can infer variable

environmental conditions lead to variable behavior as well. Together, these data suggests that behavior, or correlations between different behaviors, may be context dependent.

Eastern bluebirds in areas of high interspecific competition likely experience variable social environments due to common, but temporally intermittent, interspecific aggression from highly active tree swallows. Although nesting eastern bluebirds are likely aware of the presence of tree swallows in the surrounding area, some degree of uncertainty about the social environment likely remains because individuals have limited ability to continually assess and retain social information (Mathot et al. 2012) and because the interactions with tree swallows vary both temporally and spatially. While uncertainty about environmental conditions may affect selection for personality traits or personality dependent plasticity (Mathot et al. 2012), there may also simply be an effect of stochastic environments on the level of behavioral consistency. Thus what researchers interpret as differences in consistency may be the result of recent social events that cause short-term changes in behavior (Figure 3).

When studying box-nesting birds, it can be difficult to place nest boxes so as to mimic natural levels of competition for cavities. In the wild, availability of nesting cavities likely varies tremendously both temporally and spatially (Robertson and Rendell 1990). It may be that areas of our field site that we label as 'high competition' represent natural competition environments. Indeed, in communities that occupy natural nesting cavities, cavities tend to be rare and interspecific competition for nesting cavities is high (Robertson and Rendell 1990). The relatively unlimited availability of nesting sites in the low competition areas likely reduces both intra and interspecific competition for nesting sites initially, but higher offspring recruitment in future years should increase

intraspecific competition; however, our data demonstrate no evidence that intraspecific densities differ across the field site, and intraspecfic interactions are rare after territory establishment (Harris and Siefferman 2014). Therefore, it may be that areas with low interspecific competition better approximate laboratory (i.e., consistent) conditions and allow us to detect repeatable aggression and correlations between aggression and boldness. Perhaps, in the wild, these artificially low interspecific competition sites are not representative of the competitive environments that past generations have experienced. Therefore, the effects we measured at our low competition sites may be the result of reduced interspecific competition compared to populations occupying natural cavities. If stochastic environments lead to changes in behavior (Mathot et al. 2012) (which researchers perceive as behavioral flexibility), then studying animals in artificially consistent environments may lead researchers to conclude that behaviors are more consistent than they would be in more 'natural' environments (Figure 3). Thus, studying animals breeding in artificial nesting cavities that experience low competition environments may limit researchers' understanding of animal personality. Additionally researchers studying box-nesting species might be creating unnaturally low competition environments and could be inducing artificial selection for individuals that exhibit behavior with lower adaptive value.

Our data also demonstrate some interesting sex differences in the expression of aggression and boldness in eastern bluebirds. In the low competition sites, females, but not males, expressed repeatable territorial aggression. We suggest that the lack of repeatable behavior in males may be due to the differing roles of males and females during the breeding season. While socially monogamous, approximately 20-30% of

offspring are fathered by extra-pair males (Gowaty and Plissner 1998). Thus, male eastern bluebirds can increase fitness by investing more diligently in parental care or by seeking extra-pair mates while females tend to invest more energy in the current brood (Siefferman and Hill 2008). This greater flexibility in male behavior may be driven by selection pressures for sex-specific reproductive strategies. Furthermore, because our measurements of behavior include boldness to a potential predator and territorial aggression, there may be more variability in male behavior because males often assume more of a role in territorial defense than do females (Gowaty and Plissner 1998). Indeed, a food supplementation environment increased the repeatability of male behavior at our field site, but also increased the boldness of predator mobbing behavior that is consistent with the expectation that parents would increase investment in valuable offspring (Siefferman L, Doyle A, Harris MR, pers. obs.). Furthermore, assortative mating for behavior among eastern bluebirds leads to higher reproductive success in areas of high interspecific competition (Harris and Siefferman 2014); we suspect that males adjust their behavior to match that of their mate. Together, these data suggest that flexibility in behavior and the ability to respond to environmental conditions is an adaptive strategy of male eastern bluebirds during the breeding season.

Here, we provided evidence that the sexes differ in their behavioral strategies likely due to differences in the reproductive roles of socially monogamous eastern bluebirds. Our data further suggest that selection on behavior may act upon individuals differently depending on the intensity of interspecific competition experienced by each individual. High interspecific competition may better represent natural conditions (Robertson and Rendell 1990); there may be substantial differences in what researchers

focusing on animal behavior are measuring in natural field (i.e., unstable) versus artificial nest boxes (i.e., more stable). Moreover, one can expect an even greater difference in results measured in wild (i.e., unstable) versus laboratory (i.e., stable) conditions. Indeed, most studies of animal personality have occurred in laboratory settings under static environments (reviewed in Archard and Braithwaite 2010) and behaviors are usually measured outside of the breeding season. Future studies should follow the same animals in both the laboratory and field to attempt to disentangle the differences in behavior that occur in laboratory and field conditions. This approach should lead to the understanding of the true nature of personality/flexibility and behavioral syndromes and how these behaviors may vary depending on season or environmental stability.

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Figures

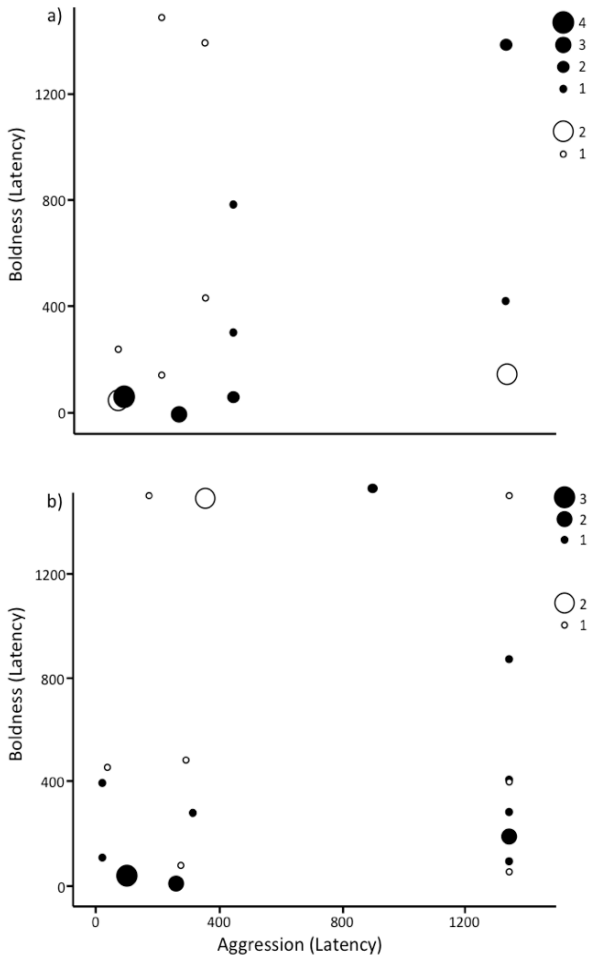

Figure 1: Scatterplot of the relationship between boldness and aggression in a) male and b) female eastern bluebirds (closed circles = low competition, open circles = high competition). The points are scaled by density of points so that overlapping points are visible. The scale at the right indicates the number of data points represented by different sized circles. Lower values for boldness and aggression = more bold/aggressive individuals.

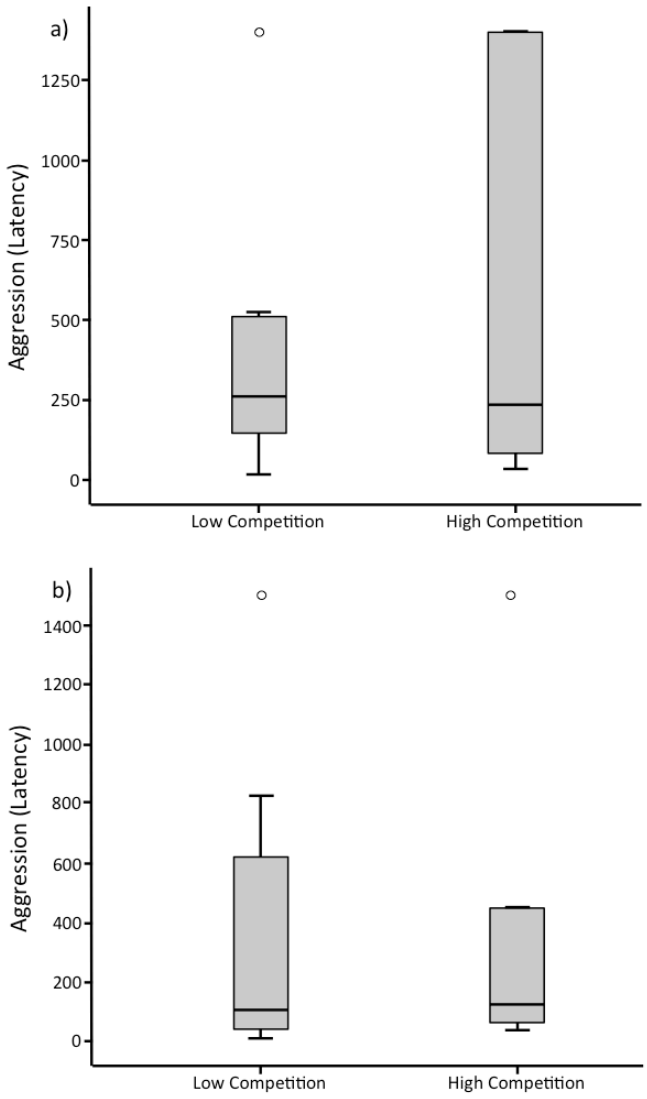

Figure 2: Boxplots of a) male and b) female aggression in high and low competition (measured as latency to approach the model crow). Note that there is more variation in male aggression in areas of high competition with tree swallows. The boxes represent the 25^{th}-75^{th} percentile, the whiskers represent the 10^{th}-90^{th} percentiles, and the line in the box represents the median. Circles represent one standard deviation away from the mean.

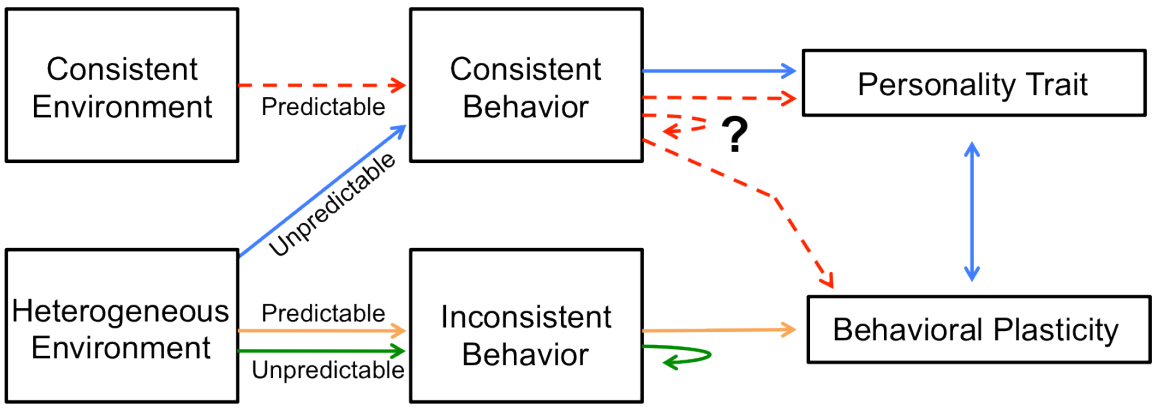

Figure 3: Conceptual diagram showing the proposed relationship between environmental consistency, heterogeneity, predictability, and the expression of personality or plasticity. The blue lines represent the lineage of what can be deemed "personality" or "behavioral syndromes." The dashed, red lines represent the proposed relationship between environmental predictability and the interpretation of behavioral consistency. The orange lines represent the relationship between heterogeneous environments and behavioral plasticity if individuals can accurately assess environmental conditions. The green lines represent the relationship between heterogeneous environments and behavioral inconsistency if individuals cannot accurately predict environmental conditions. Behavioral plasticity means that flexibility in behavior should be adaptive; therefore, the interpretation of consistent individual behavior measured in consistent environments could be a personality trait, individual behavioral plasticity (if flexibility gives the individual an advantage) that is masked by the consistent environment, or inconsistent individual behavior that is masked by the consistent environment.

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Vita

Morgan R. Harris was born in Havelock, North Carolina in 1989. He attended elementary, middle, and high school in Havelock, North Carolina. He graduated from Havelock High School in 2008, where he played Football, Baseball, and ran Cross Country. In August 2008, he enrolled at Appalachian State University and was awarded a Bachelor of Science degree in Environment Biology/Ecology with a concentration in Landscape Ecology in May 2012. In August 2012, he was awarded a teaching assistantship in the Biology Department at Appalachian State University, where he earned a Master of Science degree in Biology in May 2014. Morgan has accepted a position with the Kaua'i Endangered Seabird Recovery Program in Kaua'i, HI.