

POTENTIAL EFFECTS OF AGGRESSION, SITE, AND PROXIMATE DETERMINANTS
THAT FACILITATE TREE SWALLOW RANGE EXPANSION

A Thesis
by
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Abstract

POTENTIAL EFFECTS OF AGGRESSION, SITE, AND PROXIMATE DETERMINANTS THAT FACILITATE TREE SWALLOW RANGE EXPANSION

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Individuals within and among populations have developed behavioral strategies and physiological mechanisms such as aggression and hormonal plasticity that facilitate dispersal. Breeding range expansion occurs when individuals disperse to novel environments over successive breeding seasons and it is expected that both range expanding and native species will be affected. Dispersers are challenged with successfully colonizing new areas that may have varying abiotic and biotic environments (competition, predation, food, and weather). Additionally, native species can experience increased agonistic interactions and competition for limited resources, but they may be able to adapt by adopting behaviors such as increased aggression. Currently, tree swallows, *Tachycineta bicolor*, are undergoing a range expansion to the southeastern US, possibly as a result of decreased habitat availability in the Northeast and an increased number of nestboxes throughout the South. In Chapter 2, I investigate the effect expansion may have on a native species of eastern

bluebird, *Sialia sialis*, by comparing territorial defense behavior of bluebirds currently experiencing the tree swallow range expansion (North Carolina) and a more southern bluebird population that is not yet living in sympatry with tree swallows (Alabama). I found that, in NC bluebirds often have their nestboxes usurped by the tree swallows. My data reveal that the bluebirds in NC that are more aggressive and tend to mate with individuals of a similar behavioral type in NC compared to AL. These data suggest that bluebirds are responding behaviorally to this range expansion. In Chapter 3, I investigate differences between behavior and physiology across tree swallow populations throughout their expansion range (i.e., historical (Wisconsin, Ontario, Nova Scotia) and new (North Carolina, Indiana, Iowa) sites). My results support the prediction that tree swallows on the edge of expansion exhibit aggressive phenotypes and have elevated glucocorticoids. My thesis improves our understanding of differences between geographic populations, the effects of expansions on native species, and how individuals undergoing expansion are able to survive despite the assumed costs of novel colonization.

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Student Research, and Graduate Student Association Senate. Overall, this experience has both humbled me and strengthened me as a person, and I look forward to future adventures with my best friend Daniel Mason and my future dog.

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Foreword

All Chapters of this thesis will be submitted to *Animal Behaviour*, an international peer-reviewed journal published by Elsevier; it has been formatted according to the style guide for that journal.

Chapter 1

General Introduction

Individuals on the edge of expansion often exhibit behaviors that aid in successful colonization such as aggression (e.g., Duckworth & Badyaev, 2007), boldness (reviewed in Cote, Fogarty, Weinersmith, Brodin, & Sih, 2010), and exploration (Liebl & Martin, 2012). During expansions, native species can experience novel interactions including increased competition, and aggression (Freeman & Byers, 2006; Strauss, Lau, & Carroll, 2006). Therefore, persistence of the native species is often reliant on the ability of individuals to either cope or adapt, and if a native species can respond to challenges, they have a higher chance of survivorship (DeWitt, Sih, & Wilson, 1998). To cope, individuals may alter morphology (Freeman & Byers, 2006; Langkilde, 2009), physiology (Phillips & Shine, 2006), and/or behavior (Langkilde, 2009). For example, individuals can respond to agonism with increased aggression (e.g., Jones et al., 2016) while others may utilize mating for similar behaviors such as nest defense and feeding strategies to increase their fitness (reviewed in Schuett, Tregenza, & Dall, 2010; Schuett, Dall, & Royle, 2011; Spoon, Millam, & Owings, 2007).

However, range expanding individuals may be challenged by various habitat and ecological pressures that fluctuate along a latitudinal gradient (e.g., Addis, Davis, Miner, & Wingfield, 2011). Individuals on the edge of expansion may experience different weather, food abundance, predation, etc. and have to cope, adapt, or exhibit a certain behavioral type (e.g., boldness) to survive during environmental fluctuations. Therefore, physiology can influence expansion. Martin and Liebl (2014) showed that Kenyan house sparrows at the

edge of a range expansion have elevated glucocorticoids. Glucocorticoids regulate, for example, energy storage (Hau, Ricklefs, Wikelski, Lee, & Brawn, 2010), glucose, waste removal, and energy allocation for physiological functions during nonstressful and stressful life stages to maintain homeostasis (see Hau et al., 2010; Hau, Casagrande, Ouyang, & Baugh, 2016). Indeed, studies have recently shown evidence that elevated glucocorticoids are adaptive and aid in novel colonization (Addis et al., 2011; Martin & Liebl, 2014) and can have positive fitness effects (Bonier, Moore, Martin, & Robertson, 2009).

The focus of this thesis is to investigate multiple aspects of population differences across a latitudinal gradient including variation in competitive pressures, effects of range expansion, mechanisms that facilitate expansion, behavioral types, and hormonal phenotypes. Throughout this thesis, I focus on the ongoing range expansion of the migratory songbird, tree swallows, *Tachycineta bicolor*. Tree swallows breed throughout central and northern North America, winter along the Gulf of Mexico and northern Central America, and are loosely colonial secondary cavity nesters that readily accept manmade nest boxes (Winkler et al., 2011). Tree swallows are aerial insectivores and appear to prefer open habitats near water (Winkler et al., 2011). However, despite the fact that tree swallows are one of the most well-studied avian species in North America (Winkler et al., 2011), little research has focused on habitat preferences. Males and females demonstrate consistent individual aggression (Rosvall, 2008), often out-compete other cavity nesters for boxes, and will mob potential predators in groups (Winkler et al., 2011). Tree swallows, native to northern regions of North America, are currently expanding their breeding range to southern and mid-western North America, and have colonized much of North Carolina, Tennessee, and Iowa in the past 40 years (Shutler, Hussell, Norris, Winkler, & Robertson, 2012; Winkler et al., 2011). This

range expansion runs contrary to expectations of a 2003 global analysis that predicted songbirds to be moving to more northern breeding sites (Parmesan & Yohe, 2003; Shutler et al., 2012).

In Chapter 2, I investigated the resident species Eastern bluebird, *Sialia sialis*. In NC, bluebirds have only recently had to compete with tree swallows for breeding sites. Both species are secondary cavity nesters that compete for limited nest boxes. Tree swallows are usually dominant, and aggressively outcompete bluebirds. Tree swallows, however, have not expanded to Alabama, and indeed, the bluebirds in Alabama experience more conspecific than interspecific competition. I first established, on a small geographical scale (NC & AL), how tree swallows effect the behavior of native bluebirds. I measured bluebird response to a conspecific simulated territorial intrusion (STI) during early breeding season (i.e., nest building). I hypothesized that the presence of tree swallows in NC would influence bluebird nest defense behavior. I predicted that NC bluebirds would be more aggressive during early breeding season because they may be primed to respond aggressively to a potential intrusion. I found that NC bluebirds are more aggressive than AL bluebirds in the early breeding season, but both populations mated similarly for behavior, which may increase reproductive success in both populations.

To further investigate geographical differences in individuals undergoing range expansion, in Chapter 3, I measured differences in tree swallow behavior and hormonal profiles throughout their historic (WI, ONT, NS) and expansion range (NC, IND, IA). I investigated nest defense behavior to a STI of a mock predator, the American crow, *Corvus brachyrhynchos*, and measured physiological variation by quantifying glucocorticoids, at time 0 min (basal) and time 30 min (restraint induced). Previous studies in house sparrows,

Passer domesticus, have shown evidence of elevated glucocorticoids which may facilitate colonization during a range expansion, and western bluebirds, *Sialia mexicana*, utilize aggression during dispersal. Therefore, I predicted that tree swallows on the edge of expansion would be more aggressive and have elevated glucocorticoid levels. I found evidence that females on the edge of expansion had elevated glucocorticoid levels and increased nest defense behavior compared to those breeding in historical sites. Further, I found no evidence that behavior or physiology was a direct consequence of land use or prey availability.

My thesis provides evidence that tree swallows negatively impact native species and exhibit behaviors and physiological capabilities that aid in their ability to colonize novel environments. I predict their expansion will continue and more native species (e.g., House sparrow, House wren (*Troglodytes aedon*)) will be impacted. Therefore, tree swallows provide researchers with an important and unique species to better understand the mechanisms that facilitate range expansion.

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Chapter 2

Interspecific Competition May Drive Behavioral Differences

Among Eastern Bluebird Populations

Abstract

Aggressive interference competition for limited resources is frequently observed among animals. However, these behavioral interactions within (intraspecific) and between (interspecific) species are costly; they can be energetically expensive and cause injury or death. To avoid agonistic interactions, numerous species have altered their behaviors and resource requirements. Territorial defense behavior may vary between populations when there is variation in competitor community structure. Here, I studied territorial aggression among two Eastern bluebird (*Sialia sialis*) populations (North Carolina and Alabama, USA). The bluebirds in North Carolina experience strong interspecific competition for nesting cavities with the southern expanding tree swallow (*Tachycineta bicolor*), a pressure that is absent in Alabama populations. I found that bluebirds in North Carolina are more aggressive to simulated territorial intrusions in the early breeding season compared to Alabama. This suggests that bluebirds in North Carolina may have to maintain higher baseline aggression during territory establishment and nest construction to co-occur with highly aggressive tree swallows. I also found evidence that pairs at both sites mate similarly for nest defense behavior, and in North Carolina aggressive pairs were more likely to be mated similarly.

Introduction

When animals have to work to gain access to limited resources (e.g., territory, food, mates) they often compete either against intraspecific or interspecific competitors. Competition is a fundamental component in ecology and population biology, and for decades, researchers

have investigated how competition alters a species ecological niche and community dynamics (reviewed in Alley, 1982). The competitive exclusion principle argues that interspecific competition will eventually lead to one species out-competing the other or there will be a behavioral shift towards an ecological niche to allow co-existence (Hardin, 1960; reviewed in Mooney & Cleland, 2001). Additionally, competition pressures within a population fluctuate as resource abundance and populations change (reviewed in Alley, 1982) and can drastically be altered during invasions as nonnative species colonize (reviewed in Shea & Chesson, 2002).

When nonnative species are introduced, native species experience novel competitive, dominant, and/or aggressive interactions (Freeman & Byers, 2006; Strauss, Lau, & Carroll, 2006). One way for an individual to cope with increased agonistic interspecific interactions is to respond rapidly and appropriately, referred to as phenotypic plasticity (DeWitt, Sih, & Wilson, 1998). Responses can include alteration of morphology (Freeman & Byers, 2006; Langkilde, 2009), physiology (Phillips & Shine, 2006), and/or behavior (Langkilde, 2009). However, plasticity is expensive and requires a genotype that can respond and maintain a plastic sensory system (DeWitt et al., 1998). Therefore, not all individuals can afford to be plastic, and because invasions cause change over a short time, individuals may not have the ability to respond quickly enough. For example, aggressive house sparrows (*Passer domesticus*) that were suddenly introduced by humans in West Mexico quickly outcompeted other avian species for food and habitat (MacGregor-Fors, Morales-Pérez, Quesada, & Schondube, 2010). Consequently, these cities are now house sparrow dominant and exhibit low species richness (MacGregor-Fors et al., 2010). House sparrows have been documented as aggressively outcompeting and destroying house finch (*Carpodacus mexicanus*; Kalinoski,

1975) and Eastern bluebird (*Sialia sialis*; Gowaty, 1984) nests. House sparrows have successfully colonized many areas because their invasions are quick and they are often the more aggressive species, and native species are unable to respond quickly. Indeed, during most agonistic interactions the “winner” is more aggressive. For example, in paper wasps (*Polistes dominula*) the more aggressive individuals have more nest cells (Injaian & Tibbetts, 2015) and among range expanding western bluebirds (*Sialia mexicana*), those more aggressive phenotypes are able to obtain territories in novel environments (Duckworth & Badyaev, 2007). Individuals with aggressive phenotypes may win the limited resource but can still experience reduced fitness (Duckworth 2006). Indeed, testosterone, which mediates aggression in males and females (reviewed in Goymann & Wingfield, 2014), can cause reduced fat stores, increased injuries, and immunological suppression (reviewed in Wingfield, Lynn, & Soma, 2001). Further, the loser suffers from both energy depletion and lack of a desired resource.

Mated pairs can also utilize similar behaviors such as nest defense and feeding strategies to increase their fitness (reviewed in Schuett, Tregenza, & Dall, 2010; Schuett, Dall, & Royle, 2011; Spoon, Millam, & Owings, 2007). For example, pair similarity has positively influenced the reproductive success of zebra finches (*Taeniopygia guttata*; Schuett et al., 2011) and great tits (*Parus major*; Both, Dingemanse, Drent, & Tinbergen, 2005). Behavior of both parents may be increasingly important for cavity nesting species because both male and female defend the nest (reviewed in Schuett et al., 2010). But parents that do not mate similarly most likely have different tactics such as a division of labor that makes disassortatively mating more beneficial (reviewed in Schuett et al., 2010).

Although the influence of exploitative interactions are well studied (e.g., disease, parasitism, predation), interspecific aggression remains under studied (reviewed in Grether et al., 2013). Here, I tried to understand how a natural range expansion of an interspecific competitor affects the behavior of a native species. I studied two passerine species: the Eastern bluebird (*Sialia sialis*) and the tree swallow (*Tachycineta bicolor*). Both species are obligate secondary cavity nesters that readily use nest boxes; the cavity itself is the limiting resource that both bluebirds and swallows agonistically compete over. Both species exhibit bi-parental care of young and territorial defense (reviewed in Lambrechts et al., 2010). Eastern bluebirds breed throughout eastern and central United States. Both sexes defend the nest cavity and territory (75m radius around box) throughout the season (pairs can produce two to three broods per year) and forage on terrestrial arthropods (Gowaty & Plissner, 2015). Individual Eastern bluebirds exhibit repeatable aggressive behavior (Burtka & Grindstaff, 2013; Harris & Siefferman, 2014) and pairs have been shown to mate similarly for behaviors such as a nest defense (e.g., Burtka & Grindstaff, 2015; Harris and Siefferman, 2014).

The tree swallow is an aggressive secondary cavity nesting songbird that has recently expanded their breeding range to the southeastern United States (~40 years; Lee, 1993) and often out competes bluebirds for nesting cavities (45% usurped in 2015, pers. obs.; Harris & Siefferman, 2014). Tree swallows are semi-colonial nesters that forage on emergent aquatic insects and feed within a 300 m radius around their cavity (McCarty & Winkler, 1999). For southeastern breeding bluebirds, tree swallows represent a relatively recent interspecific competitor allowing for the unique opportunity to investigate the effects of an invasive-like competitor on a native species.

Here, I compared bluebird aggression between two breeding populations: in North Carolina where bluebirds experience interspecific competition with tree swallows and in Alabama where tree swallows have not yet colonized. Additionally, because population dynamics can be influenced by environmental factors like habitat, I also investigated various coarse measurements of habitat at each site. I hypothesized that the presence of tree swallows would influence bluebird behavior and that I would find evidence of pair similarity. I predicted that in early breeding season, bluebirds in North Carolina would defend territories more aggressively than Alabama bluebirds because 1) tree swallows are intense competitors for nest boxes and have negative effects on eastern and western bluebird species' reproductive success (Duckworth, 2006; Harris & Siefferman, 2014), and 2) having an aggressive phenotype might increase a bluebird pair's likelihood of acquiring and maintaining a cavity despite high competition with tree swallows. Additionally, because Harris and Siefferman (2014) demonstrated benefits to both aggressive and nonaggressive pair similarity in high competition zones, I predicted that at both sites pairs would mate similarly regardless of aggressive phenotype.

Methods

Field Sites

I studied Eastern bluebirds at two sites during the early breeding season: Lee Co., AL (32.5934 N 85.4952 W) from March 8-14, 2015 and Watauga Co., NC (32.2996 N 81.6765 W) from March 21-April 9, 2015. At the AL field site there is little interspecific competition (i.e., no tree swallows). Although other species occupy nest boxes in AL, bluebirds are the dominant competitors, and thus intraspecific competition likely plays a larger role than

interspecific. Site occupancy for bluebirds is ~49% of nest boxes per breeding season (65/134 boxes used) and the average distance between nearest intraspecific neighbor is 154 m. At the NC site, the bluebird population has recently experienced the arrival of tree swallows (pers. obs.; Lee, 1993). Site occupancy for bluebirds is ~32% of nest boxes per breeding season (52/159 boxes used) and the average distance between nearest intraspecific neighbor is 281 m. In 2015, bluebird nests were monitored throughout the breeding season, and success/fail rates were calculated. If a bluebird successfully fledged offspring, the nest was a success. However, if a bluebird had eggs or fledglings that did not survive or parents abandoned, the nest was a failure. If a tree swallow nest was built immediately after nest failure in the same nest box, I labeled nest as usurped.

Behavioral Trials

At both sites, I conducted simulated territorial intrusions (STIs) with an intraspecific playback (bluebird chatter) to measure aggressive behavior in the early breeding season (defined as nest building to the day the first egg was laid). I chose to use early breeding season because bluebirds compete against each other for territories in the early part of the season and most strongly against tree swallows (Harris & Siefferman, 2014; pers. obs.). Tree swallows initiate clutches ~ 1 month later than bluebirds and typically only have 1 brood per season. However, they defend cavities much earlier than nest initiation (pers. obs.), overlapping temporally with bluebirds when they initiate their first brood. After identifying an active pair of bluebirds at a nest box, I placed a speaker directly under the box and broadcasted bluebird chatter for 10 minutes. Each bird experienced the same chatter recording, which I obtained from Macaulay Library at Cornell Lab of Ornithology, recording

by G. Budney. I quantified male and female latency to approach the nest box (within ~ 1m radius of box) and the number of dives at the speaker. I used an intraspecific playback to ensure it was a stimulus the bluebirds were familiar with between both populations (North Carolina and Alabama). I chose to broadcast chatter instead of song for multiple reasons: song can be influenced by dialect while call notes are less influenced by geography (Lemon, 1975), and both sexes use and respond to chatter during territory defense and anti-predator interactions. Finally, chatter tends to elicit quicker responses from bluebirds (L. Siefferman, pers. obs.). There was also an advantage to using a playback and not a live model. With a live model, the focal bird's behavior could be influenced by the live model's behavior and may not be an accurate depiction of the individual's behavioral phenotype (see Peiman & Robinson, 2010).

Habitat Analysis

Land use/land cover (LULC) was characterized using ArcGIS v 10.2 (ESRI 2013). I obtained LULC data from the United States Geological Survey (USGS) National Land Cover Dataset (2011) for North Carolina and Alabama, USA at 30 x 30m resolution, and were projected using the Universal Transverse Mercator (16S for Alabama and 17S for North Carolina) coordinate system. I created a 75m radius foraging/territory buffer around each nest box to assess LULC within each buffer. Because bluebirds forage within a 75 m radius of the box (Gowaty & Plissner, 2015), this buffer size is most likely biologically and ecologically important for survival and reproductive success. Previous research has shown that bluebirds preferentially settle in open habitat (Gowaty & Plissner, 2015; Jones, Harris, & Siefferman, 2014). The USGS LULC data provides multiple land cover parameters that are

intercorrelated. Therefore, I combined developed-open, barren land, hay/pasture, and cultivated crops into one “open” variable.

Statistical Analysis

Statistical analyses were performed using SPSS v. 23 (IBM, 2015). Shapiro-Wilk tests demonstrated that all behavioral and habitat data deviated significantly from a normal distribution ($p < 0.05$), except Alabama percent openness ($p = 0.41$). Additionally, North Carolina territories had greater percent openness than Alabama. However, there was no correlation between percent open and behavior or habitat (i.e., latency to approach, number of dives, LULC). Therefore, I did not control for openness within each site. I investigated behavioral and habitat differences between sexes and between sites using Mann Whitney U and cross tab chi-square test. Similarity was quantified by subtracting male and female latency to approach and creating a new dependent variable (based on methods of Burtka & Grindstaff, 2015). Outliers were determined using a univariate approach for all male and female response variables. Only extreme outliers (3 x interquartile range) were removed for analysis, as anything below was biologically relevant for analysis (i.e., representative of aggressive individuals). To investigate pair similarity, pairs that were >20 seconds different to approach speaker were given a score of “dissimilar” (n=9) and all others were considered “similar” (n=20) based on the distribution of the data (Figure 1). To assess if pair similarity affected the fate of nests, a cross tabulation chi-square was performed. Additionally, I grouped males and females as aggressive or nonaggressive utilizing similar methods as previously mentioned (e.g., Figure 1). In Alabama, males and females were considered aggressive if they returned to the nest box ≤ 100 seconds and in North Carolina males were

considered aggressive at ≤ 50 seconds and females at ≤ 30 seconds to return to box. With a cross tabulation chi-square, I assessed if aggressive versus nonaggressive individuals were more or less likely to be mated similarly or dissimilarly.

Ethics Statement

This study was carried out in accordance with the recommendations for the Care and Use of Animals for Research, Teaching, or Demonstrations provided by Appalachian State University (#12-09) and Auburn University (#12-68) through Institutional Animal Care and Use Committee (IACUC) under USFWS Master Banding Permit #23563. All animals were handled in such a way to reduce stress and avoid physical harm. All adults were released in their home territory.

Results

Alabama

I found evidence for pair similarity in response to STIs. Male (median (md); md=70.00s) and female latency (md=73.50s) were significantly positively correlated ($r_s = 0.76, p < 0.001, n = 19$; Figure 2). Moreover, males and females did not differ in latency to approach the nest boxes ($U = 218.50, Z = -0.00, p = 1.00, n = 42$) and the sexes were equally likely to dive at the speaker ($\chi^2 = 1.59, p = 0.32, n = 42$). Aggressive ($n = 12$) versus nonaggressive males or females ($n = 7$) were not more likely to be similarly or dissimilarly mated ($X^2 = 1.03, df = 1, p = 0.38$; $X^2 = 4.23, df = 1, p = 0.07$ respectively).

North Carolina

Paired bluebirds behaved similarly in response to STIs: female (md=5.50s) and male latency (md=8.50s) to approach the nest box were significantly positively correlated ($r_s = 0.66$, $p < 0.001$, $n=29$; Figure 3) as were female (md=3) and male (md=5) number of dives ($r_s = 0.62$, $p < 0.001$, $n=29$). Males and females did not differ significantly in either latency to approach the nest box ($U=397$, $Z=-0.38$, $p=0.71$, $n=58$) or likelihood of diving at speaker ($\chi^2=1.10$, $p=0.50$, $n=58$). Aggressive males and females ($n=19$) were more likely to be similarly mated (89.5%) versus nonaggressive individuals ($n=10$), which were more likely to be paired dissimilarly (60%; $X^2=8.03$, $df=1$, $p=0.01$). Additionally, 23/29 early bluebird nests failed, and 13 of those were directly attributed to tree swallows. Dissimilarity did not affect the likelihood of nest fail/success ($\chi^2=0.13$, $p=0.72$, $n=29$).

Differences between field sites

Although mated pairs behaved similarly in both populations, to avoid pseudo replication, I present male and female data separately. Alabama females ($n=19$) were slower to approach the nest box ($U=131.0$, $Z=-3.07$, $p=0.002$; Figure 3) and dove less often ($U=104.5$, $Z=-3.8$, $p < 0.001$) compared to North Carolina females ($n=29$). Alabama males ($n=23$) took longer to approach nest box ($U=169.5$, $Z=-3.03$, $p=0.002$; Figure 3) and dove less often ($U=100.5$, $Z=-4.40$, $p < 0.001$) compared to North Carolina ($n=29$) males. There was no difference in the extent to which pairs showed similar behavior (i.e., female latency subtracted from male latency, described in methods) between sites ($U=216.5$, $Z=-1.36$, $p=0.175$, $n=48$).

I did not find significant correlations between land use, nesting stage, age, or bluebird behavior at either site (all $p \geq 0.09$). However, North Carolina territories had higher percent

openness than Alabama ($U=55.50$, $Z=-4.78$, $p<0.001$, $n=49$), but when our latency measurement (not split by site) was analyzed, there was no effect of openness on female ($r_s = -0.198$, $p=0.20$, $n=44$) or male latency to approach ($r_s = -0.230$, $p=0.12$, $n=48$).

Discussion

Bluebirds in North Carolina were more aggressive in response to STIs than were birds in Alabama. At both sites, mated pairs behaved similarly and behavioral phenotype did not differ between the sexes. There was no relationship between behavior and the habitat parameter (percent open) at either site, even though territories in North Carolina had a greater percentage of open habitats. Pairs in North Carolina were more likely to be aggressive and similar or nonaggressive and dissimilar, but aggression made no difference in pair similarity in Alabama.

Overall, the presence of tree swallows as an intense interspecific competitor appears to affect bluebird behavior. Among cavity nesting species, cavities are a highly contested limited resource. Therefore, when an intense competitor is introduced, individuals that are plastic can increase aggression to obtain and keep a nest cavity, even if there is a cost (see DeWitt et al., 1998). Because sensory and regulatory mechanisms are required to consistently adjust to the immediate environment, plasticity is costly and has evolutionary constraints (reviewed in DeWitt et al., 1998) and may not be necessary in all environments.

Additionally, these differences may be genetic, because tree swallows are aggressive nest box competitors, their presence may have created an environment where there is selection for aggressive bluebirds. Alternatively, it may be selection for similarly mated pairs. In NC, it was not the aggressive bluebirds that had higher reproductive success in areas of high tree

swallow competition, but those that were similarly mated (both aggressive and nonaggressive; Harris & Siefferman, 2014). However, because aggressive pairs are more likely to be mated similarly in North Carolina, during early breeding season aggression and pair similarity may not be mutually exclusive. In Oklahoma, paired Eastern bluebirds that both demonstrated high intensity nest defense behavior had more successful fledglings than dissimilar pairs. However, these findings also applied when males were slightly more aggressive than females, which may suggest in the Oklahoma population pair similarity and aggression are important (Burtka & Grindstaff, 2015).

Ultimately, for bluebirds to adapt to tree swallows, their behavior must positively affect fitness and have a heritable component (reviewed in Strauss et al., 2006). However, based on current reproductive rates that appear to be suffering, bluebirds may either not be adapting quickly enough or at all.

Repeated agonism can also contribute to elevated aggression. For example, Golden-winged warblers (*Vermivora chrysoptera*) that experienced high amounts of interspecific agonism with Chestnut-sided warblers (*Setophaga pensylvanica*) are more aggressive when consistently challenged by Chestnut-sided warblers (Jones et al., 2016). Behavior was quantified during territory acquisition and maintenance and, based on studies that have tested the challenge hypothesis, it is expected that monogamous male birds have increased amounts of testosterone that influences irritable aggression during early breeding season (reviewed in Wingfield, Hegner, Dufty, & Ball, 1990). Of course, this hypothesis also applies to AL bluebirds, but unlike NC, they are not consistently bombarded throughout the breeding season by other cavity nesting species.

As previously mentioned, bluebird pairs at both sites demonstrated strong pair similarity (both aggressive and nonaggressive phenotypes). However, whether behavior is consistent and important in mate selection or is altered after mate selection is not known (reviewed in Schuett et al., 2010). If there is selection to mate similarly, then there should be fitness benefits (see Snekser, Leese, Ganim, & Itzkowitz, 2009). For example, when pairs of cockatiels, *Nymphicus hollandicus*, behaved similarly, they displayed coordinated incubation behaviors and had higher reproductive success than dissimilar pairs (Spoon et al., 2007). However, the environment may dictate which traits are under selection (see Dingemanse, Both, Drent, & Tinbergen, 2004). In pairs that provide biparental care and defend the territories equally, aggressive phenotypes are usually necessary to obtain a limited resource, and therefore aggression may be the quality sought after by mates. Because pair similarity is beneficial to bluebirds in NC (Harris & Siefferman, 2014) and aggression may alter the likelihood of similar mating in early breeding season (see results), bluebird pairs may be under pressure to aggressively secure a nesting box but also to mate similarly. Interestingly, nonaggressive individuals were more likely to mate dissimilarly in North Carolina. However, sample size for nonaggressive individuals was low, and during breeding season, the nonaggressive individuals may not have obtained a territory and been included in this study. Therefore, I hesitate to make strong conclusions from this result. Though this study was not developed to focus on the investigation of pair similarity, it is an important component to population dynamics and requires further research.

I found no relationship between land use and behavior but recognize that the habitat parameter (i.e., percent openness) may be too coarse to identify relationships with behavior. Bluebirds settle in open habitat because open space likely allows them to better visualize and

capture insects (Gowaty & Plissner, 2015), and NC bluebirds are more likely to settle in open habitat when they breed among high densities of tree swallows (Jones et al., 2014). Further habitat analyses should be conducted to elucidate any potential effects.

To monitor population effects and fluctuations, future research should aim to investigate population responses to competitive pressures and nonnative species colonization across a spatial gradient. Currently, there is a unique opportunity to follow NC bluebirds to investigate 1) potential changes in population dynamics 2) if the bluebirds will be successful against tree swallows and 3) if the bluebirds are demonstrating phenotypic plasticity. Pair similarity should also be quantified in future studies to better understand the adaptations and selection pressures on mating between and among species.

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Figures

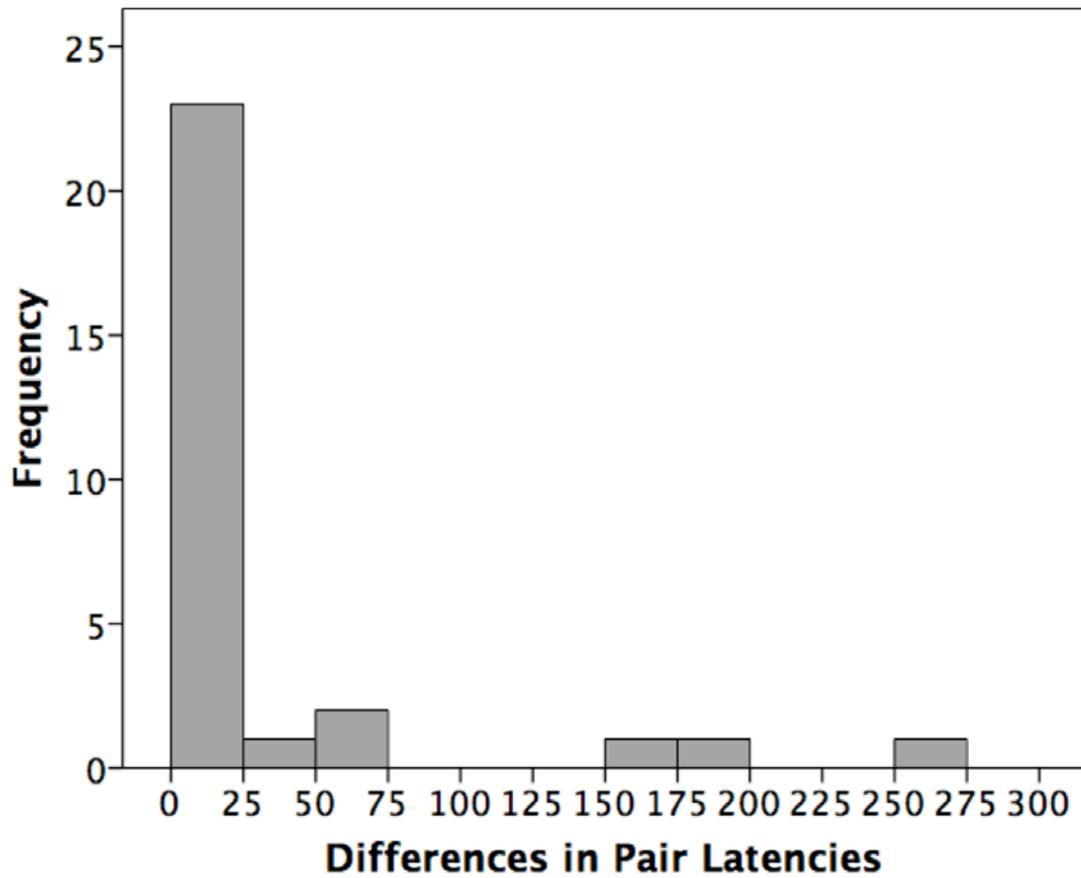


Figure 1. Histogram of pair similarity in latency to approach nest box. Latencies for each pair of male and female parents was subtracted. A pair was defined as similar if there was less than or equal to 20 second differences in time to approach box, based on distribution. Please note that in the raw data, there were no individuals at with a 25 second difference, which is why 20 seconds was used as the differentiating number.

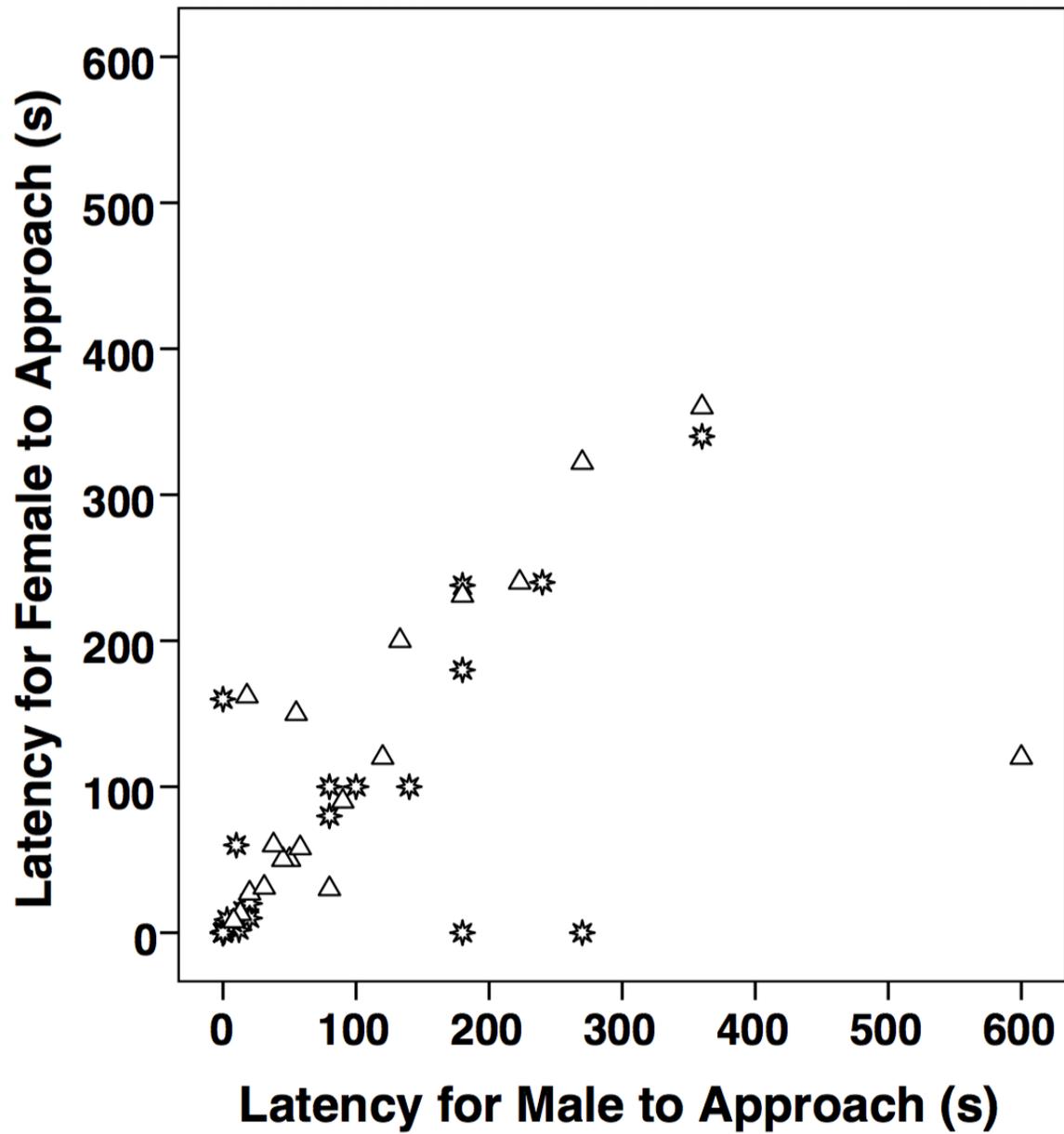


Figure 2. Male and female bluebird pair similarity in North Carolina and Alabama. Each symbol represents a mated pair of bluebirds. Gear symbol represents NC and triangles represent AL.

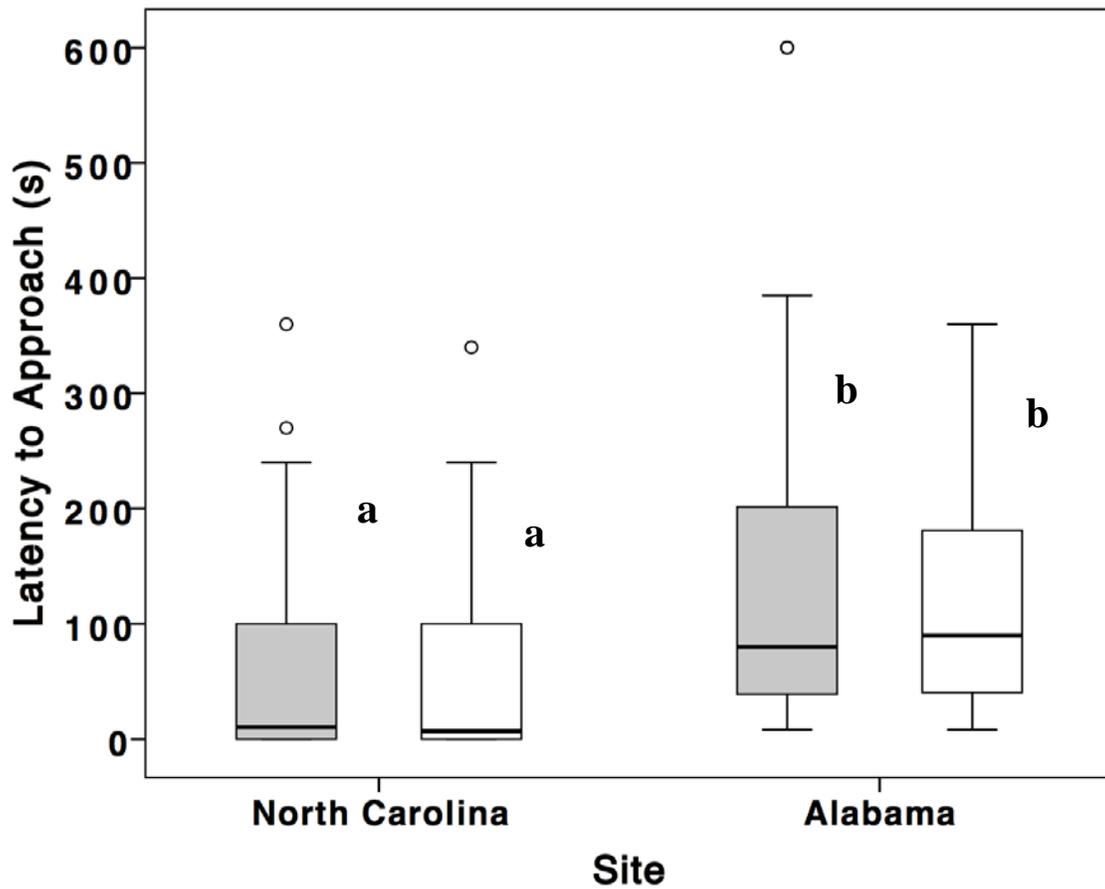


Figure 3. Box plot of male and female latency to approach nest box (within 1 meter) during STI in Alabama and North Carolina. Males are represented by shading and females are clear. Middle line represents median, bottom and top hinges represent 25th and 75th percentile, respectively. The whiskers are 1.5x hinges and points represent 1 SD above the interquartile range.

Chapter 3

Elevated Glucocorticoids Coupled with Aggression May

Facilitate Range Expansion

Abstract

Dispersal ecology is a fundamental process in the maintenance of population dynamics throughout numerous taxa. Because of this, individuals within and among populations have developed behavioral and physiological strategies that facilitate dispersal and even range expansion. Strategies include aggression, boldness, exploration, and physiological adaptations. Currently, tree swallows are undergoing a range expansion to the southeastern US possibly as a result of decreased habitat availability in the Northeast and an increased number of nestboxes throughout the south. My study provides a unique look into how tree swallows respond behaviorally and physiologically during a range expansion. I hypothesized that homeostasis is challenged by colonization of a novel environment and expect that glucocorticoids are a reliable measure of how an individual copes with change. Additionally, I hypothesized that individuals on the edge of expansion will exhibit a behavioral phenotype that may aid in colonization. During the 2015 breeding season, I investigated behavioral and glucocorticoid profiles (basal and restraint induced) of breeding female tree swallows throughout their historic and expansion range. I found evidence that females on the edge of expansion show elevated glucocorticoid levels and increased nest defense behavior compared to those breeding in historical sites. I found no evidence, however, that these differences were likely a consequence of variation in land use or prey abundance at historical versus expansion sites. Females that were incubating clutches at the expansion sites had similar basal, but increased restraint induced, glucocorticoids compared to females at historical sites.

When rearing nestlings, females at expansion sites had elevated basal and restraint induced glucocorticoid levels and protected their young more vigorously compared to females at historical sites. It may be that females on the front of the range expansion utilize a different physiology adaptation, and coupled with elevated aggression, are better able to respond quickly to stressors in novel environments.

Introduction

Dispersal is a fundamental component to population ecology across taxa (Nathan et al., 2008), and is necessary for population persistence in changing environments (reviewed by Ronce, 2007). However, there are differences in the extent to which individuals disperse and remain philopatric (do not disperse). Variation in exploratory behavior, physiology, and genotype may explain dispersal strategies (Bonte et al., 2012; see Clobert, Le Galliard, Cote, Meylan, & Massot, 2009), and individuals could use environmental cues (Verhulst, Perrins, & Riddington, 1997), be bound by a genetic predisposition (e.g., male vs. female), or use a combination of both (Bowler & Benton, 2005). Dispersal advantages include: decreased inbreeding, kin competition, and intraspecific competition (Clobert et al., 2009). However, dispersal is costly because individuals have less information about habitats, neighbors and the ability to acquire breeding territories (Bowler & Benton, 2005).

When populations spread out from a central location via dispersal to novel environments in successive breeding seasons, this is referred to as a range expansion (e.g., Duckworth, 2008; Lee, 1993). The ability of individuals to adjust physiologically and behaviorally to novel environments likely influences their ability to succeed in unfamiliar locations. Thus, range expansions require adaptations and strategies that increase

survivorship in novel environments (Clobert et al., 2009; Duckworth & Badyaev, 2007) such as aggressive phenotypes (Duckworth 2006), exploratory behavior (Dingemanse, Both, Van Noordwijk, Rutten, & Drent, 2003), and/or physiological flexibility (see Liebl & Martin, 2012). Indeed, aggression facilitates successful colonization of male western bluebirds, *Sialia mexicana* (Duckworth & Badyaev, 2007), and house sparrows, *Passer domesticus*, on the edge of expansion have more exploratory phenotypes (Liebl & Martin, 2012).

In novel environments, stressors such as competition, predation, food, and weather are unpredictable and may challenge homeostasis (Wingfield et al., 1998). Homeostasis is the maintenance of critical biological ranges, which survival is dependent on, that support a constant internal environment (e.g., glucose, oxygen, waste removal; Goodman, 2010). Therefore, challenges accompanied with novel colonization such as new predators and adverse weather may require glucocorticoid levels to be modified. Glucocorticoids function to maintain physiological homeostasis (Romero, 2004), and can indicate an individual's internal response to their environment (e.g., Addis, Davis, Miner, & Wingfield, 2011). During a stressor or challenge, glucocorticoids elevate within 2-3 minutes and peak between 15-30 minutes from time of stress to maintain homeostasis and increase survivorship (Hau, Ricklefs, Wikelski, Lee, & Brawn, 2010). Glucocorticoids will reach target cells where they bind to intracellular receptors and initiate gene transcription (Goodman, 2010). Once transcribed, cellular products such as proteins will aid the body in dealing with challenges. Increased levels can promote adaptive behaviors such as increased foraging or blood and oxygen circulation to tissues (Sapolsky, Romero, & Munck, 2000). According to the cort-fitness hypothesis, elevation of glucocorticoids may cause poor body condition and decrease fitness (reviewed in Bonier, Martin, Moore, & Wingfield, 2009). However, studies have

shown deviations from the cort-fitness hypothesis and demonstrate the adaptability of elevated glucocorticoids (see Bonier, Moore, Martin, & Robertson, 2009; Bonier & Robertson, 2011). For example, Bonier, Moore, et al. (2009) found females rearing nestlings with elevated glucocorticoids had evidence of higher reproductive success. Elevated glucocorticoids may also be adaptive during range expansions. In White-crowned sparrows, *Zonotrichia leucophrys*, which are undergoing a high altitude range expansion, have significantly higher basal and elevated glucocorticoid levels compared to non-range expanding conspecifics (Addis et al., 2011). The authors suggest that because higher altitudes have harsher weather, the energy demand is greater and elevated glucocorticoid aid the individual to meet increased metabolic needs.

In addition to behavior and physiology, environmental pressures can influence dispersal. New environments may contain unsuitable habitat, new predation risks, and variable hetero and conspecific competition (Edelaar, Siepielski, & Clobert, 2008; Stamps, 2001). However, new environments could also have suitable habitat and good resources (e.g., increased food availability). Life history strategies such as the sociability may attribute to dispersal distance (reviewed in Cote, Fogarty, Weinersmith, Brodin, & Sih, 2010). For example, group composition is a primary determinant for the invasive mosquitofish, *Gambusia affinis*, to disperse: asocial individuals 1) disperse farther and 2) tend to disperse more if their school is asocial (Cote et al., 2010). Overall, success may not only be dependent on the individual but also the environmental factors surrounding dispersal.

Tree swallows, *Tachycineta bicolor*, are loosely colonial secondary cavity nesters (Winkler et al. 2004) that demonstrate consistent individual aggression (i.e., animal personality; Rosvall 2008) and often out-compete other secondary cavity nesters for limited

nesting sites. Before readily available nest boxes, tree swallows probably utilized natural tree snags and dammed water from beavers (Lee, 1993). Tree swallows are a passerine native to northern North America, and have been undergoing a rapid range expansion into the southeastern United States for the last 40 years (Lee, 1993; Shutler, Hussell, Norris, Winkler, & Robertson, 2012; Winkler et al., 2011). This range expansion runs contrary to expectations of a 2003 global analysis that predicts songbirds will move to more northern breeding sites (Parmesan & Yohe, 2003). Their movement to the southeast is most likely due to urbanization in northeastern North America coupled with beaver dam loss and reappearance plus the widespread establishment of manmade nestbox trails (Askins, 1995; Lee, 1993; Robbins, Sauer, Greenberg, & Droege, 1989). Since the 1960s, bird enthusiasts have erected artificial cavities (nestboxes) all over the southern United States to counter the decline of Eastern bluebirds, *Sialia sialis*. These nestbox trails could encourage tree swallow range expansion (i.e., more habitat available for them; Lee, 1993).

Because previous studies have shown that glucocorticoid levels are elevated during range expansion (e.g., Addis et al., 2011; Martin & Liebl, 2014) and aggression can aid dispersal (e.g., Duckworth, 2006), I hypothesized that aggression and hormonal phenotype have facilitated the ongoing range expansion of tree swallows. I measured the avian glucocorticoid, corticosterone (cort; basal and restraint induced) and behavioral phenotype (via a simulated territorial intrusion) of female tree swallows throughout their historic (i.e., Wisconsin, Ontario, Nova Scotia) and expansion range (i.e., Indiana, Iowa, North Carolina). I predicted that individuals breeding on the expansion edge would be more aggressive and have significantly higher cort levels compared to those breeding in historical range. Further,

because site differences in habitat could also influence behavior and physiology, I quantified land use and insect abundance.

Methods

General Field Methods

In this study, I focused on females because they were easier to capture and they disperse further than males (Greenwood, 1980). Because female tree swallows display delayed plumage maturation, second year (SY) females have brown body plumage while after-second year (ASY) females have iridescent body plumage (Bentz, Navara, & Siefferman, 2013). Thus, misidentifying the age of female tree swallows was unlikely. However, ASY females and males are difficult to distinguish, therefore, upon capture I colored all females with a colored Sharpie over the white breast feathers for identification during behavioral trials.

Study Sites

I monitored seven populations of established tree swallow nestbox breeding sites in May and June 2015. Expansion sites included Davidson, North Carolina (35.438 N, 80.697 W); Boone, North Carolina (36.196 N, 81.783 W); Bloomington, Indiana (39.142 N, 86.602 W); and Ames, Iowa (42.073 N, 93.635 W). Historical sites were Saukville, Wisconsin (43.382 N, 88.023 W); Long Point, Ontario (42.623 N, 80.465 W); and Wolfville, Nova Scotia (45.107 N, 64.378 W). Historical sites have been documented in tree swallow historical breeding range since the mid-1800s (Winkler et al., 2011) and expansion sites have had an increase in tree swallow presence during the breeding season since the 1960s (Lee, 1993; A.

Bruner, pers. comm; Sauer et al., 2011). I collected GPS coordinates at each nestbox where an adult female was captured using a Garmin GPSmap 78s.

Adult Capture

At each site, I captured 20-30 nesting females between the hours of 0900-1130 and 1300-1630. I collected blood twice to yield both basal and restraint induced cort. Within 3 min of capture, I collected an initial blood sample ~80 μ l (time 0 min; basal cort). I drew blood from the alar wing vein using a 26.5-gauge needle and kept on ice until centrifugation. Following initial blood draw, I gave birds a USGS band, and measured wing and tail length, and body mass. I recorded female age SY or ASY using plumage coloration (Bentz et al., 2013). I then placed birds in paper bag until 30 minutes post capture, time immediately began from when bird first captured, and then took another blood sample to measure restraint induced plasma cort. I captured females opportunistically, because of this, females were captured either during incubation or when rearing 6-10 day old nestlings.

Behavior

Twenty-four hours post capture, I conducted simulated territorial intrusions (STIs) for each breeding female tree swallow. Behavioral trials were coordinated with time of day that cort was collected the day prior (e.g., a bird captured at 10am was given an STI between 9am-11am on the following day). I did this to eliminate time of day bias as cort is on a diurnal rhythm mediated by the hypothalamic-pituitary axis (Goodman, 2010). Once the female tree swallow was identified at her box, I mounted a model American crow (*Corvus brachyrhynchos*), a natural nestling predator, 0.3 m above the box to simulate flying, and played crow calls using portable speakers. I measured latency for female to come within 1

meter of the crow, the number of dives mounted toward the model (Siefferman et al., unpubl. data). I quantified aggression as both continuous variables (seconds to respond and number of dives).

Characterization of Land use, and Prey Abundance

I characterized land use/land cover (LULC) using ArcGIS 10.2 (ESRI, Redlands, California). LULC data was obtained from the United States Geological Survey (USGS) National Land Cover Dataset (2011) for sites that were in the United States (IA, IND, NC, WI) with 30 x 30m resolution. LULC data for Nova Scotia and Ontario was acquired through the Gouvernement du Canada Land Use (2010) with 30 x 30m resolution. USGS and Canadian LULC categories were recoded using the descriptions provided to create new categories for each land type that were comparable across both countries. No land types were deleted, and all LULC categories were represented. Categories included: open water, developed open space (including primary, secondary, and tertiary roads), developed and urban, barren land, forested area (mixed, deciduous, and evergreen), shrub, herbaceous, hay/pasture land, cultivated crops, woody wetlands, and emergent herbaceous wetlands. Each site was analyzed on a different ArcGIS file so each state or province could be analyzed in its correct UTM Zone. I used WGS 1984 for each coordinate system and Transverse Mercator for projection. Once LULC for each state was acquired, a foraging buffer was created around each nestbox to assess LULC within each buffer. Because tree swallows forage within a 300 m radius of the nestbox (McCarty & Winkler, 1999), the habitat each bird is experiencing within this buffer is most likely biologically and ecologically important for food and survival for themselves and their offspring.

To investigate food availability, I quantified insects at four sites (Valle Crucis NC, IA, WI, ONT) over two nights and three days with a Bug Dorm[®] malaise trap (165 x 110 cm with 96 x 26 mesh/square inch; #BT1001). Malaise traps have the ability to capture high diversities of flying insects (reviewed in Campbell & Hanula, 2007; Juillet, 1963). At each of the four field sites, three traps were evenly distributed at 3pm on day 1 and taken down at 9am on day 3 during blood and behavior collection. Insects were trapped in a 500 mL bottle provided with the trap with water and not preservative. Therefore, once the traps were taken down, I drained the water through a paper towel, quantified wet mass, and identified insects to order.

Hormone Assays

I quantified plasma corticosterone levels using enzyme immunoassay kits (Cayman ELISA #500655; assay sensitivity 30 pg/mL). This assay has been utilized to measure plasma corticosterone in multiple songbird species with comparable corticosterone levels (see Davis & Guinan, 2014; Rosvall, Reichard, Ferguson, Whittaker, & Ketterson, 2012). I followed the manufacturer's instructions with minor modifications. Specifically, I added 10uL of plasma to 200uL of ultrapure H₂O. I then extracted samples three times with diethyl ether, dried with N₂, and reconstituted with 600uL of assay buffer. I ran the reconstituted samples on the plate in duplicate, alongside a pooled plasma standard that served as an intra- and inter-plate control. Bleeding timepoints (i.e., basal or restraint induced) and site locations were dispersed evenly among plates. I quantified corticosterone concentrations using a four-point logistic standard curve analyzed via Gen5 software (v2.09, BioTek, Winooski, VT, USA). Inter-plate variability was 10.2%, and intra-plate ranged from 3.7-12.4% (mean: 7.7%). In a

separate subset of samples, I titrated hormones to estimate average extraction efficiency. To do so, I added 20uL of H3-corticosterone (~2500 CPM) to each 10uL sample (n=10), which was then processed and extracted exactly as described above. Average extraction efficiencies were = 97.7%.

Statistical Analysis

I analyzed data using SPSS v. 23.0 (IBM Corp, 2015). I tested continuous variables for normality using Shapiro-Wilkes test. I identified outliers using a univariate technique between breeding stage without separating between expansion and historic sites. I only removed extreme outliers (3 times interquartile range) in the data, and individuals that were outside the interquartile range but under extreme outlier range were not removed for cort analysis, as high values of cort are most likely relevant for this study.

I initially explored cort using a repeated measures general linear model (GLM) following Field (2015) guidelines with basal and restraint induced cort as within subject variables and the seven field and breeding stage as the between subject factors to assess whether 1) the protocol induced an elevated restraint response within individual birds and 2) the response was influenced by site. I then separated basal and restraint induced cort for further analyses because mineralocorticoid receptors have shown flexibility in regulation uncoupled with glucocorticoid receptor flexibility (which has shown to be heritable; Hau, Casagrande, Ouyang, & Baugh, 2016). This suggests that basal cort is not completely coupled with elevated cort, and can be investigated separately.

I investigated aggression using generalized linear models (Poisson log linear link function), and either latency to approach crow or number of dives was the response variable, and site type (historic or range) and breeding stage were factors. Once I split data, continuous

dependent variables were analyzed via independent samples *t*-tests if data were normally distributed and Mann-Whitney U if distribution deviated significantly from a normal distribution.

I used a univariate analysis to assess the relationships between cort and behavior. In all models, I split the data by breeding stage as cort and breeding stage have a significant interaction (see previous). First, I utilized a univariate analysis with cort as the dependent variable (1 model included basal and the other investigated restraint induced), site type was the fixed factor, and for the behavior models latency to approach crow and number of dives were covariates. However, in the land use models, percent open were covariates, but the rest remained the same. I also utilized univariate analysis split by breeding stage to investigate potential effects of land use (percent open) on behavior. In the model either latency to approach crow or number of dives was the dependent variable and percent open was a covariate.

Results

Repeated Measures Corticosterone

Basal and restraint induced cort deviated from normality (Shapiro Wilkes $p < 0.05$), therefore cort was log transformed (Shapiro Wilkes $p > 0.05$). There was a significant elevation of cort; cort increased from time 0 (basal) to time 30 (during the restraint protocol) ($F(1,117)=234.77$, $r=0.82$, $p < 0.001$; Figure 1). Site (defined here as individual field site) did not significantly affect cort ($F(6, 117)=0.73$, $p=0.63$). Therefore, for all further analyses, site is referring to historical versus expansion.

When field sites were grouped into either historical or range expansion sites, expansion sites had higher elevation in cort ($t=-3.52$, $df=119$, $p=0.001$; Figure 1), but there

was a significant main effect of breeding stage on cort ($F(1,117)=5.10$, $r=0.21$, $p=0.03$).

Therefore, for further analyses, I split the dataset by females captured during incubation and nestling rearing.

Corticosterone

During incubation, basal cort did not differ significantly between historical and range expanding sites ($t=-0.53$, $p=0.60$, $df=70$; Figure 2), however, restraint induced cort was significantly higher among the females in the expansion sites ($t=-2.23$, $p=0.03$, $df=70$; Figure 3). Females rearing nestlings exhibited significantly higher basal and restraint induced cort in expansion sites compared to the historical sites (basal: $t=-2.26$, $p=0.03$, $df=51$, Figure 4; restraint induced: $t=-3.55$, $p=0.001$, $df=51$, Figure 5).

Additionally, for the females that were incubating, body mass did not differ significantly between expansion and historic sites ($t=-0.55$, $p=0.59$, $n=94$; Figure 6). However, among the females that were rearing nestlings, females at historic sites were significantly heavier compared to females at expansion sites ($t=2.83$, $p=0.01$, $n=69$; Figure 7). Among incubating females, body mass was not significantly correlated with cort in historic (basal: $r=-0.26$, $p=0.11$, $n=39$; restraint induced $r=-0.28$, $p=0.09$, $n=39$) or expansion sites (basal: $r=-0.17$, $p=0.36$, $n=30$; restraint induced $r=-0.34$, $p=0.07$, $n=30$). Among the females rearing nestlings, female body mass was not significantly correlated with cort in historic (basal: $r=-0.09$, $p=0.64$, $n=24$; restraint induced $r=-0.01$, $p=0.95$, $n=25$) or expansion sites (basal: $r=-0.26$, $p=0.17$, $n=29$; restraint induced $r=-0.32$, $p=0.13$, $n=28$).

Capture date nor capture time had an effect on cort (r ranged from -0.03 to -0.15, all $p > 0.07$), and within each breeding stage, there was not a significant effect of adult female age on cort (incubation: $t = -0.322$, $p = 0.75$, $df = 51$; rearing nestlings: $t = 1.46$, $p = 0.15$, $df = 52$).

Land use and Prey Abundance

Territories at historic sites (median (md) = 64.4%) exhibited significantly lower percent of open habitat compared to territories in expansion sites (md = 71.5%) ($U = 2686.00$, $Z = -2.2$, $p = 0.03$, $n = 164$; Figure 8). All sites had more Diptera than any other order (Table 1). Boone, NC had the highest number of Diptera and the greatest number of orders ($n = 8$) compared to IA ($n = 3$), WI ($n = 3$), and ONT ($n = 4$).

Behavior

The latency model showed no significant site * breeding stage interaction ($X^2 = 1.16$, $p = 0.281$, $n = 92$) but the main effects of site ($p < 0.001$) and breeding stage ($p < 0.001$) were statistically significant. I did find an interaction between site type and breeding stage ($X^2 = 4.53$, $p = 0.03$, $n = 107$). To appropriately investigate main effects and account for interaction, I split the data by breeding stage. Within expansion and historic range, I found no significant differences in behavior of females that were incubating and rearing nestlings (historic: $U = 277.00$, $Z = -0.45$, $p = 0.65$, $n = 49$; expansion $U = 377.50$, $Z = -0.68$, $p = 0.50$, $n = 58$).

For incubating females, those at historical and expansion sites did not differ significantly in latency to approach the crow ($U = 784.00$, $Z = -1.87$, $p = 0.06$, $n = 90$; Figure 9) or in number of dives toward the crow ($U = 283.50$, $Z = -1.49$, $p = 0.14$, $n = 54$; Figure 10). Females that were rearing nestlings at the expansion sites dove more often at the crow compared to

females at historical sites ($U=161.00$, $Z=-2.78$, $p=0.01$, $n=51$; Figure 11), but did not differ in latency to approach the crow ($U=166.50$, $Z=-0.99$, $p=0.32$, $n=41$; Figure 9).

Behavior and Corticosterone

Because cort was previously found to have an interaction with breeding stage, data was split for behavioral analysis. For incubating females, there was no significant relationship of latency to approach crow ($F(1,37)=1.73$, $p=0.06$) or number of dives ($F(1,37)=1.73$, $p=0.06$) to basal or restraint induced cort (latency: $F(1,33)=1.23$, $p=0.28$; dives: $F(1,33)=0.98$, $p=0.33$). Indeed, when females had nestlings latency to approach crow ($F(1,27)=0.40$, $p=0.54$) nor number of dives ($F(1,27)=0.10$, $p=0.77$) was related to basal or restraint induced cort (latency: $F(1,25)=1.44$, $p=0.24$; dives: $F(1,33)=0.07$, $p=0.80$).

Land use, Density, and Corticosterone

Among the incubating females, there was no significant effect of land cover ($F(1,64)=1.51$, $p=0.23$) on basal or restraint induced cort (basal: $F(1,64)=0.15$, $p=0.70$; restraint induced: $F(1,64)=4.06$, $p=0.06$). Likewise, among the females rearing nestlings, I found no significant effect of land cover ($F(1,46)=3.30$, $p=0.08$) on basal or restraint induced cort (basal: $F(1,47)=0.01$, $p=0.99$; restraint induced: $F(1,47)=0.47$, $p=0.50$).

Land use and Behavior

There was no significant effect of percent openness of territories ($F(1,43)=1.83$, $p=0.18$) on number of dives or latency to approach crow (percent open: $F(1,47)=1.78$, $p=0.18$; density: $F(1,47)=0.03$, $p=0.86$) when females were incubating. Additionally, when females had

nestlings, there was no effect of percent open ($F(1,40)=0.01, p=0.65$) or density ($F(1,40)=0.17, p=0.68$) on latency to approach crow or number of dives (percent open: $F(1,33)=3.16; p=0.08$; density: $F(1,33)=0.68, p=0.42$).

Discussion

As expected, female tree swallows on the edge of range expansion had elevated cort levels and increased aggression, but there was little evidence of field site-specific differences in those measures. Moreover, breeding stage was a primary factor in the investigation of both behavior and physiology- females that were incubating eggs tended to show lower cort than those rearing nestlings and this is consistent with the cost of reproduction (Martin, 1987). Females in expansion sites had higher restraint induced cort during both incubation and nestling rearing stages, but only exhibited elevated basal cort when rearing nestlings. Additionally, the restraint protocol utilized in this study did elicit an elevated cort response (Figure 1). During incubation, females at historical versus expansion sites did not differ in body mass, however, when rearing nestlings, females at expansion sites were lighter. When responding to the mock predator trials, females at historical and expansion sites did not differ in how quickly they approached the crow model but females in the expansion site dove at the crow more (Table 2).

In expansion sites, only females with nestlings exhibited elevated basal cort. However, these results may be evidence to support the cort-adaptation hypothesis that states elevated levels of cort can be adaptive. Bonier, Moore, et al. (2009) found female tree swallows rearing nestlings (10-12 days old) had elevated basal cort compared to when females were incubating. However, females with elevated basal cort invested more in

reproduction (via greater brood mass). When basal cort was elevated during incubation, the females had decreased reproductive success. This may be indicative that the cort-fitness hypothesis in tree swallows is dependent on the life history stage and is stronger support for the cort-adaptation hypothesis. Increased basal cort may be adaptive so females can respond to greater energetic demands required to provision nestlings (Bonier, Moore, et al., 2009). Females that had low cort during incubation but elevated during nestling phase had the heaviest broods. Females with low incubation cort may have arrived to breeding site in good quality and invest large amounts of energy towards reproduction (e.g., more eggs). However, once hatched, more eggs mean more nestlings to feed, and elevated cort will help to reallocate resources to assist high reproductive demands.

Because females in historic and expansion sites had low basal cort during incubation, and expansion females exhibited elevated restraint induced cort, my results may support that cort-adaptation is associated with colonization. However, I did not measure the same females from incubation to rearing nestlings like Bonier, Moore, et al. (2009), so this is speculative. Because tree swallows are undergoing a successful range expansion, this study may be additional evidence that elevated cort can be adaptive. Females in expansion sites with nestlings do have lower body mass, which may indicate a poor body condition during nestling rearing. However, I did not measure fitness of individuals so I cannot say if this had any effect on fledgling success or brood mass. Additionally, expansion sites had no obvious invertebrate shortages and territories tended to have more open habitat – which tree swallows prefer for foraging (Winkler et al., 2011), and percent openness per territory was not correlated to basal cort or body mass.

In addition to the cort-adaptation hypothesis, house sparrows in Kenya undergoing range expansion exhibit elevated restraint induced cort, similar to the expansion tree swallows in the current study (Martin & Liebl, 2014). The authors suggest that elevated cort enables individuals to meet the challenges of an unpredictable and novel environment and keep up with the energy demands of new locations. Although chronically high levels of cort are potentially harmful, and should be selected against, they should eventually subside to mirror levels of tree swallows in historic sites (see Liebl, Shimizu, & Martin, 2013).

I found some evidence to corroborate Duckworth and Badyaev's research that suggest individuals utilize aggression at expansion sites (2007). Tree swallow females with nestlings at expansion sites dove more often at the model compared to those in historical locations. At each site sampled, the females rearing nestlings commenced breeding earlier in the season than did the incubating females, which is often indicative of a high quality individual (e.g., Siefferman & Hill, 2005). Therefore, it is possible the females rearing nestlings possess an intrinsic quality that assists the females in maintaining an aggressive phenotype and that aggression may benefit fitness of range expanding females. Within expansion and historic sites, there were not differences in the number of dives between incubation and females with nestlings. Therefore, even though the interaction between breeding stage and range location was statistically significant, it may not be biologically meaningful, and should be acknowledged that the overall expansion population had more dives (Figure 8). Interestingly, latency to respond to the mock predator was not a significant measurement of aggression. It may be that latency is a more subjective measure; I acknowledge more confidence in correctly identifying dives compared to approach.

Additionally, the distance from the box the female went after the startle of my approach may influence her ability to detect the model crow and time to return to box.

I did not find evidence that behavior is directly mediated by cort, which may not be surprising as cort is a metabolic hormone. However, if homeostasis is compromised and individuals elevate cort, then this should reduce energy reserves (Hau et al., 2016) and their ability to maintain aggression. Elevated cort and reduced body condition at expansion sites could also be caused by reduced habitat suitability for tree swallows. Yet, I found little consistent evidence that expansion sites are lower quality breeding locations. In expansion sites, birds tend to breed in more open habitat and may experience higher prey availability. My measures of territory land use and prey availability, however, were coarse and possibly are an incomplete representation of habitat parameters (see Johnson, 2007). The malaise traps did not show any obvious differences in insect availability at the sites, indeed, Boone NC had the highest wet mass and greatest diversity, suggesting it may have the highest prey availability. Currently, tree swallow prey preference and habitat preferences are not well known and may be site specific (e.g., Hussell, 2012; McCarty & Winkler, 1999) and can change in a short time, even throughout a breeding season (reviewed in Johnson, 2007). Finally, if habitat differences were driving these range expansion trends in hormones and behavior, I would expect to find significant correlations between those measures and land use. Nonetheless, I cannot rule out the possibility that at other, unmeasured aspects of habitat select for both elevated cort and aggression among females at expansion sites.

Alternatively, the physiological and behavioral traits that facilitate dispersal may be maternally and environmentally influenced prior to novel colonization (Meylan, Belliure, Clobert, & de Fraipont, 2002; Meylan & Clobert, 2005). It may also be that individuals are

physiologically and/or behaviorally plastic (i.e., the ability of genotype to alter phenotype based on environment), and are thus better able to cope with fluctuations in new environment (reviewed in Cote et al., 2010; Nussey, Postma, Gienapp, & Visser, 2005; e.g., Martin & Liebl, 2014). Unfortunately, my data do not allow me to differentiate between genetic influences or plasticity as alternative causal explanations for the successful range expansion of tree swallows.

In this study, I found evidence that cort and behavior may be facilitating the range expansion of tree swallows. I also may have evidence to support the cort-adaptation hypothesis coupled with the importance of investigating breeding stage on a much larger scale than previously researched. To my knowledge, studies that quantify behavior and physiology across a species' historic and expansion sites are limited, and this study may increase knowledge on how populations successfully colonize. There are many other possibilities that should be investigated in the future to determine which behaviors facilitate range expansion. If tree swallows have adapted to maintain aggression despite the assumed costs (i.e., lower reproductive success), and adaptively respond physiologically, I predict their expansion will continue to the southern US. However, further research is required to elucidate the role of physiology that mediate dispersal.

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Figures

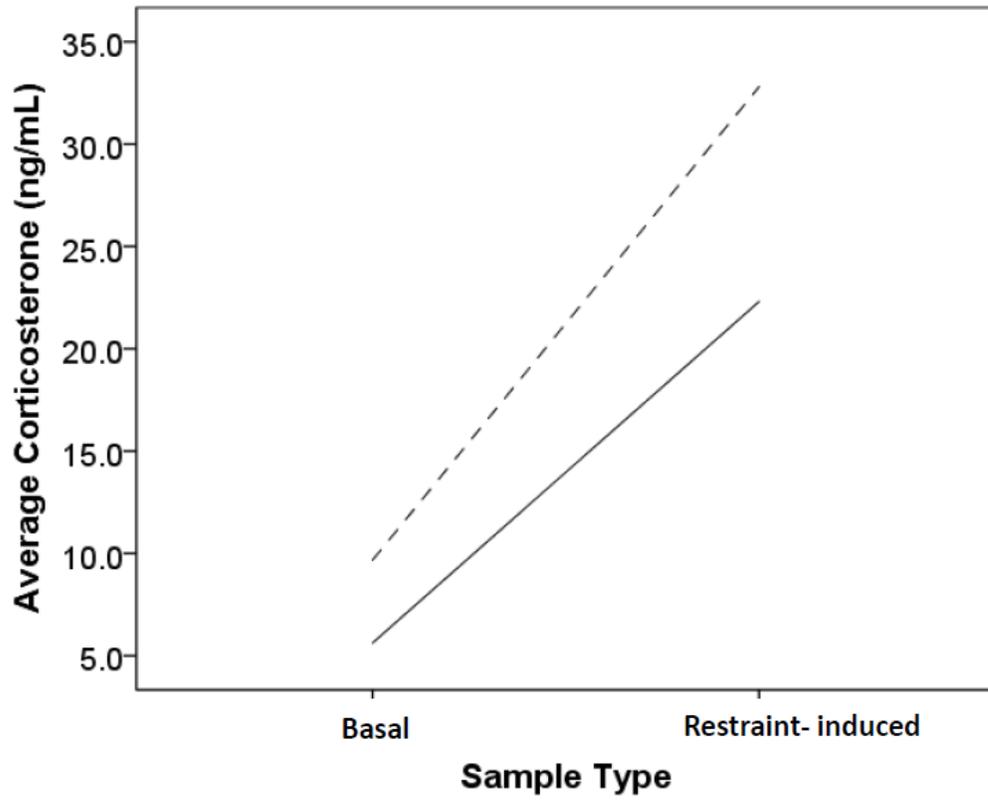


Figure 1. Overall average of change in corticosterone from basal to restraint induced in historic (solid line) and expansion (dashed line) sites.

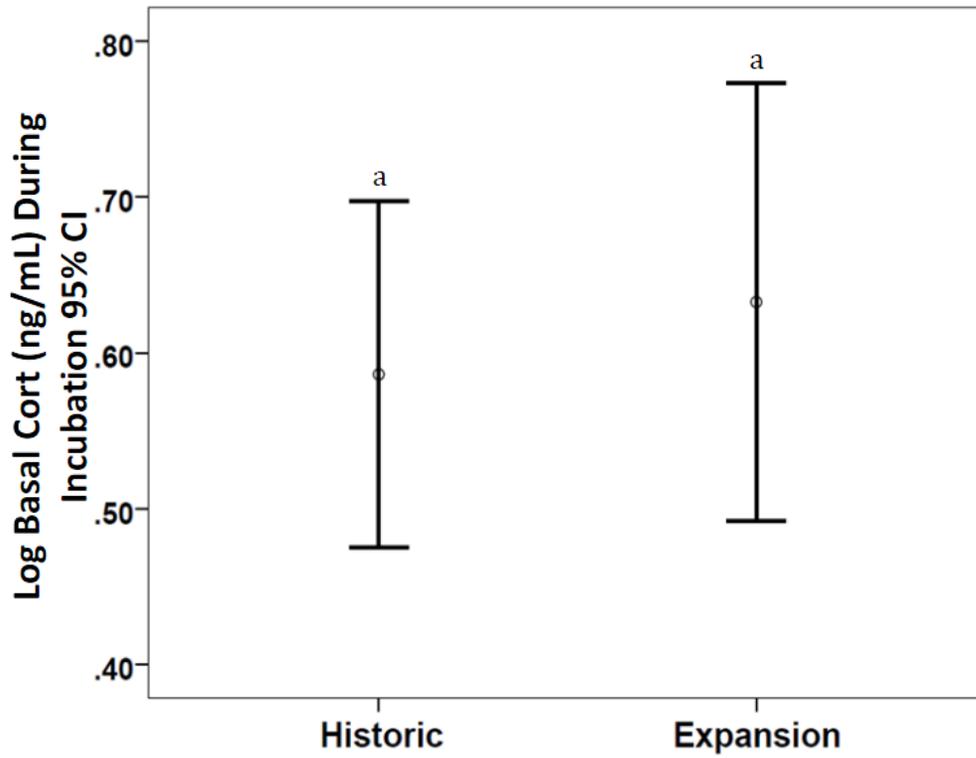


Figure 2. Comparison of the mean +/- 95% confidence intervals of basal cort (ng/mL) in historic and expansion sites in incubating females. There was no difference in basal cort in expansion versus historical sites. Letters denote statistical significance at the 0.05 level.

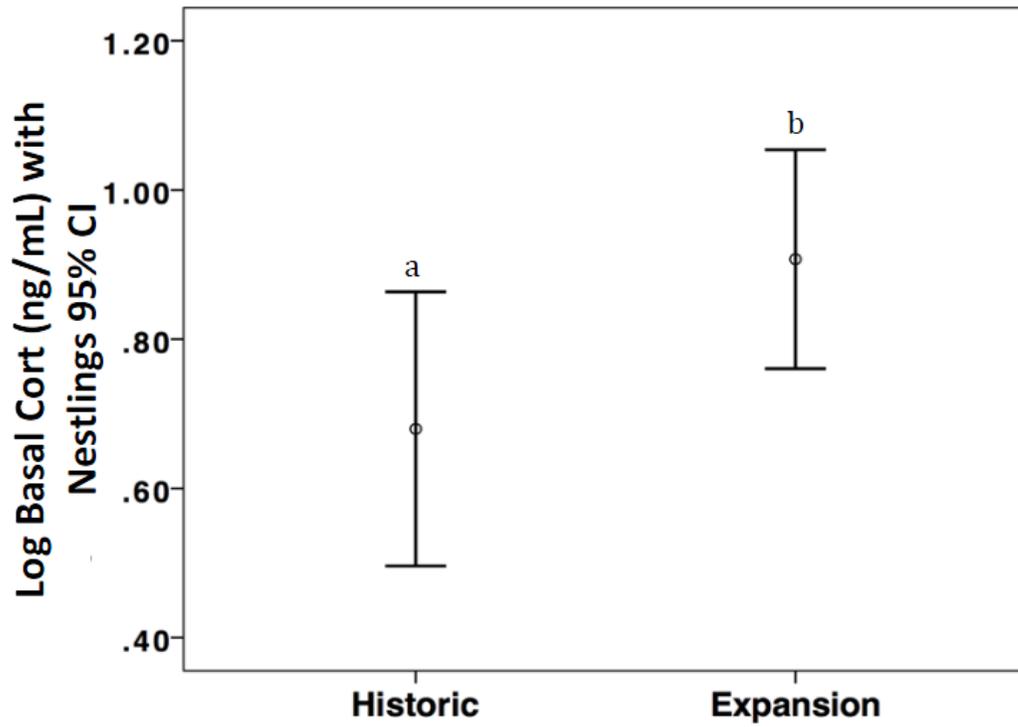


Figure 3. Comparison of the mean +/- 95% confidence intervals of basal cort (ng/mL) in historic and expansion sites when females have nestlings. Expansion females had elevated restraint induced cort when rearing nestlings. Letters denote statistical significance at the 0.05 level.

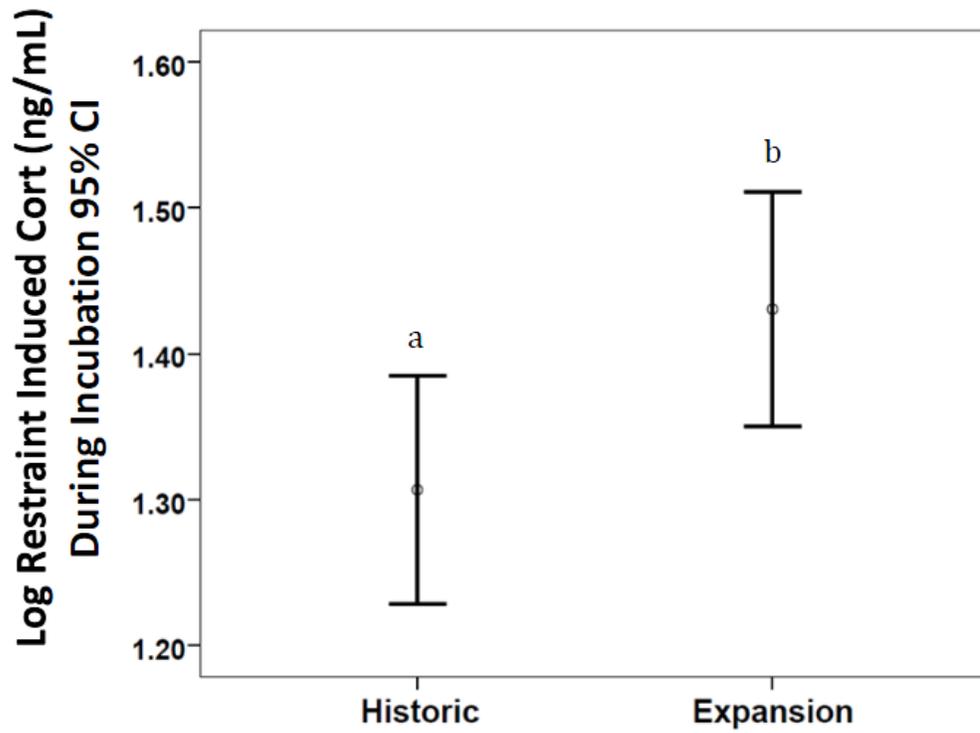


Figure 4. Comparison of the mean \pm 95% confidence intervals of restraint induced cort (ng/mL) in historic and expansion sites when females are incubating. Expansion females had elevated restraint induced cort. Letters denote statistical significance at the 0.05 level.

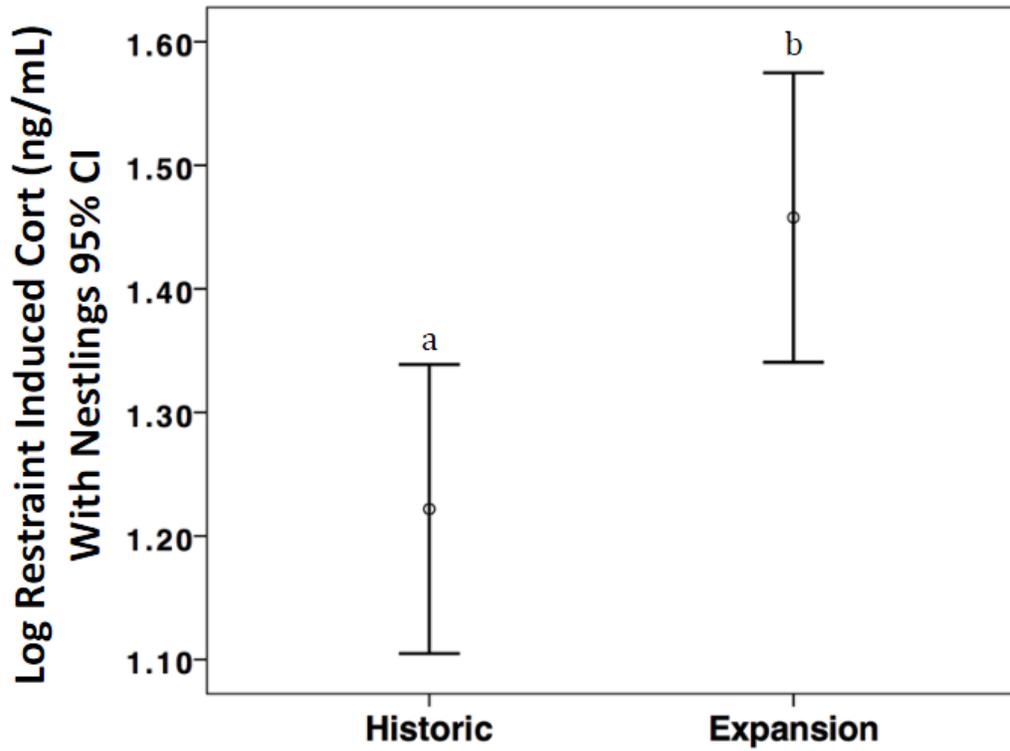


Figure 5. Comparison of the mean \pm 95% confidence intervals of restraint induced cort (ng/mL) in historic and expansion sites when females have nestlings. Expansion females had elevated restraint induced cort. Letters denote statistical significance at the 0.05 level.

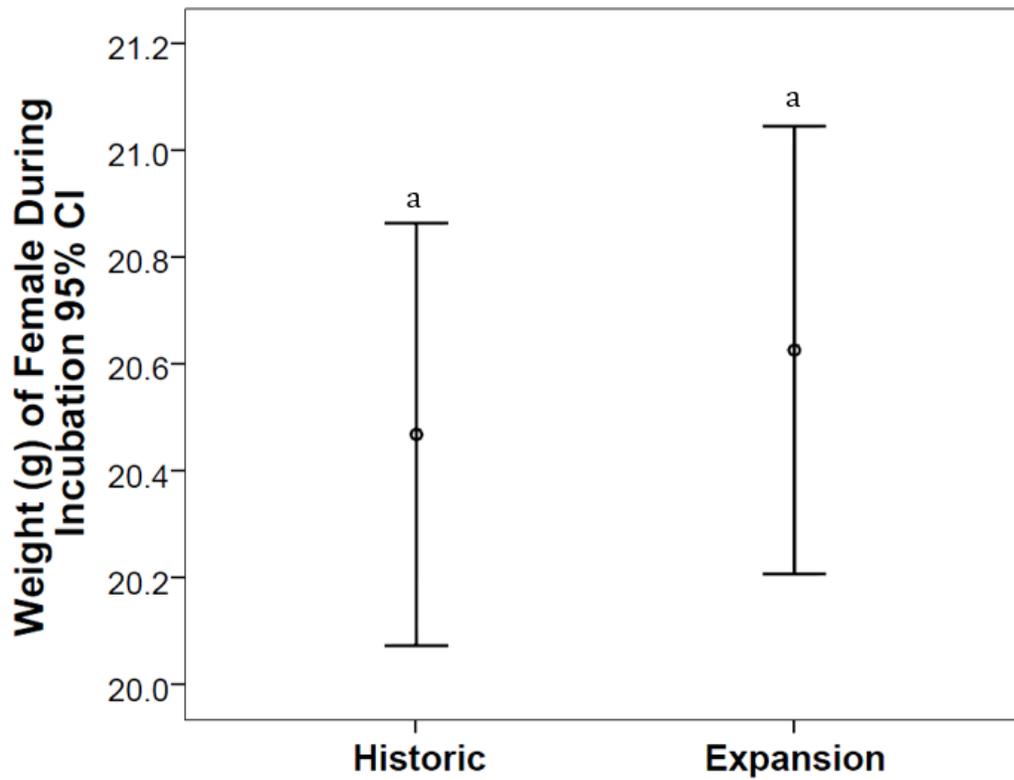


Figure 6. Comparison of the mean \pm 95% confidence intervals of mass (g) of breeding female tree swallows in historic and expansion sites during incubation. Weight was not significantly different. Letters denote statistical significance at the 0.05 level.

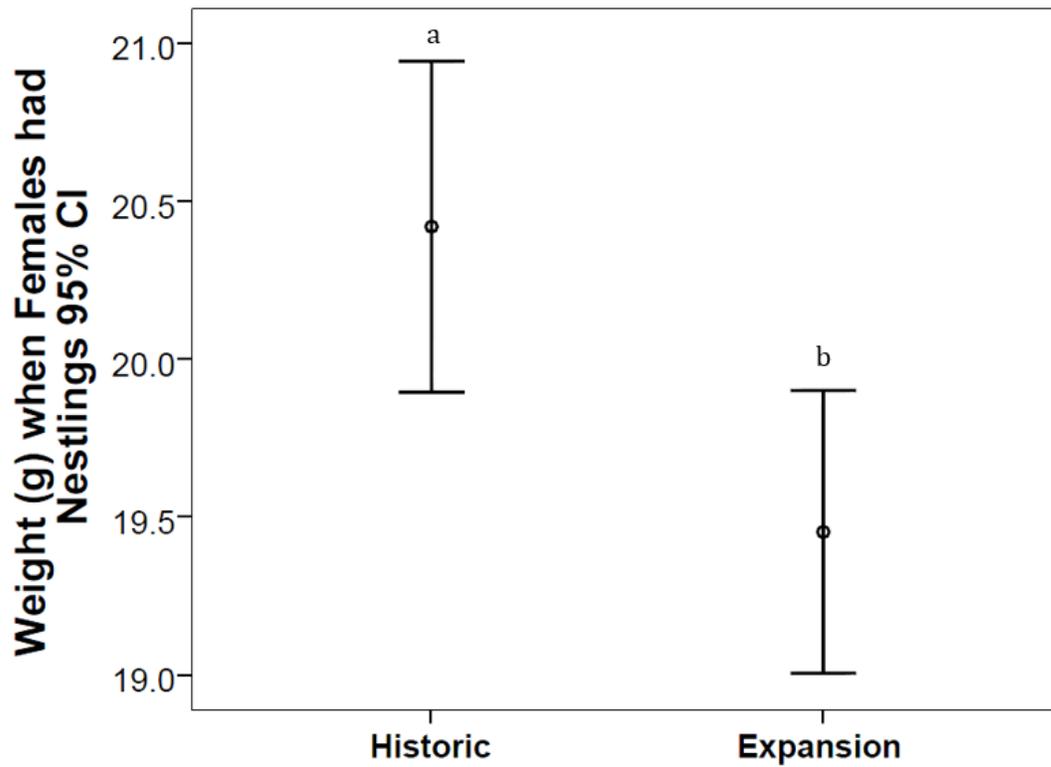


Figure 7. Comparison of the mean \pm 95% confidence intervals of mass (g) of breeding female tree swallows in historic and expansion sites when females had nestlings. Expansion females weighed less than historic females. Letters denote statistical significance at the 0.05 level.

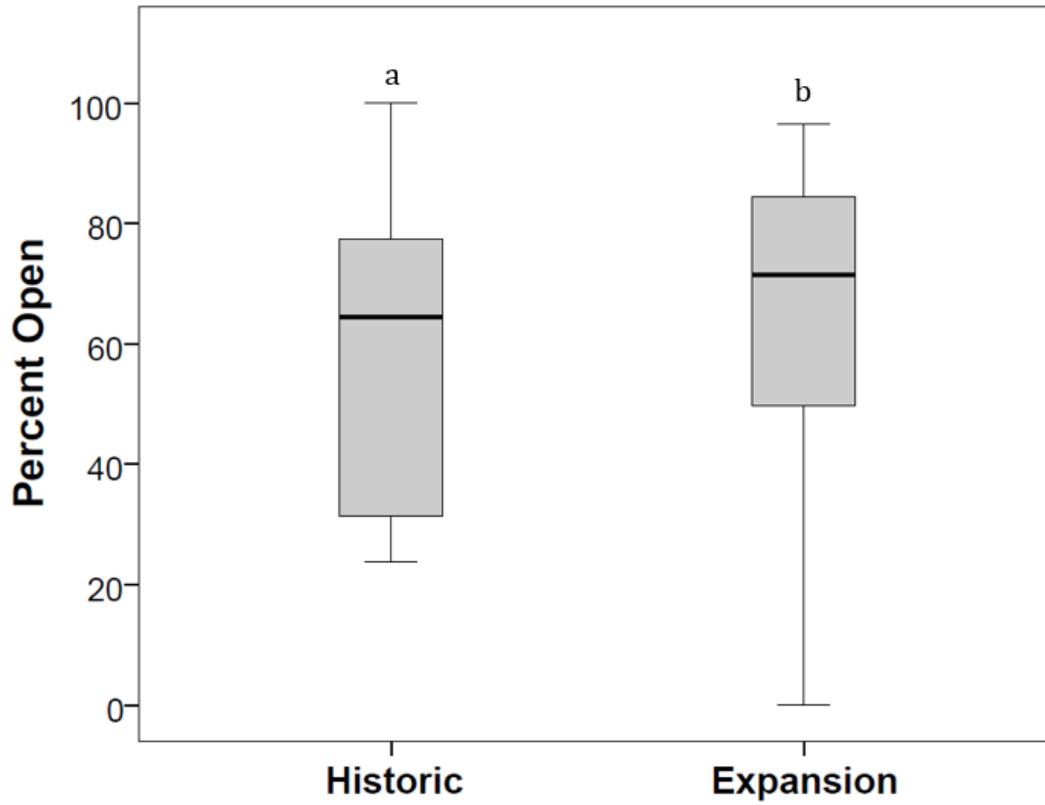


Figure 8. Percentage of open land (calculated by a 300 m radius at each nestbox) in historic and expansion sites. Expansion sites had more open territories. Letters denote statistical significance at the 0.05 level.

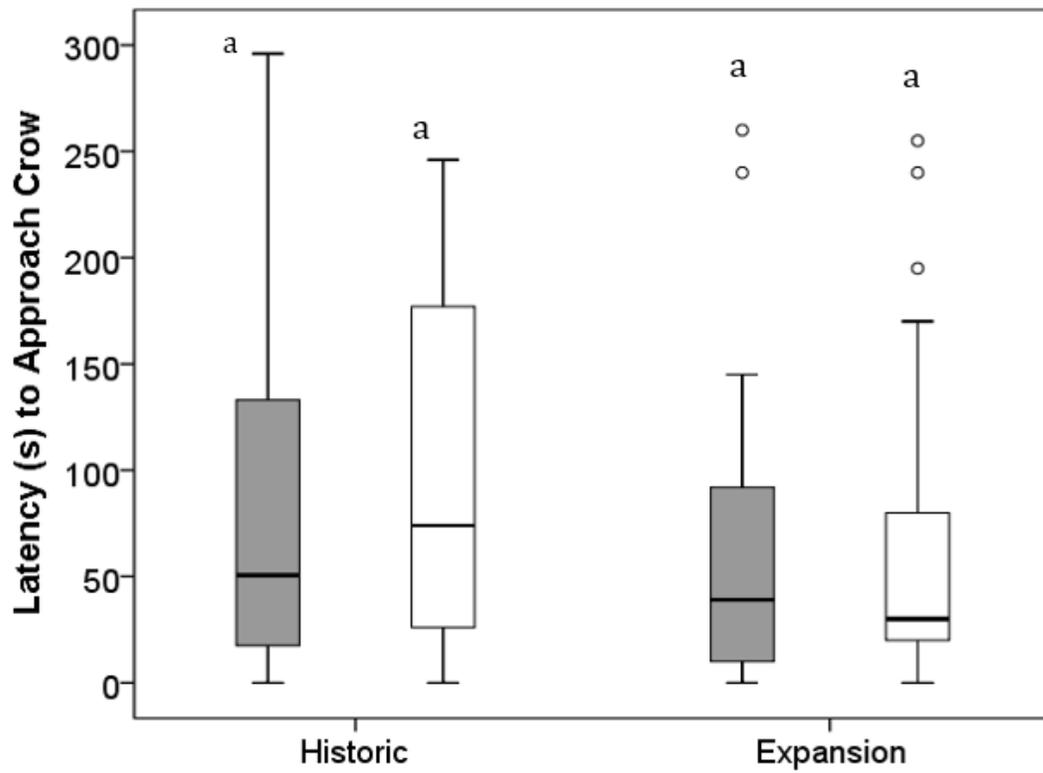


Figure 9. Latency (s) to for incubating females (solid) and females with nestlings (white) approach the crow within 1 meter. There was no significant differences in latency. Letters denote statistical significance at the 0.05 level.

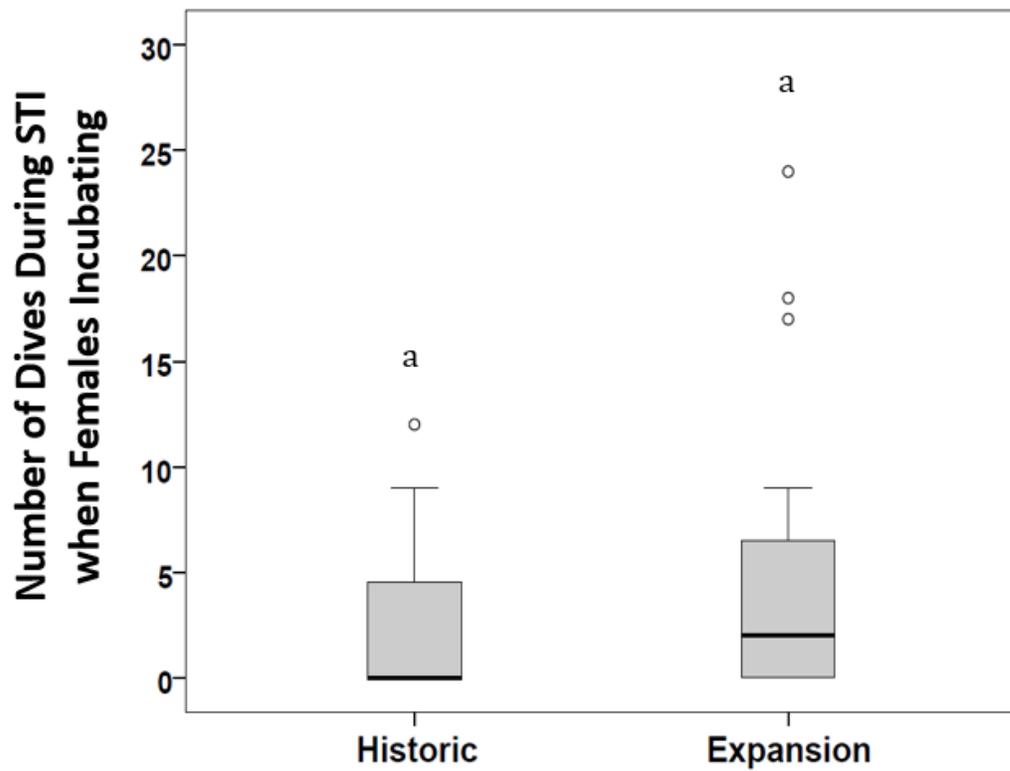


Figure 10. Number of dives at the model crow during STI by incubating females. Females did not dive more during incubation. Letters denote statistical significance at the 0.05 level.

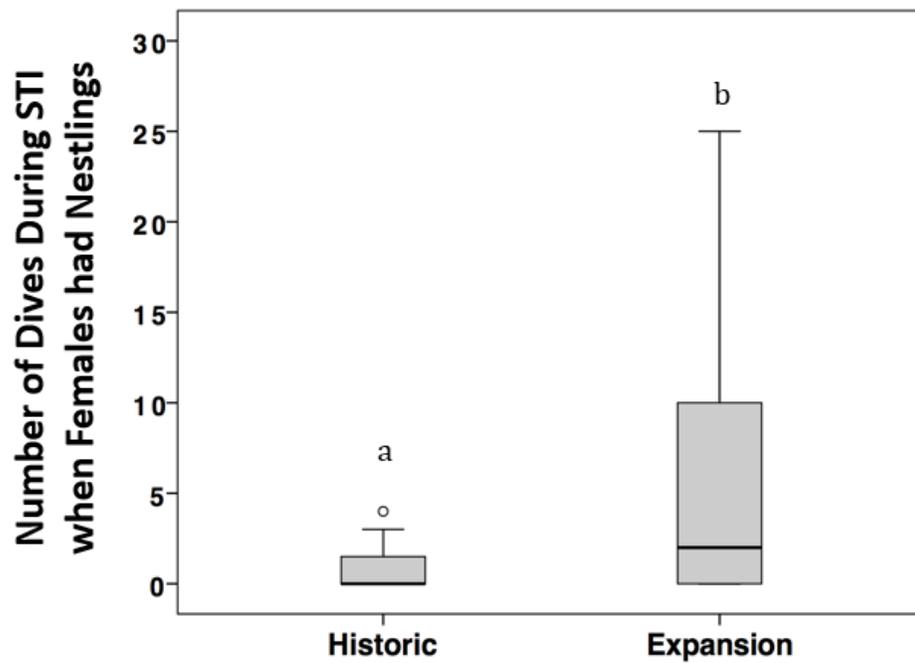


Figure 11. Number of dives at the model crow during STI by females with nestlings. Females in the expansion sites dove more when they had nestlings. Letters denote statistical significance at the 0.05 level.

Site	Mass(g)	Order	Description	Quantity
Iowa (Expansion)	10.99	Diptera	True Flies	67
		Hymenoptera	Wasps, Bees	6
		Coleoptera	Beetle	1
Valle Crucis, NC (expansion)	13.45	Diptera	True Flies	137
		Hymenoptera	Wasps, Bees	14
		Coleoptera	Beetle	10
		Lepidoptera	Moths	5
		Araneae	Spiders	1
		Hemiptera	Shield Bugs	10
		Plecoptera	Stoneflies	2
		Trichoptera	Caddisflies	6
Wisconsin (Historic)	10.74	Diptera	True Flies	47
		Hymenoptera	Wasps, Bees	6
		Araneae	Spiders	1
Ontario (Historic)	11.32	Diptera	True Flies	87
		Hymenoptera	Wasps, Bees	3
		Lepidoptera	Moths	3
		Araneae	Spiders	1

Table 1. Summary of invertebrate order, mass, and description of what was found in malaise traps

Expansion (vs. Historic) Not split for breeding stage	Expansion (vs. Historic) split by stage	Expansion (vs. Historic) split by stage
	Incubation	Nestlings
↑Change in cort	= Basal cort	↑Basal cort
↑Percent Open	↑ Restraint induced cort	↑ Restraint induced cort
	= Latency to approach	= Latency to approach
	= Number of dives	↑Number of dives

Table 2. Summary of results comparing expansion sites to historic sites 1) overall, 2) during incubation, and 3) when females had nestlings

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Vita

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