

INFLUENCE OF MATERNAL AGGRESSION AND STRESS RESPONSE ON OFFSPRING
QUALITY IN TREE SWALLOWS

by

Kimberly Rebecca Todd

Honors Thesis

Appalachian State University

Submitted to the Department of Biology
and The Honors College
in partial fulfillment of the requirements for the degree of

Bachelor of Science

May, 2020

Approved by:

Lynn Siefferman, Ph.D., Thesis Director

Jon Davenport, Ph.D., Second Reader

Lynn Siefferman, Ph.D., Departmental Honors Director

Jefford Vahlbusch, Ph.D., Dean, The Honors College

Abstract

Mounting evidence suggests wild animals possess unique personalities that, while consistent within individuals, differ across individuals in the population. Conversely, the glucocorticoid profiles of animals can show high within-individual plasticity. The repeatability of some traits coupled with the degree to which other traits vary across time and contexts should be considered complementary aspects of animals' coping styles. Behavior-physiology interactions and their fitness consequences have only recently surfaced in the literature, yet these phenotypic combinations are heritable, fitness-related, and shaped by evolutionary forces and thus represent an adaptive strategy for coping in a dynamic environment. A behavioral reaction norm (BRN) is a modelling approach used to quantify the degree of within- and between-individual personality ('intercept') and plasticity ('slope'). We use a 3-year dataset collected on a breeding population of tree swallows (*Tachycineta bicolor*) in the southern Appalachians to assess how female personality (nest defense aggression) and glucocorticoid plasticity (baseline corticosterone/CORT slope) interact to influence offspring quality across multiple years. We found that females with aggressive and nonaggressive personalities adjusted baseline CORT differently across the breeding stage. Nonaggressive females tended to experience increased baseline CORT from the early to late nestling stage, consistent with a 'cost of reproduction,' whereas aggressive females did not. Personality alone did not predict reproductive success, but there was a personality-by-CORT-slope interaction. Baseline CORT slope predicted nestling quality, but only among aggressive females which maintained a constant level of baseline CORT in 2015 and reduced baseline CORT in 2016. Overall, our results suggest that aggressive females can produce high-quality young without enduring a physiological 'cost of reproduction.' Comparable fitness despite differences in glucocorticoid plasticity among females of different

personalities may be driven by changing environmental contexts, individual attributes, and unique physiological optima that aid individuals in striking a personalized balance between energy use and allocation to offspring.

Introduction

The phenomenon known as ‘animal personality’ has long captivated behavioral ecologists and evolutionary biologists. Animal personality exists when a population exhibits within-individual repeatability coupled with consistent between-individual differences in a phenotype across time and contexts (Dingemanse et al. 2010; Hau & Goymann 2015). Personality research encompasses a broadening array of taxa from three-spined sticklebacks (*Gasterosteus aculeatus*; Harcourt et al. 2009), to aphids (*Acyrtosiphon pisum*; Schuett et al. 2011), to great tits (*Parus major*; Hollander et al. 2008). Assessments of personality include traits such as exploratory behavior (Verbeek et al. 1994), boldness (Réale et al. 2009), neophobia (Ensminger & Westneat 2012), and aggression (Betini & Norris 2012). Individuals can exhibit suites of correlated repeatable behaviors, or behavioral syndromes (Sih et al. 2004; van Oers et al. 2004), such as aggressive-bold (Huntingford 1976) and aggressive-exploratory syndromes (Verbeek et al. 1994).

Other animal behaviors are characterized by their lability. That is, individual animals from the same population may adjust their behavior differently in response to variation in environmental conditions or physiological stressors; this is referred to as ‘phenotypic plasticity.’ Plasticity is defined as a change in the expressed phenotype of a genotype as a function of the environment (Sih et al. 2004), or as the responsiveness of an individual’s physiology and/or behavior to environmental variation (Dingemanse et al. 2010; Cockrem 2013). Traits known to

show intra-individual plasticity include reproductive timing (Nussey et al. 2005a; Nussey et al. 2005b), sperm morphometry (Immler et al. 2010), and stress response (Angelier & Wingfield 2013; Cockrem 2013; Lendvai et al. 2015).

Personality and hormonal plasticity can interact as ‘coping styles,’ or combinations of the behavioral and physiological responses of an individual characterizing its reaction to stressors (Koolhaas et al. 1999; Dingemanse et al. 2010; Gangloff 2016). These interactions have been documented in numerous taxa including dogs (Corson & Corson 1976), primates (Sapolsky 1990), and birds (Stöwe et al. 2010). This concept assumes a negative association between aggression and hypothalamic–pituitary–adrenal (HPA) axis reactivity (Grace & Anderson 2014): individuals can be ‘proactive’ with high aggression and low stress response, or ‘reactive’ with low aggression and high stress response (Sih et al. 2004; Dingemanse et al. 2010; Cockrem 2013). Aggressive individuals are frequently proactive and respond to stressors through confrontation, whereas nonaggressive individuals are typically reactive and respond to stressors through acclimation and immobility (Benus 1988; Hessing 1994; Cockrem 2013). Studies have shown that coping styles are heritable (Boake 1994), associated with fitness-related behaviors (e.g. foraging, exploration, and aggression; Dingemanse et al. 2002; Dingemanse & Reale 2005), and shaped by evolutionary forces (Bell et al. 2009).

The interaction of personality and plasticity has been explored through a modeling approach known as a ‘behavioral reaction norm’ (BRN). BRNs quantify the degree of individual plasticity as well as mean population-level plasticity under two or more environmental conditions (Dingemanse et al. 2010; Cockrem 2013). These models portray the range of phenotypes individuals within a population can express in a given set of conditions; the resultant slope measures the degree of individual plasticity (Dingemanse et al. 2010; Cockrem 2013). The

intercept, or ‘elevation,’ of a BRN is determined by an individual’s personality and signifies an individual’s response under average conditions (Dingemanse et al. 2010). The covariance between a BRN’s intercept and slope mathematically represents a coping-style (Dingemanse et al. 2010).

Corticosterone (hereafter termed ‘CORT’), the primary avian glucocorticoid, enables birds to respond to environmental and physiological stressors (Landys et al. 2006). Baseline CORT regulates daily metabolic demands and mediates tradeoffs between energy use and allocation to tasks such as raising a brood (Landys et al. 2006; Angelier & Wingfield 2013; Guindre-Parker et al. 2019). Baseline CORT is highly plastic within individual birds and responds to environmental conditions as well as an individual’s energetic reserves (Bonier et al. 2009; Angelier & Wingfield 2013; Cockrem 2013; Hau & Goymann 2015; Akçay et al. 2016). An increase in baseline CORT throughout a reproductive attempt cues allocation of resources to reproduction through increased foraging and provisioning behaviors, ultimately leading to higher fitness (‘CORT-Adaptation Hypothesis’; Bonier et al. 2009). A high initial level of baseline CORT at the onset of a reproductive attempt indicates individuals in poor condition; these individuals must reallocate resources from reproduction to stressor-response, leading to reduced fitness (CORT-Fitness Hypothesis; Bonier et al. 2009; Bonier et al. 2011). Poor-quality individuals often launch a more acute stress response which inhibits sexual and parental care behaviors, adversely affecting fitness (Angelier & Wingfield 2013). Variation in CORT response is also attributable to resource availability, social context, age, and life history stage (Bonier et al. 2009; Angelier & Wingfield 2013; Hau & Goymann 2015).

Aggression, on the other hand, is a well-established personality trait in free-living birds and manifests in territorial and nest defense behaviors associated with breeding (Montgomerie &

Weatherhead 1988; Sih et al. 2004; Both et al. 2005; Betini & Norris 2012). For obligate secondary cavity-nesters which rely upon pre-excavated cavities for nest-building, competition for limited cavities is intense and aggression-mediated (Newton 1994). Indeed, aggression is an important determinant of territory acquisition (Both et al. 2005). Rosvall (2008) found that in tree swallows, aggressive females obtain nesting cavities more frequently than nonaggressive females. In socially monogamous birds, nest defense aggression can be vital for brood survival, though it may incur substantial fitness costs in the form of reduced parental survival (Montgomerie & Weatherhead 1988). Further, studies of both male (Duckworth 2006; Pryke and Griffith 2009) and female (Rosvall 2010) birds demonstrate a trade-off between aggression and parental care wherein highly aggressive individuals invest less in parental care, adversely affecting fitness ('cost of aggression').

Tree swallows (*Tachycineta bicolor*) are loosely colonial, secondary cavity nesters that readily nest in manmade boxes. Due to the limited availability of nest boxes, tree swallows compete for and defend these cavities against both conspecific nest usurpers and nest predators (Robertson et al. 1992). Tree swallows breed in fields and marshes throughout central and northern North America and winter along the Gulf of Mexico as well as northern Central America (Winkler et al. 2011). In the past 40 years, tree swallows have expanded their range to the southeastern U.S. (Winkler et al. 2011) and developed a suite of behavioral strategies and physiological mechanisms such as aggression and glucocorticoid plasticity to facilitate their expansion (Albers 2016). Tree swallows in the expansion zone exhibit higher aggression and CORT levels compared to historic populations (Albers 2016), which may be advantageous in the colonization of novel and unpredictable environments (Cockrem 2013). In our southern-breeding population of tree swallows, individuals show highly repeatable nest defense aggression within

and across years, whereas baseline CORT shows high within-individual plasticity (Content 2017). Further, baseline CORT shows a population-level increase from the early to late nestling stage due to the physiological costs of raising a brood, but individual females vary in how their baseline CORT changes (Content 2017).

How endocrine signals mediate behavior and *vice versa* in wild birds is well-studied; however, less is known about how hormones and behavior, glucocorticoid plasticity and personality, interact to influence offspring quality. In this study, we investigate the interactive effects between maternal aggression and baseline CORT on offspring quality across multiple years. Whereas behavior relates to food acquisition and energy expenditure, physiology is associated with energy allocation and mobilization, generating a trade-off between survival and reproduction in wild populations where resources are limited and fluctuating (Gangloff 2016). Thus, we hypothesize that the reproductive success of aggression-CORT combinations is context-dependent due to temporal fluctuations in available resources, and the consequent trade-off between maternal energy use and allocation to offspring. Specifically, we ask how aggression and baseline CORT profiles interact to influence offspring growth, and how these interactions vary with year. This study aims to elucidate how the link between personality and glucocorticoid plasticity influences the reproductive success of a free-living passerine, as well as how annual variability shapes these interactions.

Methods

Fitness and Adult Captures

We studied wild breeding tree swallows from May to July of 2014, 2015, and 2016 in Watauga County, North Carolina. In 2014, we monitored active nests in Meat Camp, NC (n=58

nests; 36.299 N, 81.676 W), and in 2015 and 2016, we monitored active nests at two sites, Meat Camp and Valle Crucis, NC (2015: n=90 nests; 2016: n=85 nests; 36.209 N, 81.778 W). We monitored nest building, egg laying, hatching, and fledging success. We fitted nestlings with a United States Geological Survey (USGS) aluminum band at 8 days old (day 1 = hatch day), and measured nestling mass (± 0.1 g). Nestling tree swallow growth asymptotes at ~ 12 days old; therefore, the mass of nestlings at 8 days old is indicative of the period of rapid mass gain (McCarty 2001).

Female tree swallows were captured in nest boxes twice using trapdoors (Stutchbury & Robertson 1986), once during late incubation (day 10 incubation ± 3 days; ‘early nestling stage’) and once when nestlings were 10 days old (± 3 days; ‘late nestling stage’), and all captures occurred between the hours of 06:00-15:00. Upon first capture, we banded females with a USGS aluminum band and one colored plastic band, as well as measured body mass (± 0.1 g), wing length, and tail length. It can be challenging to visually determine the sex and identity of tree swallows by plumage and bands; therefore, we also colored the white abdominal feathers with either red, green, or blue marker (Sharpie®) for remote identification. We started a timer as soon as we captured each bird and collected an initial blood sample ($64 \pm 24 \mu\text{L}$) within 3 min to measure hematocrit and baseline CORT levels. Blood was drawn from the alar wing vein using a 26.5-gauge needle, transferred to a 1.5-mL tube, and kept on ice until centrifugation. We then stored the plasma at -80°F until processing.

Nest Defense Aggression and Reaction Norms

Approximately 24-30 hr after each adult capture, we conducted a behavioral assay of maternal aggression in response to a simulated nest predator as modified from (Winkler 1992;

Winkler 1994). Behavioral trials were conducted when nestlings were 2 days old (± 3 days; ‘early nestling stage’) and 11 days old (± 3 days; ‘late nestling stage’). Our predator decoy was an American crow (*Corvus brachyrhynchos*), which was suspended 0.3 m above the nest box using a wire such that it moved in a semi-natural flight position. Trials began by visually identifying the female and then deploying the decoy. For 5 min from a distance of 40 m, we measured the number of dives females performed toward the model within 10 m of the nest box. We then used a BRN to measure the intercept (i.e. initial level during incubation) of aggression (see Content 2017 for details), and classified females as high- or low-aggression. High-aggression females had an intercept of >0.98 , whereas low-aggression females had an intercept of <0.98 .

CORT Assays and Reaction Norms

We extracted and quantified plasma CORT using an enzyme immunoassay kit (ENZO Life Sciences, Cat. No. ADI 901-097; Donkey anti-Sheep IgG; assay sensitivity 27 pg/mL). Duplicates of individual samples were assayed with 5 standards that represented the standard curve ranging from 32 to 20,000 pg/mL, blanks, and positive controls. In 2014, CORT was measured across 5 assays with a 2.01% inter-assay variation, and the average intra-assay variation was 2.04%. In 2015, CORT was measured across 5 assays with a 3.14% inter-assay variation, and the average intra-assay variation was 1.89%. In 2016, CORT was measured across 3 assays with a 1.19% inter-assay variation, and the average intra-assay variation was 1.94%. We then used a BRN to measure the intercept (i.e. initial level during incubation) and slope (i.e. plasticity from the early to late nestling stage) of baseline CORT across the 11-day breeding period (see Content 2017 for details).

Statistical Analyses

We analyzed CORT and behavior using SPSS v. 26 (IBM Corp 2019). All tests were set at a significance level of $p \leq 0.05$. We used a Student's T-test to investigate whether maternal aggression predicts baseline CORT slope, first egg date, clutch size, brood size, and number fledged with high- and low-aggression females as the t-test groups. We then fit a Linear Mixed Model (LMM) with nest ID as a random effect to test whether year, maternal aggression, and baseline CORT slope interact to influence nestling mass. To compare nestling mass across years, we fit an LMM with nest ID as a random effect and year as a fixed effect. We performed the same analysis to investigate year effects on maternal aggression as well as baseline CORT intercept and slope. We then proceeded to split the data by year and run an LMM with nest ID as a random effect to test whether maternal aggression and baseline CORT slope interact to influence nestling mass in individual years. We report nestling mass at age day 8 post-hatch, as this age is indicative of the period of rapid mass gain (McCarty 2001) and therefore high sensitivity to parental efforts.

Ethical Note

This study followed the guidelines for the Care and Use of Animals for Research, Teaching, or Demonstrations at Appalachian State University (#16-16). This study was also conducted under the Institutional Animal Care and Use Committee (IACUC) under USGS master banding permit #23563 (Lynn Siefferman). Each bird was minimally handled to reduce stress and physical harm.

Results

High- and low-aggression females adjusted baseline CORT differently across the breeding stage. Low-aggression females (n=35) increased baseline CORT, whereas high-aggression females (n=21) reduced baseline CORT ($t=2.25$, $p=0.028$, $df=54$; Fig. 1).

Reproductive parameters (date of first-laid eggs, clutch size, brood size, and number of offspring fledged) did not significantly differ between high- and low-aggression females (Table 1).

We found significant interactions between year, maternal aggression, and baseline CORT slope on nestling mass ($F_{2,203}=8.07$, $p<0.001$). Nestling mass was significantly highest in 2015, but only marginally ($F_{2,765}=3.19$, $p=0.042$; Fig. 2). Maternal aggression was significantly lowest in 2015 ($F_{2,112}=9.52$, $p<0.001$; Fig. 3). Maternal baseline CORT intercept was significantly lowest in 2016 ($F_{2,68}=5.69$, $p=0.005$; Fig. 4). Maternal baseline CORT slope was not significantly different across years ($F_{2,68}=1.86$, $p=0.164$; Fig. 5).

We found significant interactions between maternal aggression and baseline CORT slope on nestling mass in individual years (2014: $F_{1,32}=13.34$, $p=0.001$; 2015: $F_{1,51}=5.89$, $p=0.019$; 2016: $F_{1,105}=0.56$, $p=0.456$). In 2015, high-aggression females that did not change their baseline CORT across the breeding stage reared the largest nestlings ($R^2=0.83$, $F=4.47$, $p=0.047$, $n=21$; Fig. 6), and no significant trend was found among low-aggression females. In 2014 and 2016, high-aggression females that reduced their baseline CORT reared the largest nestlings (2016: $R^2=0.10$, $F=4.49$, $p=0.041$, $n=40$; Fig. 7), and no significant trend was found among low-aggression females.

Discussion

Our data demonstrate that tree swallow personalities predicted changes in baseline glucocorticoids when mothers were sampled at the incubation and late nestling stages. While the nonaggressive females showed an increase in baseline CORT from the early to late nestling stage (Fig. 1), aggressive females tended to either maintain a consistent baseline CORT (Fig. 6) or experience a reduction across the breeding period (Fig. 7). Aggressive and nonaggressive females did not differ in several measures of reproductive success (first-egg date, clutch size, brood size, and number of offspring fledged). However, we did find that interactions between personality and glucocorticoids predicted nestling quality, but these relationships were complex and context-dependent. Aggressive females reared larger nestlings by maintaining consistent baseline CORT in one year and by showing a decrease in baseline CORT in another year. For the nonaggressive females, however, nestling mass was not predicted by variation in baseline CORT. While we focus here on identifying glucocorticoid levels associated with the highest fitness for individuals of different personality types, our data suggest environmental context matters.

Organisms that reproduce sexually must balance allocation of limited resources between current and future reproductive efforts. This ‘cost of reproduction’ is a classical life-history trade-off (Williams 1966) that has been demonstrated in myriad taxa both vertebrate (Descamps et al. 2009) and invertebrate (Kotiaho & Simmons 2003). An increase in baseline CORT throughout a current reproductive attempt is thought to reallocate resources from self-maintenance to reproduction, representing the ‘cost of reproduction’ (Hanssen et al. 2005); thus, baseline CORT slope is a measure of this cost. Additionally, ‘coping styles’ provide a basis for explaining the physiological underpinnings of animal personality, and how selection on behavior

also shapes physiological stress response and *vice versa* (Grace & Anderson 2014). Consistent between-individual differences in baseline CORT slope can emerge across a range of environmental conditions or life-history contexts (Lendvai et al. 2014; Lendvai et al. 2015). Our data indicate that in a North Carolina population of tree swallows, maternal personality and stress physiology interact to mediate the cost of reproduction such that females of different personalities adjust baseline CORT differently in response to mounting reproductive demands. Whereas the baseline CORT of low-aggression females increased as the breeding stage progressed, the baseline CORT of high-aggression females tended to remain stable or decrease across this period. Thus, it appears that low-aggression females paid the cost of reproduction while high-aggression females did not.

The relationship between glucocorticoids and personality traits including aggression is evident in domestic species such as chickens (*Gallus gallus*; reviewed in Cockrem 2007); however, it is more equivocal in wild avian populations (Kralj-Fišer et al. 2010; Garamszegi et al. 2012). Even so, wild populations exhibiting ‘proactive’ and ‘reactive’ phenotypes have been documented (Aplin et al. 2014; Grace & Anderson 2014; Jacques-Hamilton et al. 2017), and these coping styles are subject to selection (Carere et al. 2003; Stöwe et al. 2010). The question remains of what drives the variation in female coping styles within our North Carolina population of tree swallows, where nonaggressive females show consistent elevations in baseline CORT while aggressive females respond little, and inconsistently. Wong et al. (2015) demonstrated that proactive and reactive zebrafish (*Danio rerio*) lines possess different whole-brain transcriptome profiles consisting of genes associated with stress and anxiety-related behaviors. For example, reactive individuals showed significantly higher expression of the genes associated with elevating and deactivating glucocorticoids (Wong et al. 2015). Further, these

reactive individuals released cortisol faster within the first 6 min of exposure to a novel stressor, and then restored basal cortisol levels more quickly (Wong et al. 2019). Faster post-stressor release of CORT has also been documented in selectively bred reactive great tits (Baugh et al. 2012).

Additionally, Vitousek et al. (2014) suggested that the traditional lack of association between baseline CORT and behavior in models of reproductive success can stem from non-linear relationships between CORT and fitness. We found significant interactions between year and baseline CORT slope on nestling mass among the aggressive females, including a non-linear association between baseline CORT and nestling mass in 2015. Aggressive females that maintained a constant level of baseline CORT across the breeding stage reared the largest nestlings in 2015 (Fig. 6). Those that increased or decreased their baseline CORT reared smaller, poorer-quality nestlings. Overall, 2015 seemed to be an unusual year because baseline CORT at the population level did not vary across the breeding stage (Content 2017)—females did not show a ‘cost of reproduction’ (Vitousek et al. 2018a). Based on an annual summary of climatological data from the nearest National Oceanic and Atmospheric Administration (NOAA) weather station (Boone, NC), 2015 corresponded with levels of precipitation that far exceeded the long-term average. NOAA’s National Climate Report for 2015 additionally reports that most rainfall occurred in May as a product of tropical storm Ana. High precipitation, which is negatively associated with both foraging (Irons et al. 2017) and reproductive (Whitehouse et al. 2013) success in tree swallows, has been known to cause 90% of nests to fail in some populations (Ouyang et al. 2015) due to reductions in aerial insect abundance (Winkler et al. 2013). It is plausible that the female tree swallows at our study sites experienced high baseline CORT during incubation due to a reduced ability to forage, particularly as wet weather alters the

abundance and/or timing of insect emergence (Imlay et al. 2018). Additionally, because nestlings are featherless and thus incapable of thermoregulation early on, females may have had to increase their nest box occupancy when periods of heavy rainfall inflated brooding requirements (Radford et al. 2001). Subsequently, these females may have lacked additional energetic reserves to allocate towards reproduction in the late nestling stage which could explain the consistent level of baseline CORT across the breeding period. As to why aggressive females that experienced a reduction in baseline CORT produced lower-quality nestlings, it could be that these females did not re-allocate enough resources toward their brood, hindering nestling growth.

This same strategy was more successful in 2016—aggressive females that showed a decrease in baseline CORT reared the largest nestlings, and the relationship was linear (Fig. 7). Past studies (Sih & Bell 2008; Biro et al. 2010; Mathot et al. 2011; Dingemanse & Wolf 2013) have urged for a greater understanding of the extent to which individual plasticity is or is not consistent across time or contexts. Here, we demonstrate that the trajectory of glucocorticoid plasticity across individuals can change over time (e.g. from non-linear to linear) as it tracks changes in the relationship between baseline CORT slope and nestling quality. These complex year effects on the association of baseline CORT slope and nestling quality may be indicative of variation in environmental variables such as food availability, predation rates, and weather conditions. Moreover, Arnold et al. (2001) and Calsbeek et al. (2012) postulated that environmental variation creates an adaptive endocrine landscape dependent upon a combination of biotic and abiotic factors, a landscape expected to shift with seasonal, developmental, or life-history context. The influence of year on how aggressive females modulate baseline CORT across the breeding stage suggests that the costs and benefits of aggression and its interaction with CORT vary with this environmentally-driven landscape.

Nussey et al. (2007) similarly surmised that the presence of intraspecific variation in plasticity within a population points to environmental causes as a driving force. For example, Eurasian blue tits (*Cyanistes caeruleus*) increase CORT in response to lower temperatures, higher precipitation, and lower territory-scale oak density; however, low temperatures alone reduce nestling mass (Henderson et al. 2017). Glucocorticoid plasticity can also differ among populations—tree swallows in Wyoming appear to upregulate baseline CORT levels in response to atypically low temperatures and high precipitation, whereas tree swallows in Tennessee, which experience both a longer breeding season and more predictable conditions, maintain consistently low baseline CORT across the nestling period (Zimmer et al. 2019). It is also possible that females of different personalities differ in how their glucocorticoid profiles are affected by environmental variables such as temperature. Betini and Norris (2012), for instance, determined that in an Ontario tree swallow population, aggressive individuals are better able to adjust to variation in temperature though this does not confer any fitness advantages. Further, previous analyses in our population indicate that individuals differ in how their baseline CORT responds to variation in temperature (Content 2017). It is conceivable that variation in environmental conditions across years influences the relationship between CORT and fitness in some species or populations (Henderson et al. 2017), particularly given the role of baseline CORT in moderating an individual's energetic state (Angelier & Wingfield 2013).

We also found that nestlings were largest and maternal aggression lowest in 2015. However, these annual trends in nestling mass, despite being statistically significant, were relatively weak (Fig. 2), and therefore may not be biologically consequential. With regards to maternal aggression, previous studies have shown that proactive (bold, aggressive) individuals are more 'risk-prone' (Groothuis & Carere 2005) and experience reduced survival (reviewed in

Smith & Blumstein 2008). In our study population, it could be that maternal survival and return rates were influenced by personality, reducing the number of returning aggressive females and thereby generating a disproportionate number of nonaggressive breeders. This could have manifested as the low maternal aggression observed in 2015.

Maternal baseline CORT during incubation was lowest in 2016. Baseline CORT levels vary with factors such as resource availability, an individual's fat stores, and habitat quality (Bonier et al. 2009). NOAA weather data indicate that our study sites experienced below-normal precipitation as well as above-average summer temperatures in 2016. NOAA's National Climate Report for 2016 attributes the dryness to a summer drought that afflicted the southern Appalachians from April to November. Previous studies have shown that in addition to precipitation, ambient temperatures largely predict insect availability (Winkler et al. 2013) due to low temperatures negatively affecting insect flight activity (Dunn et al. 2011). Thus, the availability of insect prey and the profitability of foraging upon them increases with ambient temperature (Winkler et al. 2013). A low baseline CORT intercept coupled with warm temperatures and low precipitation in 2016 suggests that females experienced favorable environmental conditions, and consequently had more energy to allocate to their clutches during incubation. Elevated baseline CORT during incubation can adversely affect parental investment (e.g. yolk compound deposition; Bowers et al. 2016) and this negative association can intensify under poor environmental conditions (Vitousek et al. 2018b). A four-year study of tree swallows in New York found that during incubation, interactions between baseline CORT and year predicted reproductive success (Vitousek et al. 2018b). Specifically, low temperatures in 2013 reduced food availability and induced higher baseline CORT levels during incubation which, in

turn, led to decreased fledging success, a pattern unseen in milder years when baseline CORT was lower (Vitousek et al. 2018b).

In our study, aggressive females that reduced baseline CORT across the breeding stage reared the highest-quality offspring in 2016. These findings are contrary to Bonier et al. (2009)'s CORT-Adaptation Hypothesis predicting that an elevation in baseline CORT enhances reproductive success during the energetically taxing life history stage in which parents provision their offspring. A plausible explanation for this discrepancy may lie in Bonier and Cox (2019)'s 'Optimal Endocrine Phenotype Hypothesis,' which suggests that endocrine variation reflects ongoing adaptive adjustment (plasticity) of endocrine phenotypes in response to ever-shifting environmental optima, which tend to vary among individuals. It could be that for aggressive females, elevating baseline CORT across the breeding stage is maladaptive. Our data suggest that the extent to which aggressive females maintain or reduce their baseline CORT levels in different years has direct consequences for nestlings. Perhaps each year presents a novel environmental optimum that provokes a unique response from aggressive females, but not from nonaggressive females which consistently respond by elevating CORT per the CORT-Adaptation Hypothesis. In 2016, favorable environmental conditions (i.e. warm temperatures and low precipitation) may have enabled aggressive females to down-regulate CORT while still rearing large offspring. Vitousek et al. (2018b) found evidence of the CORT-Adaptation Hypothesis, but only in milder years, and increases in baseline CORT were coupled with a low acute stress response. There may be a trade-off between glucocorticoid-mediated reproductive strategies wherein parents benefit either from 1) an up-regulation of baseline CORT that facilitates nestling provisioning, or 2) maintaining a strong acute stress response that aids in nest defense or response to environmental stressors (Vitousek et al. 2018b).

How aggressive females rear large nestlings without experiencing physiological stress, especially given the associated fitness costs of aggression, remains speculative. Dingemanse and Wolf (2013) contend that the optimal degree of plasticity (e.g. baseline glucocorticoid levels) is a function of individual attributes (e.g. energetic state) that impact the costs and benefits associated with plasticity. Because individuals that achieve high fitness may possess certain glucocorticoid profiles that are near-optimal and thus selected for (Lande & Arnold 1983), it may be that the aggression-CORT profiles of female tree swallows represent different optima that enable high reproductive success. Past research suggests that the maintenance of distinct coping styles within populations results from different fitness optima in changing environments (Dochtermann & Dingemanse 2013; Sih et al. 2015). These optima may be collectively determined by an individual's genetic makeup, environmental or social context, and constraints brought on by the expression of other traits (Angelier & Wingfield 2013; Hau et al. 2016; Taff & Vitousek 2016). Finally, glucocorticoids are not the only measure of stress response. In laying hens subjected to an unpredictable feeding schedule, proactive brown hens had more responsive heterophil:lymphocyte ratios, whereas reactive white hens had more responsive heat shock protein expression; these different reactions represent alternative coping strategies to the same stressor (Pusch et al. 2018).

Although our data suggest low-aggression females paid the cost of reproduction while high-aggression females did not, reproductive success did not differ between females of contrasting aggressive personalities. Alternative explanations to high- and low-aggression females possessing different optimal glucocorticoid profiles are that aggressive females can achieve high fitness without elevating baseline CORT because 1) their partners contribute more to offspring care, 2) personality influences foraging or parenting behavior, or 3) aggressive

females out-compete nonaggressive females for nesting sites and thus settle in higher-quality territories. Although we lack data to suggest that the partners of aggressive females invest more in parental care (authors' unpublished data), there is evidence from a Pennsylvania population that female tree swallows adjust their reproductive investment (e.g. clutch allocation) as a function of their mate's personality (Rosvall 2010). Further, assortative mating for personality leads to high offspring quality in great tits (Both et al. 2005). In our population of tree swallows, mated pairs tend to display similar aggressive personalities and this assortative mating appears to increase provisioning efficiency and, subsequently, offspring growth (Pyle 2016). There is no evidence in our population, however, that assortative mating or male personality are associated with female glucocorticoid profiles (authors' unpublished data).

Personality may also influence territory acquisition and foraging or parenting behavior such that aggressive parents defend higher-quality territories (Both et al. 2005) whereas nonaggressive pairs forage more efficiently (Verbeek et al. 1994), enabling both strategies to yield high fitness. Although there has been no research addressing whether personality is linked to foraging behavior or habitat quality in tree swallows, weather drives fluctuations in prey abundance and, consequently, reproductive success (Winkler et al. 2013). Individuals must modulate baseline glucocorticoids in response to changes in food availability (Landys et al. 2004), and responses can vary within and among individuals. House sparrows (*Passer domesticus*) exposed to *ad libitum* and food-limited conditions show inter- and intra-individual differences in baseline CORT plasticity such that some birds, but not others, increase CORT under food-limited conditions (Lendvai et al. 2014). Additionally, rainfall appeared to vary substantially across our study period, which can predict the abundance and timing of the aerial insects that tree swallows rely upon exclusively to feed their offspring (Winkler et al. 2013), as

well as impact tree swallow foraging efficacy (Irons et al. 2017). Because natural selection maintains intrasexual aggression in female tree swallows due to competition for limited nesting cavities (Rosvall 2008), the aggressive females in our population may be more likely to secure high-quality territories with greater food resources. Nonaggressive females, on the other hand, may need to forage more diligently in order to feed offspring optimally, which could cause an increase in baseline CORT. Future research should investigate potential associations between personality, settlement patterns, physical habitat, and prey abundance in tree swallows.

Conclusion

Our results indicate that the interaction of maternal personality and glucocorticoid plasticity in a southern tree swallow population is likely driven by complex intrinsic and extrinsic mechanisms. Wolf et al. (2008) predicted that the coupling of resource competition and spatiotemporal variation in the environment can lead to adaptive differences in plasticity. Interindividual differences in plasticity within a population, such as the differences in baseline CORT slope between aggressive and nonaggressive personalities reported here, could moderate population-level response to novel or changing environments (Wolf & Weissing 2012). Indeed, it could be that these selective forces shape the differences in glucocorticoid signaling observed among high- and low-aggression female tree swallows. Additionally, our study highlights the significance of year effects in shaping the complex, multidimensional relationships among hormones, behavior, and reproductive success. Year effects likely represent the integration of multiple, long-term sources of variation such as social context, predation pressures, and potential carryover effects from conditions encountered during migration or at the wintering grounds (Vitousek et al. 2018b). Future research should address the prospect of fluidity in the

associations between personality, glucocorticoids, and fitness as a function of changing environmental contexts (Vitousek et al. 2018b). Finally, a more thorough understanding of aggression-CORT phenotypes and their fitness consequences, as well as what factors maintain variation in these phenotypes, is essential to elucidating how female tree swallows of different personalities strike a personalized balance between energy use and allocation to offspring.

Literature Cited

- Akçay, Ç., Lendvai, Á. Z., Stanback, M., Hausmann, M., Moore, I. T., & Bonier, F. 2016. Strategic adjustment of parental care in tree swallows: life-history trade-offs and the role of glucocorticoids. *Royal Society Open Science* 3(12): 160740.
- Albers, A. N. 2016. Potential effects of aggression, site, and proximate determinants that facilitate tree swallow range expansion (Master's thesis). Appalachian State University, Boone, NC, USA.
- Angelier, F., & Wingfield, J. C. 2013. Importance of the glucocorticoid stress response in a changing world: theory, hypotheses and perspectives. *General & Comparative Endocrinology* 190: 118-128.
- Aplin, L. M., Farine, D. R., Mann, R. P., & Sheldon, B. C. 2014. Individual-level personality influences social foraging and collective behaviour in wild birds. *Proceedings of the Royal Society B: Biological Sciences* 281(1789): 20141016.
- Arnold, S. J., Pfrender, M. E., & Jones, A. G. 2001. The adaptive landscape as a conceptual bridge between micro-and macroevolution. *In* *Microevolution Rate, Pattern, Process* (pp. 9-32). Springer, Dordrecht, Netherlands.
- Baugh, A. T., Schaper, S. V., Hau, M., Cockrem, J. F., de Goede, P., & van Oers, K. 2012. Corticosterone responses differ between lines of great tits (*Parus major*) selected for divergent personalities. *General & Comparative Endocrinology* 175(3): 488-494.
- Bell, A. M., Hankison, S. J., & Laskowski, K. L. 2009. The repeatability of behaviour: a meta-analysis. *Animal Behaviour* 77(4): 771-783.

- Benus, R. F. 1988. Aggression and coping: differences in behavioural strategies between aggressive and nonaggressive male mice (Ph.D. thesis). University of Groningen, Groningen, Netherlands.
- Betini, G. S., & Norris, D. R. 2012. The relationship between personality and plasticity in tree swallow aggression and the consequences for reproductive success. *Animal Behaviour* 83(1): 137-143.
- Biro, P. A., Beckmann, C., & Stamps, J. A. 2010. Small within-day increases in temperature affects boldness and alters personality in coral reef fish. *Proceedings of the Royal Society B: Biological Sciences* 277(1678): 71-77.
- Boake, C. R. (Ed.). 1994. Quantitative genetic studies of behavioral evolution. University of Chicago Press, Chicago, Illinois, USA.
- Bonier, F., & Cox, R. M. 2019. Do hormone manipulations reduce fitness? A meta-analytic test of the Optimal Endocrine Phenotype Hypothesis. *Molecular & Cellular Endocrinology* 110640.
- Bonier, F., Moore, I. T., Martin, P. R., & Robertson, R. J. 2009. The relationship between fitness and baseline glucocorticoids in a passerine bird. *General & Comparative Endocrinology* 163(1-2): 208-213.
- Bonier, F., Moore, I. T., & Robertson, R. J. 2011. The stress of parenthood? Increased glucocorticoids in birds with experimentally enlarged broods. *Biology Letters* 7(6): 944-946.
- Both, C., Dingemanse, N. J., Drent, P. J., & Tinbergen, J. M. 2005. Pairs of extreme avian personalities have highest reproductive success. *Journal of Animal Ecology* 74(4): 667-674.

- Bowers, E. K., Bowden, R. M., Thompson, C. F., & Sakaluk, S. K. 2016. Elevated corticosterone during egg production elicits increased maternal investment and promotes nestling growth in a wild songbird. *Hormones & Behavior* 83: 6-13.
- Calsbeek, R., Gosden, T. P., Kuchta, S. R., & Svensson, E. I. 2012. Fluctuating selection and dynamic adaptive landscapes. *The Adaptive Landscape in Evolutionary Biology* 89-109.
- Carere, C., Groothuis, T. G. G., Möstl, E., Daan, S., & Koolhaas, J. M. 2003. Fecal corticosteroids in a territorial bird selected for different personalities: daily rhythm and the response to social stress. *Hormones & Behavior* 43(5): 540-548.
- Cockrem, J. F. 2007. Stress, corticosterone responses and avian personalities. *Journal of Ornithology* 148: 169–178.
- Cockrem, J. F. 2013. Corticosterone responses and personality in birds: individual variation and the ability to cope with environmental changes due to climate change. *General & Comparative Endocrinology* 190: 156-163.
- Content, K. R. 2017. Individual variation in stress hormones and behavioral profiles represented by personality and plasticity in tree swallows (Master's thesis). Appalachian State University, Boone, NC, USA.
- Corson, S. A., & Corson, E. O. L. 1976. Constitutional differences in physiologic adaptation to stress and distress. *In Psychopathology of Human Adaptation* (pp. 77-94). Springer, Boston, MA, USA.
- Descamps, S., Gilchrist, H. G., Bêty, J., Buttlar, E. I. & Forbes, M. R. 2009. Costs of reproduction in a long-lived bird: large clutch size is associated with low survival in the presence of a highly virulent disease. *Biology Letters* 5: 278–81.

- Dingemanse, N. J., Both, C., Drent, P. J., van Oers, K., & Van Noordwijk, A. J. 2002. Repeatability and heritability of exploratory behaviour in great tits from the wild. *Animal Behaviour* 64(6): 929-938.
- Dingemanse, N. J., Kazem, A. J., Réale, D., & Wright, J. 2010. Behavioural reaction norms: animal personality meets individual plasticity. *Trends in Ecology & Evolution* 25(2): 81-89.
- Dingemanse, N. J., & Reale, D. 2005. Natural selection and animal personality. *Behaviour* 142: 1159-1184.
- Dingemanse, N. J., & Wolf, M. 2013. Between-individual differences in behavioural plasticity within populations: causes and consequences. *Animal Behaviour* 85(5): 1031-1039.
- Dochtermann, N. A., & Dingemanse, N. J. 2013. Behavioral syndromes as evolutionary constraints. *Behavioral Ecology* 24(4): 806-811.
- Duckworth, R. A. 2006. Behavioral correlations across breeding contexts provide a mechanism for a cost of aggression. *Behavioral Ecology* 17(6): 1011-1019.
- Dunn, P. O., Winkler, D. W., Whittingham, L. A., Hannon, S. J., & Robertson, R. J. 2011. A test of the mismatch hypothesis: how is timing of reproduction related to food abundance in an aerial insectivore?. *Ecology* 92(2): 450-461.
- Ensminger, A. L., & Westneat, D. F. 2012. Individual and sex differences in habituation and neophobia in house sparrows (*Passer domesticus*). *Ethology* 118(11): 1085-1095.
- Gangloff, E. J. 2016. Ecology and evolution of physiological phenotypes in garter snakes (*Thamnophis* spp.). Graduate Theses and Dissertations 15914.

- Garamszegi, L. Z., Rosivall, B., Rettenbacher, S., Markó, G., Zsebők, S., Szöllősi, E., ... & Török, J. 2012. Corticosterone, avoidance of novelty, risk-taking and aggression in a wild bird: no evidence for pleiotropic effects. *Ethology* 118(7): 621-635.
- Grace, J. K., & Anderson, D. J. 2014. Corticosterone stress response shows long-term repeatability and links to personality in free-living Nazca boobies. *General & Comparative Endocrinology* 208: 39-48.
- Groothuis, T. G., & Carere, C. 2005. Avian personalities: characterization and epigenesis. *Neuroscience & Biobehavioral Reviews* 29(1): 137-150.
- Guindre-Parker, S., Mcadam, A. G., Van Kesteren, F., Palme, R., Boonstra, R., Boutin, S., ... & Dantzer, B. 2019. Individual variation in phenotypic plasticity of the stress axis. *Biology Letters* 15(7): 20190260.
- Hanssen, S. A., Hasselquist, D., Folstad, I., & Erikstad, K. E. 2005. Cost of reproduction in a long-lived bird: incubation effort reduces immune function and future reproduction. *Proceedings of the Royal Society B: Biological Sciences* 272(1567): 1039-1046.
- Harcourt, J. L., Sweetman, G., Johnstone, R. A., & Manica, A. 2009. Personality counts: the effect of boldness on shoal choice in three-spined sticklebacks. *Animal Behaviour* 77(6): 1501-1505.
- Hau, M., Casagrande, S., Ouyang, J. Q., & Baugh, A. T. 2016. Glucocorticoid-mediated phenotypes in vertebrates: multilevel variation and evolution. *Advances in the Study of Behavior* 48: 41-115.
- Hau, M. & Goymann, W. 2015. Endocrine mechanisms, behavioral phenotypes and plasticity: known relationships and open questions. *Frontiers in Zoology* 1: S7.

- Henderson, L. J., Evans, N. P., Heidinger, B. J., Herborn, K. A., & Arnold, K. E. 2017. Do glucocorticoids predict fitness? Linking environmental conditions, corticosterone and reproductive success in the blue tit, *Cyanistes caeruleus*. *Royal Society Open Science* 4(10): 170875.
- Hessing, M. J. C. 1994. Individual behavioural characteristics in pigs and their consequences for pig husbandry (Ph.D. thesis). Agricultural University Wageningen, Wageningen, Netherlands.
- Hollander, F. A., Van Overveld, T., Tokka, I., & Matthysen, E. 2008. Personality and nest defence in the great tit (*Parus major*). *Ethology* 114(4): 405-412.
- Huntingford, F. A. 1976. The relationship between antipredator behavior and aggression among conspecifics in the three-spined stickleback. *Animal Behaviour* 24: 245–260.
- Imlay, T. L., Mills Flemming, J., Saldanha, S., Wheelwright, N. T., & Leonard, M. L. 2018. Breeding phenology and performance for four swallows over 57 years: relationships with temperature and precipitation. *Ecosphere* 9(4): e02166.
- Immler, S., Pryke, S. R., Birkhead, T. R., & Griffith, S. C. 2010. Pronounced within-individual plasticity in sperm morphometry across social environments. *Evolution: International Journal of Organic Evolution* 64(6): 1634-1643.
- Irons, R. D., Harding Scurr, A., Rose, A. P., Hagelin, J. C., Blake, T., & Doak, D. F. 2017. Wind and rain are the primary climate factors driving changing phenology of an aerial insectivore. *Proceedings of the Royal Society B: Biological Sciences* 284(1853): 20170412.

- Jacques-Hamilton, R., Hall, M. L., Buttemer, W. A., Matson, K. D., da Silva, A. G., Mulder, R. A., & Peters, A. 2017. Personality and innate immune defenses in a wild bird: evidence for the pace-of-life hypothesis. *Hormones & Behavior* 88: 31-40.
- Koolhaas, J. M., Korte, S. M., De Boer, S. F., Van Der Vegt, B. J., Van Reenen, C. G., Hopster, H., ... & Blokhuis, H. J. 1999. Coping styles in animals: current status in behavior and stress-physiology. *Neuroscience & Biobehavioral Reviews* 23(7): 925-935.
- Kotiaho, J. S. & Simmons, L. W. 2003. Longevity cost of reproduction for males but no longevity cost of mating or courtship for females in the male-dimorphic dung beetle *Onthophagus binodis*. *Journal of Insect Physiology* 49: 817–22.
- Kralj-Fišer, S., Weiß, B.M. & Kotrschal, K. 2010. Behavioural and physiological correlates of personality in greylag geese (*Anser anser*). *Journal of Ethology* 28: 363–370.
- Lande, R., & Arnold, S. J. 1983. The measurement of selection on correlated characters. *Evolution* 37(6): 1210-1226.
- Landys, M. M., Ramenofsky, M., Guglielmo, C. G., & Wingfield, J. C. 2004. The low-affinity glucocorticoid receptor regulates feeding and lipid breakdown in the migratory Gambel's white-crowned sparrow *Zonotrichia leucophrys gambelii*. *Journal of Experimental Biology* 207(1): 143-154.
- Landys, M. M., Ramenofsky, M., & Wingfield, J. C. 2006. Actions of glucocorticoids at a seasonal baseline as compared to stress-related levels in the regulation of periodic life processes. *General & Comparative Endocrinology* 148(2): 132-149.
- Lendvai, Á. Z., Giraudeau, M., Bókony, V., Angelier, F., & Chastel, O. 2015. Within-individual plasticity explains age-related decrease in stress response in a short-lived bird. *Biology Letters* 11(7): 20150272.

- Lendvai, A. Z., Ouyang, J. Q., Schoenle, L. A., Fasanello, V., Hausmann, M. F., Bonier, F., & Moore, I. T. 2014. Experimental food restriction reveals individual differences in corticosterone reaction norms with no oxidative costs. *PLoS One* 9(11).
- Mathot, K. J., van den Hout, P. J., Piersma, T., Kempenaers, B., Réale, D., & Dingemanse, N. J. 2011. Disentangling the roles of frequency-vs. state-dependence in generating individual differences in behavioural plasticity. *Ecology Letters* 14(12): 1254-1262.
- McCarty, J. P. 2001. Variation in growth of nestling tree swallows across multiple temporal and spatial scales. *The Auk* 118(1): 176-190.
- Montgomerie, R. D., & Weatherhead, P. J. 1988. Risks and rewards of nest defence by parent birds. *The Quarterly Review of Biology* 63(2): 167-187.
- Newton, I. 1994. The role of nest sites in limiting the numbers of hole-nesting birds: a review. *Biological Conservation* 70(3): 265-276.
- NOAA National Centers for Environmental Information. 2016. State of the Climate: National Climate Report for Annual 2015. Retrieved from <https://www.ncdc.noaa.gov/sotc/national/201513>.
- NOAA National Centers for Environmental Information. 2017. State of the Climate: National Climate Report for Annual 2016. Retrieved from <https://www.ncdc.noaa.gov/sotc/national/201613>.
- Nussey, D. H., Clutton-Brock, T. H., Elston, D. A., Albon, S. D., & Kruuk, L. E. 2005a. Phenotypic plasticity in a maternal trait in red deer. *Journal of Animal Ecology* 74(2): 387-396.
- Nussey, D. H., Postma, E., Gienapp, P., & Visser, M. E. 2005b. Selection on heritable phenotypic plasticity in a wild bird population. *Science* 310(5746): 304-306.

- Nussey, D. H., Wilson, A. J., & Brommer, J. E. 2007. The evolutionary ecology of individual phenotypic plasticity in wild populations. *Journal of Evolutionary Biology* 20(3): 831-844.
- Ouyang, J. Q., Lendvai, Á. Z., Dakin, R., Domalik, A. D., Fasanello, V. J., Vassallo, B. G., ... & Bonier, F. 2015. Weathering the storm: parental effort and experimental manipulation of stress hormones predict brood survival. *BMC Evolutionary Biology* 15(1): 219.
- Pryke, S. R., & Griffith, S. C. 2009. Socially mediated trade-offs between aggression and parental effort in competing color morphs. *The American Naturalist* 174(4): 455-464.
- Pusch, E. A., Bentz, A. B., Becker, D. J., & Navara, K. J. 2018. Behavioral phenotype predicts physiological responses to chronic stress in proactive and reactive birds. *General & Comparative Endocrinology* 255: 71-77.
- Pyle, T. J. 2016. Personality seals the bid: influence of pair personality in provisioning coordination and reproductive success in tree swallows (Honors thesis). Appalachian State University, Boone, NC, USA.
- Radford, A. N., McCleery, R. H., Woodburn, R. J. W., & Morecroft, M. D. 2001. Activity patterns of parent great tits *Parus major* feeding their young during rainfall. *Bird Study* 48(2): 214-220.
- Réale, D., Martin, J., Coltman, D. W., Poissant, J., & Festa-Bianchet, M. 2009. Male personality, life-history strategies and reproductive success in a promiscuous mammal. *Journal of Evolutionary Biology* 22(8): 1599-1607.
- Robertson, R. J., Stutchbury, B. J., & Cohen, R. R. 1992. Tree swallow (*Tachycineta bicolor*). American Ornithologists' Union, Washington, DC, Maryland, USA.

- Rosvall, K. A. 2008. Sexual selection on aggressiveness in females: evidence from an experimental test with tree swallows. *Animal Behaviour* 75(5): 1603-1610.
- Rosvall, K. A. 2010. Do males offset the cost of female aggression? An experimental test in a biparental songbird. *Behavioral Ecology* 21(1): 161-168.
- Sapolsky, R. M. 1990. Stress in the wild. *Scientific American* 262(1): 116-123.
- Schuett, W., Dall, S. R., Baeumer, J., Kloesener, M. H., Nakagawa, S., Beinlich, F., & Eggers, T. 2011. Personality variation in a clonal insect: the pea aphid, *Acyrtosiphon pisum*. *Developmental Psychobiology* 53(6): 631-640.
- Sih, A., & Bell, A. M. 2008. Insights for behavioral ecology from behavioral syndromes. *Advances in the Study of Behavior* 38: 227-281.
- Sih, A., Bell, A., & Johnson, J. C. 2004. Behavioral syndromes: an ecological and evolutionary overview. *Trends in Ecology & Evolution* 19(7): 372-378.
- Sih, A., Mathot, K. J., Moiron, M., Montiglio, P. O., Wolf, M., & Dingemanse, N. J. 2015. Animal personality and state-behaviour feedbacks: a review and guide for empiricists. *Trends in Ecology & Evolution* 30(1): 50-60.
- Smith, B. R., & Blumstein, D. T. 2008. Fitness consequences of personality: a meta-analysis. *Behavioral Ecology* 19(2): 448-455.
- Stöwe, M., Rosivall, B., Drent, P. J., & Möstl, E. 2010. Selection for fast and slow exploration affects baseline and stress-induced corticosterone excretion in great tit nestlings, *Parus major*. *Hormones & Behavior* 58(5): 864-871.
- Stutchbury, B. J., & Robertson, R. J. 1986. A simple trap for catching birds in nest boxes. *Journal of Field Ornithology* 57(1): 64-65.

- Taff, C. C., & Vitousek, M. N. 2016. Endocrine flexibility: optimizing phenotypes in a dynamic world? *Trends in Ecology & Evolution* 31(6): 476-488.
- van Oers, K., Drent, P. J., De Goede, P., & Van Noordwijk, A. J. 2004. Realized heritability and repeatability of risk-taking behaviour in relation to avian personalities. *Proceedings of the Royal Society B: Biological Sciences* 271(1534): 65-73.
- Verbeek, M. E., Drent, P. J., & Wiepkema, P. R. 1994. Consistent individual differences in early exploratory behaviour of male great tits. *Animal Behaviour* 48(5): 1113-1121.
- Vitousek, M. N., Jenkins, B. R., & Safran, R. J. 2014. Stress and success: individual differences in the glucocorticoid stress response predict behavior and reproductive success under high predation risk. *Hormones & Behavior* 66(5): 812-819.
- Vitousek, M. N., Taff, C. C., Ardia, D. R., Stedman, J. M., Zimmer, C., Salzman, T. C., & Winkler, D. W. 2018a. The lingering impact of stress: brief acute glucocorticoid exposure has sustained, dose-dependent effects on reproduction. *Proceedings of the Royal Society B: Biological Sciences* 285(1882): 20180722.
- Vitousek, M. N., Taff, C. C., Hallinger, K. K., Zimmer, C., & Winkler, D. W. 2018b. Hormones and fitness: evidence for trade-offs in glucocorticoid regulation across contexts. *Frontiers in Ecology & Evolution* 6: 42.
- Whitehouse, M. J., Harrison, N. M., Mackenzie, J., & Hinsley, S. A. 2013. Preferred habitat of breeding birds may be compromised by climate change: unexpected effects of an exceptionally cold, wet spring. *PLoS One* 8(9).
- Williams, G. C. 1966. Natural selection, the costs of reproduction, and a refinement of Lack's principle. *American Naturalist* 100: 687-690.

- Winkler, D. W. 1992. Causes and consequences of variation in parental defense behavior by tree swallows. *The Condor* 94(2): 502-520.
- Winkler, D. W. 1994. Anti-predator defence by neighbours as a responsive amplifier of parental defence in tree swallows. *Animal Behaviour* 47(3): 595-605.
- Winkler, D. W., Hallinger, K.K., Ardia, D.R., Robertson, R.J., Stutchbury, B. J., & Cohen, R. R. 2011. Tree swallow (*Tachycineta bicolor*). In *The Birds of North America Online*. Cornell Lab of Ornithology, Ithaca, NY, USA.
- Winkler, D. W., Luo, M. K., & Rakhimberdiev, E. 2013. Temperature effects on food supply and chick mortality in tree swallows (*Tachycineta bicolor*). *Oecologia* 173: 129–138.
- Wolf, M., Van Doorn, G. S., & Weissing, F. J. 2008. Evolutionary emergence of responsive and unresponsive personalities. *Proceedings of the National Academy of Sciences* 105(41): 15825-15830.
- Wolf, M., & Weissing, F. J. 2012. Animal personalities: consequences for ecology and evolution. *Trends in Ecology & Evolution* 27(8): 452-461.
- Wong, R. Y., French, J., & Russ, J. B. 2019. Differences in stress reactivity between zebrafish with alternative stress coping styles. *Royal Society Open Science* 6(5): 181797.
- Wong, R. Y., Lamm, M. S., & Godwin, J. 2015. Characterizing the neurotranscriptomic states in alternative stress coping styles. *BMC Genomics* 16(1): 425.
- Zimmer, C., Taff, C. C., Ardia, D. R., Rose, A. P., Aborn, D. A., Johnson, S. L., & Vitousek, M. N. 2019. Environmental unpredictability shapes glucocorticoid regulation across populations of tree swallows. *bioRxiv*.

Tables

Table 1. Comparison of the baseline CORT slope and reproductive parameters of high- versus low-aggression female tree swallows. Data are combined 2014-2016.

Source	F	t	df	P-value
Baseline CORT slope	3.20	2.25	54	0.028
First Egg Date	0.52	-0.66	113	0.51
Clutch Size	0.90	1.14	113	0.26
Brood Size	0.01	0.92	113	0.36
Number Fledged	0.63	0.30	113	0.76

Figures

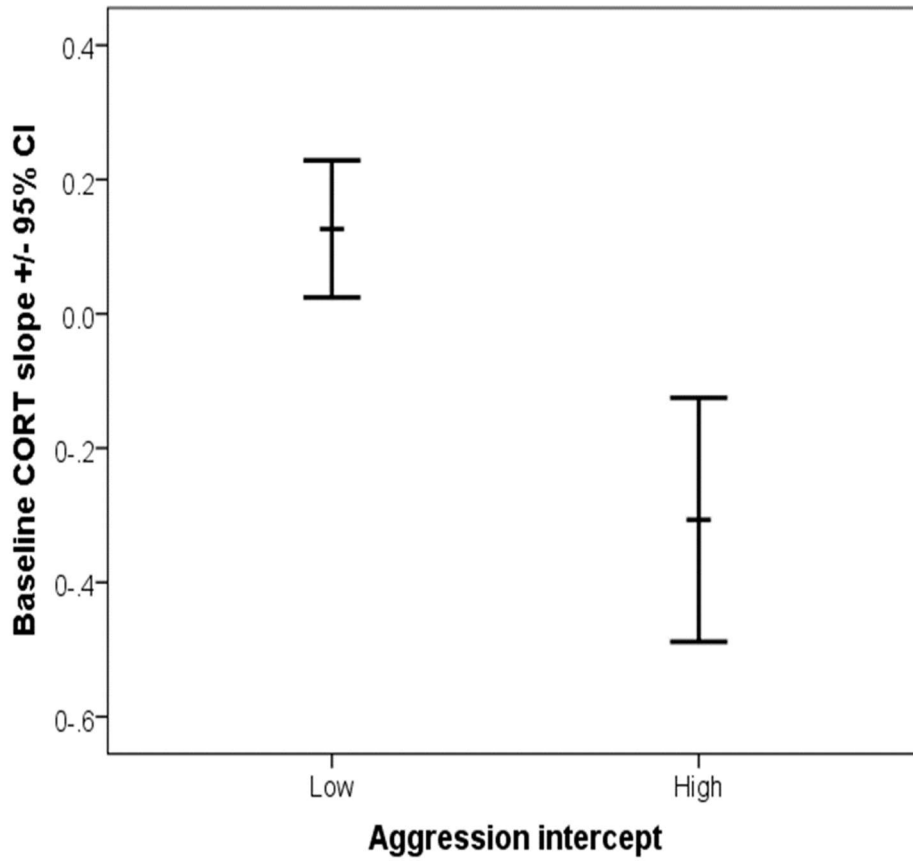


Figure 1. High- (n=21) and low-aggression (n=35) females adjusted baseline CORT differently across the breeding stage. Low-aggression females appear to pay a higher cost of reproduction ($t=2.25$, $p=0.028$, $df=54$). The bars represent the 95% confidence intervals for the means.

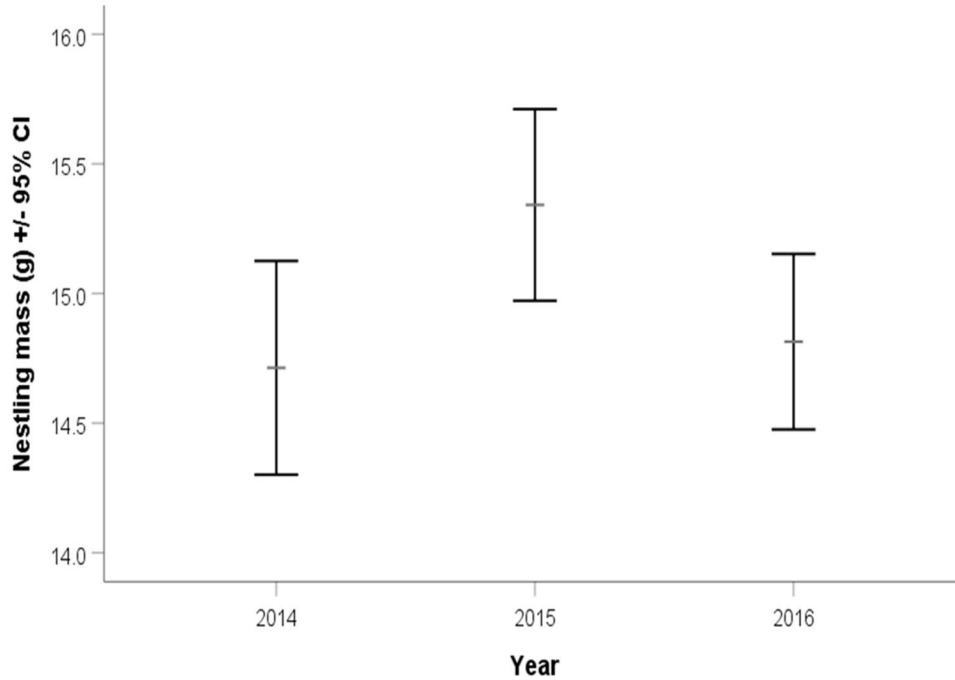


Figure 2. Comparison of mean nestling mass (g) of 8-day old tree swallows across the 3-year study; nestling mass was highest in 2015 ($F_{2,765}=3.19$, $p=0.042$). The bars represent the 95% confidence intervals for the means.

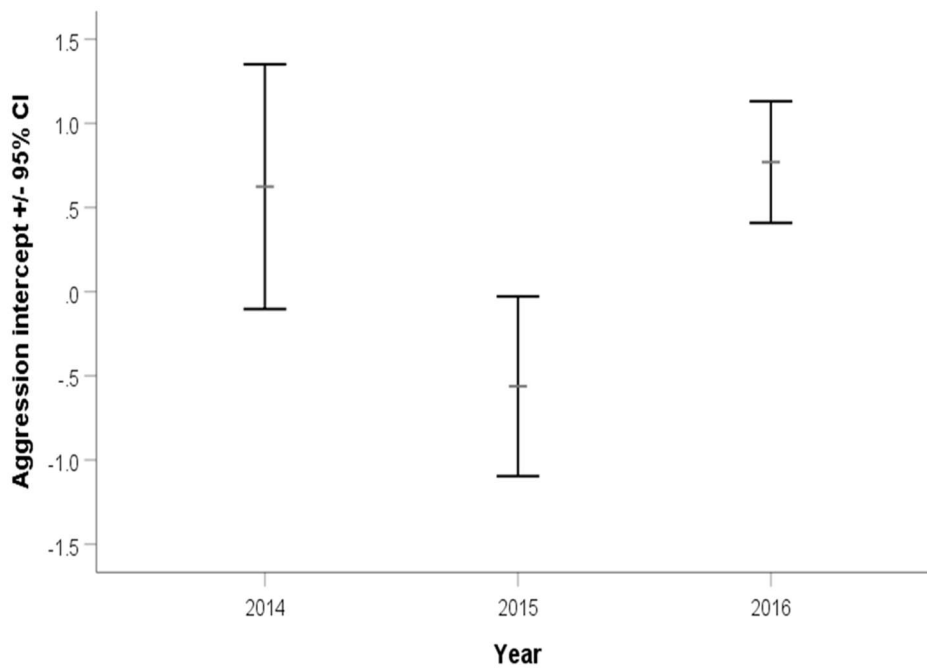


Figure 3. Comparison of nest defense aggression of female tree swallows measured when nestlings were 2 days old ('early nestling stage') across the 3-year study; aggression was lowest in 2015 ($F_{2,112}=9.52$, $p<0.001$). The bars represent the 95% confidence intervals for the means.

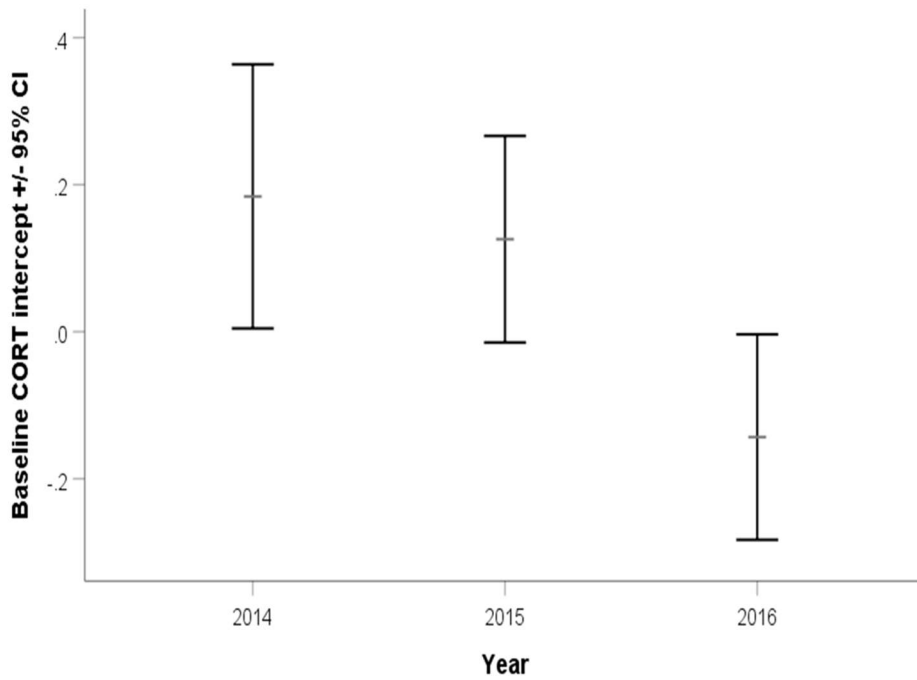


Figure 4. Comparison of baseline CORT intercept of female tree swallows measured during incubation ('early nestling stage') across the 3-year study; baseline CORT intercept was lowest in 2016 ($F_{2,68}=5.69$, $p=0.005$). The bars represent the 95% confidence intervals for the means.

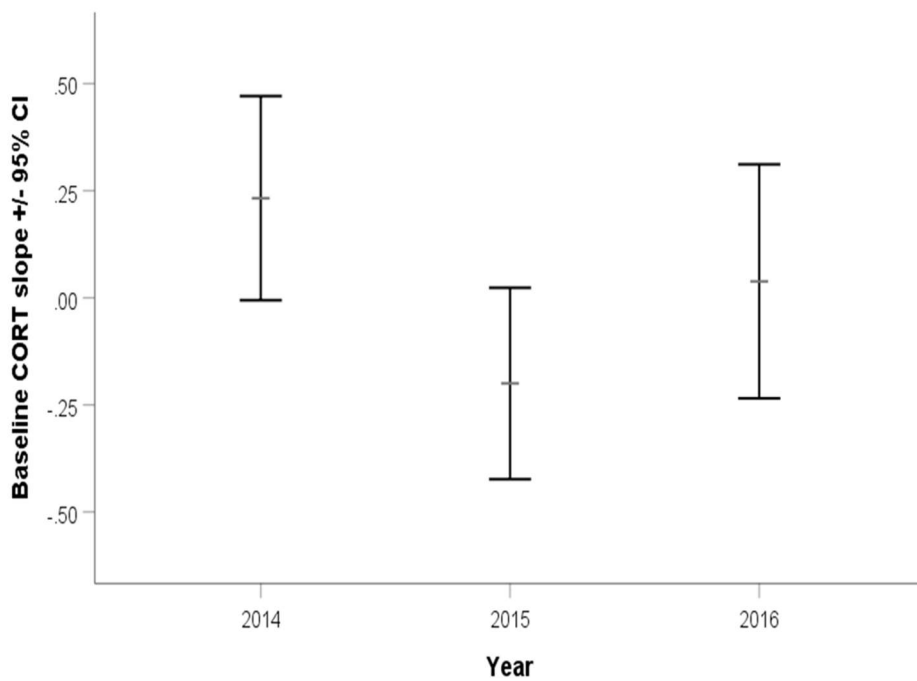


Figure 5. Comparison of baseline CORT slope of female tree swallows measured in the early and late nestling stages across the 3-year study with no significant differences ($F_{2,68}=1.86$, $p=0.164$). The bars represent the 95% confidence intervals for the means.

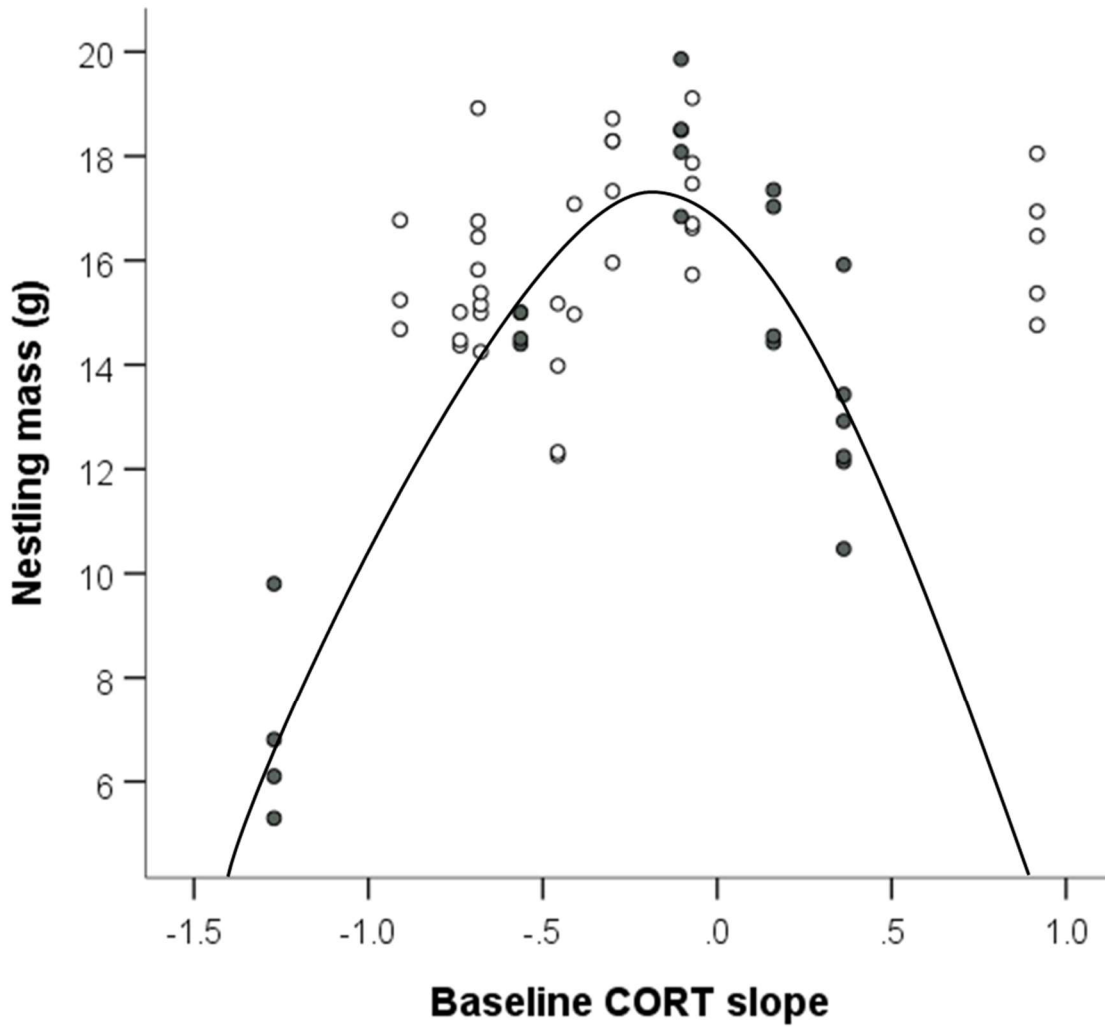


Figure 1. Relationship between maternal baseline CORT slope and nestling mass (at age 8 days post-hatch) in 2015. Data split by high- (dark circles) and low- (white circles) aggression females. The trend was only significant for high-aggression females ($R^2 = 0.83$, $F=4.47$, $p=0.047$, $n=21$).

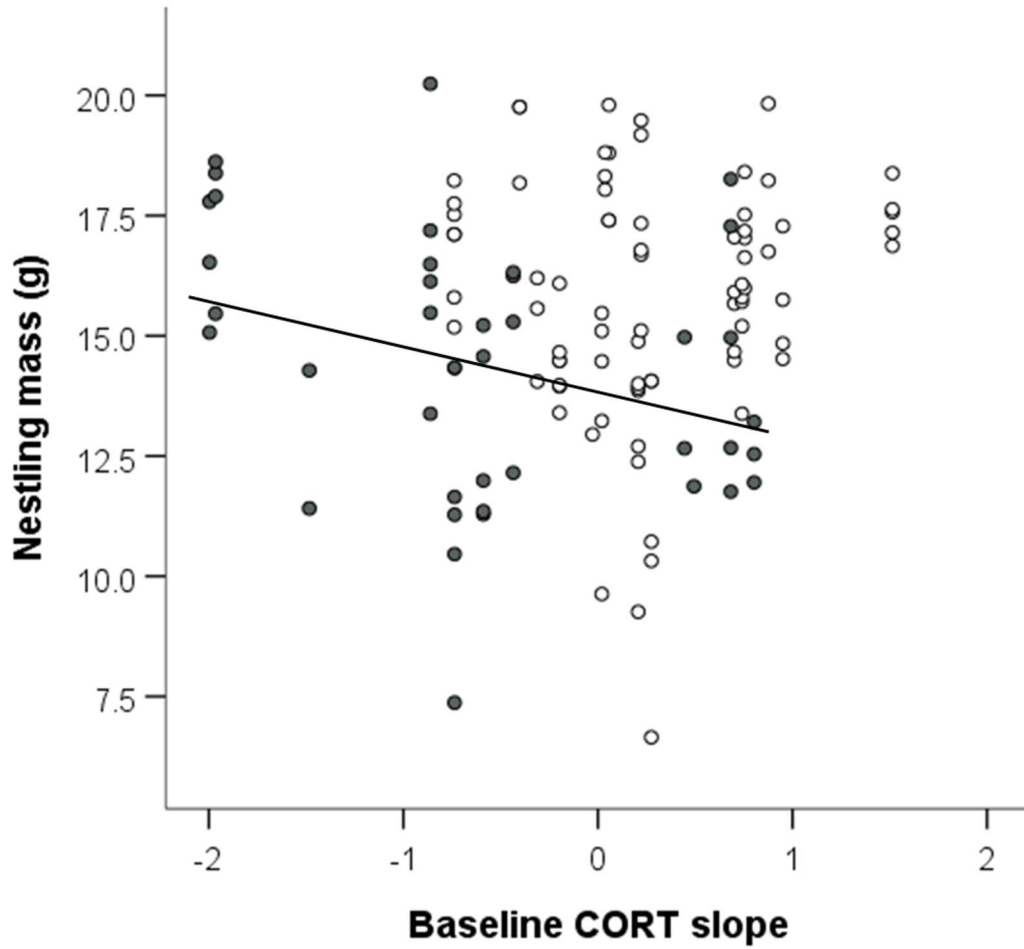


Figure 2. Relationship between maternal baseline CORT slope and nestling mass (at age 8 days post-hatch) in 2016. Data split by high- (dark circles) and low- (white circles) aggression females. Similar trend observed in 2014. The trend was only significant for high-aggression females ($R^2=0.10$, $F=4.49$, $p=0.041$, $n=40$).