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**The Influence of Breeding Density on Female Aggression, Parental Care, and  
Ornamentation in a Secondary-Cavity Nesting Warbler**

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science  
in Biology at Virginia Commonwealth University

By

Elsa B. Chen  
Bachelor of Arts, Skidmore College, 2015

Thesis Advisor: Lesley P. Bulluck, PhD  
Assistant Professor, Center for Environmental Studies  
Virginia Commonwealth University

Virginia Commonwealth University  
Richmond, VA  
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## Abstract

### **The Influence of Breeding Density on Female Aggression, Parental Care, and Ornamentation in a Secondary-Cavity Nesting Warbler**

By Elsa B. Chen, M.S.

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in Biology at Virginia Commonwealth University

Virginia Commonwealth University, 2020

Thesis Advisor: Lesley P. Bulluck, PhD,  
Assistant Professor, Center for Environmental Studies

Tradeoffs between individual survival and reproductive success associated with aggressive behaviors are a driving force of evolution, but these tradeoffs are often overlooked for aggressive conspecific interactions between females. For avian males, it is well documented that more aggressive individuals tend to provide less parental care. In the few studies that address this in females, the tradeoffs seem to be more context-dependent, varying due to factors such as predation pressure and habitat quality. The relationship between female ornamentation and aggression is similarly understudied, but evidence suggests that both aggression and ornamentation are important traits involved in social selection – the competition for resources other than mates. This study assessed the tradeoffs of female aggression related to parental care and reproductive success within the context of breeding density in the Prothonotary Warbler (*Protonotaria citrea*), a secondary cavity-nesting warbler that readily uses nest boxes. Breeding density is a proxy for reproductive resource availability in box nesting species. During incubation, we conducted staged nest intruder trials with a female decoy “perched” on the box, paired with playback of female chips, and recorded the focal female’s response. We also examined whether breast and crown feather coloration were correlated with female aggressive

response. Our results show that females nesting in high-density environments were less aggressive and provisioned their young more often. We also observed that total nestling provisioning (male and female) was lower in pairs with more aggressive females. Additionally, one female breast feather ornamentation metric (yellow intensity) was negatively associated with aggression regardless of density, while another (carotenoid content) was positively associated with aggression only in high-density environments. Together with previous studies in this system that have found positive relationships between female ornamentation and individual fitness, our results suggest that female ornamentation may provide both inter- and intra-sexual signals and therefore function in both sexual and social selection, respectively. Through explicit consideration of the potential tradeoffs of female aggression, our results also suggest that the costs associated with female competitive traits can be mediated by breeding density.



## Introduction

Sexual selection is the competition for access to mates and has resulted in the evolution of physiological (e.g. armaments or ornaments) or behavioral (e.g. elaborate displays or aggression) traits to increase fitness. Behavioral and anatomical traits such as these are often energetically costly and can negatively affect survival (Liker and Székely 2005). For males, the benefit of higher reproductive success due to increased access to females balances the costs of expressing these competitive traits (Andersson 1994, Galimberti et al. 2007). However, the function and associated tradeoffs of these traits in females is poorly understood. Thus, social selection, the competition for resources such as nest sites or food, may be a more effective framework than sexual selection for explaining the evolution of competitive traits in females (Lyon and Montgomerie 2012, Cain and Rosvall 2014).

In avian systems, plumage features are one of the most prominent signals for intra- and inter-sexual communication (Santos et al. 2011, Enbody et al. 2018, Fan et al. 2018). Since they tend to be more colorful and conspicuous, males have similarly been the primary focus of these studies (Roberts et al. 2009, Jones et al. 2016). Male plumage is correlated with aggression and can serve as an intrasexual badge of dominance and/or as an intersexual signal of individual quality (Garamszegi et al. 2006, Griggio et al. 2011). In the last 20 years, there has been growing interest in the evolution and function of female ornamentation. For example, aggression in female Blue Tits (*Cyanistes caeruleus*) was related to individual blue crown and yellow breast coloration (Midamegbe et al. 2011). Recent studies suggest that female avian ornaments can also be honest signals of individual quality, but that instead of mate acquisition, the function of female ornaments is more often related to competition for resources; their evolution may therefore be driven more by social rather than sexual selection (Tobias et al. 2012, Cantarero et

al. 2015, Bulluck et al. 2017, Plaza et al. 2018). Despite this growing understanding, the function of female ornamentation related to aggression, as well as the associated tradeoffs with aggression, are not well understood (Heygi et al. 2008, Kötél et al. 2016).

Competitive behavioral traits like aggression also have important implications for individual fitness and reproductive success. In avian systems, a negative association with the degree of parental care (i.e., nestling provisioning) is an established tradeoff of male conspecific aggression—communicated with overly hostile actions, posturing, and/or song (Fitzpatrick et al 1995, Duckworth 2006, Barnett et al. 2012). However, the costs and benefits of aggression in females are less clear. More aggressive female Tree Swallows (*Tachycineta bicolor*) acquired nest boxes, but also had lower quality nestlings (Rosvall 2008, 2011). This suggests that aggressiveness is important in female-female competition for crucial breeding resources, but also may lead to less energy allocated towards parental care, which can negatively affect reproductive success. Because females direct more energy towards parental care (i.e., egg production and brooding), females may suffer greater costs for being aggressive (Fitzpatrick et al. 1995); however, recent research suggests that, similar to males, the tradeoffs of female aggression can be context-dependent (Cain and Ketterson 2013, Cain and Rosvall 2014, Krieg and Getty 2020). In lower-quality habitat with unequal resource distribution, female Superb Fairy-wrens (*Malurus cyaneus*) exhibited stronger overall aggressive responses to intruders and more aggressive females had lower reproductive success; however, in higher-quality habitat, more aggressive females had higher reproductive success (Cain and Langmore 2016). More studies are needed in different systems to fully understand the costs and benefits of female aggression and the contexts in which it may present a selective advantage (Cain and Ketterson 2013, Cain and Rosvall 2014).

Though rarely examined, breeding density may be another factor influencing the tradeoffs of female aggression, especially in box nesting species where it can be manipulated and serves as a proxy for resource availability (Rosvall 2011, Cain and Langmore 2016). Interpopulation differences in male territorial aggression can be explained by differences in breeding density, with individuals in higher-density populations exhibiting more aggression (Yoon et al. 2012, Araya-Ajoy and Dingemanse 2017). This agrees with social selection theory, which suggests that competitive traits (i.e., high levels of aggression) will be advantageous in more competitive environments (West-Eberhard 1983). An increase in breeding density results in an increased chance for more conspecific aggressive interactions, creating a more competitive environment. However, resource distribution and availability likely influence the tradeoffs of competitive traits such as aggression as well (Grant 1993, Grant et al. 2000, Cain and Rosvall 2014, Cain and Langmore 2016). Under social selection theory, the benefits of female aggression (i.e., as improved access to limited nesting sites) are likely to outweigh the costs (i.e., reduced energy for parental care) at a high-density site with increased competitive interactions, similar to what has been observed in males. Alternatively, under resource defense theory, the benefits of female aggression are likely to outweigh the costs at a low-density site with limited nesting sites and fewer competitors (Figure 1). To our knowledge, the influence of breeding density on the tradeoffs of female aggression has not been explicitly examined.

In this study, we examined the costs and benefits of female aggression in the Prothonotary Warbler (*Protonotaria citrea*), a secondary cavity-nesting warbler, and considered the influence of breeding density at two field sites that differ in mean breeding density due to nest box availability. In addition to site-level density, we also assessed the influence of local density around each nest box on the costs and benefits of female aggression. We are specifically

interested in whether our results will support social selection theory, where more aggressive females nesting at higher densities will experience higher reproductive success, or if our results will support resource defense theory, where more aggressive females nesting at lower densities will experience higher reproductive success. We also examined whether female ornamentation is related to aggression, and if so, if they are the same plumage traits related to individual quality.

## **Methods**

### *Study Species*

The Prothonotary Warbler serves as an excellent study species to explore the potential relationships between aggression, reproductive success, plumage, and breeding density. These secondary cavity-nesting warblers readily breed in artificial nest boxes, which provide several advantages for a behavioral/breeding ecology study: females and males are easily captured, nests are easily monitored, and breeding density can be manipulated. Furthermore, Prothonotary Warblers double-brood, initiating their first nests in late April and continuing to lay eggs into late June/early July, allowing us to examine the potential effects of season on aggression. The signaling function of female ornamentation can also be examined in this species, as previous studies have shown that male and female Prothonotary Warbler breast coloration is correlated with nest box acquisition (Beck 2013), and that female plumage quality (carotenoid content) is predictive of reproductive success (number of young fledged) and provisioning rates (Bulluck et al. 2017). Carotenoids must be acquired through diet and provide signals about individual quality (Olson and Owens 1998, 2005; Blount 2004). Finally, Prothonotary Warblers frequently fan out their tails as part of an aggressive stance, which displays structurally based white tail spots that vary in size (Petit 1999). In other passerines, these tail spots are honest indicators of individual

quality; females preferred males with larger amounts of white in their tails, and males with more tail white were socially dominant (Hill et al. 1999, McGlothlin et al. 2008, Griggio et al. 2011)

### *Study Site*

Our study populations are located along tributaries of the tidal freshwater portion of the James River, ~20 - 40 km southeast of Richmond, Virginia at two sites with established nest boxes placed over water. All boxes are monitored from a canoe. Deep Bottom Park (DBP) has 65 boxes (density ~2 birds/ha, comparable to the ~1.8 birds/ha at the Great Dismal Swamp, a nearby high-density natural cavity nesting site; Bulluck, unpublished data) and the VCU Rice Rivers Center (RRC) has 25 boxes (density < 1 bird/ha). The DBP population is part of a long-term study of Prothonotary Warbler breeding ecology initiated in 1987 (Blem 1991), while the RRC boxes were installed in 2010. Nest box competition is high at DBP, with 74% of boxes occupied by Prothonotary Warblers in 2019, and a few instances of nest box takeover through egg burial are observed most years (Tucker and Bulluck 2018; 1 instance of burial at DBP in 2019). Additional information about DBP, such as the dominant tree species, is detailed in Dodson et al. (2016). RRC is approximately 28 km downstream from DBP and has a similar vegetative composition (tidal freshwater wetland and bottomland hardwood forest), but with a higher proportion of bald cypress (*Taxodium distichum*) than DBP. At RRC, the lower box density may result in fewer competitive interactions. Though a small number of individuals nest in nearby natural cavities at both sites, there is a preference for nest boxes since they are over water and therefore experience less predation; thus, box density provides an accurate proxy for local breeding density (Bulluck unpublished data, Hoover 2006, Beck 2013, Tucker et al. 2016)

During nest checks that occurred every 2-3 days throughout the 2019 breeding season (mid-April to mid-July), we recorded the number of eggs, number of nestlings, and nest fate

(signs of fledging, mortality, or predation). During incubation and brooding, we captured females with a mesh net placed over the nest box hole and banded them with an aluminum USGS band (permit #23486) and a unique combination of 2-3 color bands (VCU IACUC #AM10232). We opportunistically captured and banded males during nestling provisioning or with the use of mist nets in established territories.

### *Breeding Density*

In addition to the site-level densities of breeding birds/ha described above, we were interested in incorporating the local density of breeding Prothonotary Warblers around each focal female at the time of the aggression trial/incubation. Previous research on a Prothonotary Warbler population in the Illinois Cache River watershed found that ~ 75% of extra-pair young were sired by neighboring males within 200 m of the focal nest, and that decisions regarding breeding dispersal are influenced by conspecific interactions at the same scale (Schelsky 2010). In other species, local density at a finer scale (the number of neighbors within 50 - 65 m) influences aggressive responses (Bhardwaj et al. 2015) or reproductive success (Woodworth et al. 2017, O'Shea et al. 2018). Thus, to measure local density in our study populations, we used the Generate Spatial Weights Matrix tool in the Spatial Statistics toolbox in ArcMap to calculate the number of neighbors in a 60 m radius within 10 days from hatch date for each nest (ESRI, Redlands, CA). This 20-day window around hatch date was chosen to encompass when females might be interacting aggressively with other nearby nesting females. For nests that did not hatch (N = 5), we used the date halfway between nest initiation and nest fate determination.

### *Aggression Trials*

Our behavioral assay consisted of a 5-minute staged nest intruder (SNI) presented during incubation (3-10 days after the last egg is laid). Aggression assays typically consist of a live bird

or decoy accompanied by a recording of territorial vocalizations, with observers noting behaviors such as vocalization rate, focal individual perching location, physical contact with the SNI, and threatening actions such as dives and flights within close proximity to the SNI (Rosvall 2008, Barnett et al. 2012, Cain and Ketterson 2013). We used one of three decoys and three playback recordings for each trial to minimize pseudoreplication and selected the playback and decoy stimuli combination with a random number generator ( $N = 9$ ). The decoys were 3D-printed and painted with acrylics to resemble a female Prothonotary Warbler. The 10-minute playbacks consisted of repeating chip note sequences (25 seconds of chips and 5 seconds of silence) from three individual females recorded using a Tascam DR-05 and a shotgun microphone early in the field season (late April 2019). In Audacity 2.3.0 (Audacity Team 2018), background noises (ovenbird songs, boat motors, etc.) were reduced with the Noise Reduction function and a high-pass filter of 4.5k (RC11 was processed with a high-pass filter of 5.5k), and the sequences were then normalized. In the field, all playback stimuli were broadcast at  $\sim 80$  dB at 1 m away (measured with Tascam DR-05).

During incubation, we approached active nest boxes, placed the decoy on top of the pole supporting the nest box, and hung the audio equipment under the nest box (Figure 2). During our approach, we attempted to “soft flush” the female by tapping the sides of our canoe with the paddle; if that failed, we knocked on the side of the box before opening it to “hard flush” the female. If the incubating female flushed within sight, we immediately set-up the trial, retreated to a distance  $\geq 10$  m away, and started the playback. If the female seemed to flush deep into the forest/across the river/etc., the playback was left on for 7.5 minutes, and then we waited an additional  $\geq 15$  minutes for the female to return to start a trial. If females entered the box as we were setting up or approaching, we waited  $\geq 5$  minutes and then flushed her. If the box was

unoccupied at the time of the approach, we waited  $\geq 15$  minutes and aborted the attempt if there was no sign of the focal female nearby. A single observer (EBC) conducted all trials and used an Olympus WS-821 digital voice recorder to document behaviors. A Tascam DR-05 placed behind the nest box was used to record and identify vocalizations made by the focal female (chips/minute). Female Prothonotary Warblers rarely sing (Matthews et al. 2017), but display aggression by fanning their tail, approaching the threat, and repeatedly chipping. We developed an ethogram based on known aggressive behaviors in this species and on previous female aggression studies (Rosvall 2008, Cain and Ketterson 2013). The first five SNI trials were used to modify the protocol and ethogram to best quantify aggression in this species and were not used for analysis. Details of recorded behaviors can be found in Table 1.

#### *Aggression Scores*

A single researcher (EBC) scored all trials by processing the recordings in BORIS (Friard and Gamba 2016). The trial portion selected for analysis began two seconds (to the nearest 10th of a second) before the first chip note in the playback and lasted 5 minutes. The 5-minute trials were binned into sixty 5-second intervals where intervals were scored as 1 if any aggressive behavior occurred during that time (Table 1). Trials were only included for further analysis if the female was present for more than half the trial ( $\geq 2.5$  min). Others using a similar protocol for female Tree Swallows have found scores from these SNIs to be highly repeatable ( $r = 0.79$ ) within individuals (Rosvall 2008).

Females varied considerably in their responses to the SNI, which included interacting aggressively with the decoy, remaining close to the decoy/nest box ( $\leq 3$  m), leaving the area, and resuming incubation. Due to this variation, two aggression metrics were calculated similar to those created by Cain and Ketterson (2013): one, “Aggression,” only included 5-second intervals



when the focal female exhibited overtly aggressive actions (Peck, On decoy, On box, Flybys within 1 m), while the other, “Persistence,” also included intervals when the focal female was perched within 3 m of the decoy. Similar studies have used time within 0.25 m and 1-5 m as a measure of aggression (Cain and Ketterson 2013), but because the boxes are over water, limiting the availability of nearby perches, a distance of 3 m was chosen as it encompassed the nearest available perch for all trials. These two scores allowed us to evaluate individuals that were not overtly aggressive but were continually present and responding to the SNI (Figure 3).

Repeatability of these two metrics was calculated both within ( $N = 3$ ) and between clutches ( $N = 8$ ) using the ICC package in R (Lessells and Boag 1979, Wolak et al. 2012, R Core Team 2019).

#### *Quantifying Parental Care and Reproductive Success*

Parental nestling provisioning rate was measured with video observation during the mid-late nestling stage (6-10 days after hatching) on days without rain. During this stage, we filmed each nest for ~2-hours (mean = 2.63 hrs, range = 1.83 – 3.11 hrs) in the morning (6:00 AM – 12:30 PM) and standardized the number of parental visits by the number of nestlings and the video length (i.e., number of visits chick<sup>-1</sup> hour<sup>-1</sup>), following a protocol previously used in this study system (Dodson et al. 2016). Provisioning effort from all videos was recorded by one individual (EBC). Although previous studies found male and female Prothonotary Warbler provisioning effort to be correlated (Bulluck et al. 2017), this was not the case during the 2019 breeding season ( $r = 0.186$ ,  $p = 0.307$ ), so the number of male visits was not used as a covariate in models predicting female visits. Because we were interested in using total visits as a metric of pair parental effort in nestling condition models, we also examined whether female aggression metrics were related to total (female + male) provisioning effort.

Reproductive success was quantified for each female as the residuals from a generalized linear regression (Poisson distribution and log link) of the number of young fledged across the season and the initiation date of her first nest. Using these residuals instead of the total number of young fledged accounts for the fact that females who initiate nests earlier in the season tend to have larger clutches and are more likely to double brood (Bulluck et al. 2013). We also calculated a mean nestling body condition index (BCI) for each nest as a measure of fitness because nestling mass is an indicator of post-fledging survival (Maness and Anderson 2013). BCI was calculated as the residuals from a linear regression of nestling mass and log (nestling age in days); Individuals with positive residual values (BCI) are larger than average for their age and those with negative residuals are smaller than average for their age.

### *Quantifying Ornamentation*

We collected six crown and nine breast feathers from each focal female and mounted them on black cardstock. Feather reflectance was measured using an Ocean Optics JazPX spectrometer, and ornamentation metrics representing the relative contribution of several specific wavelength ranges/hues to total brightness (S1U Chroma = ultraviolet, S1B Chroma = violet-blue) were calculated with the R package pavo (Maia et al. 2019). We calculated violet blue (VB) chroma as the total reflectance in the violet-blue region,  $R_{400-510 \text{ nm}}$ , divided by the total reflectance in the entire measured spectrum,  $R_{300-700 \text{ nm}}$  (Shawkey et al. 2006). By modifying the code in from pavo, we created a function to calculate Yellow Intensity as the average reflectance in the yellow (500-700 nm) region minus the minimum reflectance in the blue (435-500 nm) region (Montgomerie 2006). We examined both VB chroma and yellow intensity because VB chroma is inversely related to carotenoid content while yellow intensity is related to feather structure (Saks et al. 2003, Shawkey and Hill 2005), and previous research indicates that they

have different signaling functions in this species (Beck 2013, Bulluck et al. 2017). As VB Chroma is highly correlated with UV Chroma (breast  $r = 0.76$ , crown  $r = 0.75$ ; Figure 4), the latter was not analyzed further. To quantify the size of the white tail spots, we collected one outer tail feather (when all tail feathers were present) and measured the area and proportion of white using ImageJ software (Rueden et al. 2017).

### *Statistical Analysis*

#### *Predictors of Aggression/Persistence*

All analyses were conducted in R 3.5.3 and RStudio 1.2.5001 (R Core Team 2019, R Studio Team 2019). Before proceeding with using aggression and persistence scores as independent variables, we first assessed whether they varied significantly with playback file, decoy ID, flush type, incubation stage, or SNI trial date using zero-inflated models with a negative binomial (nbinom1) distribution in the glmmTMB package (Brooks et al. 2017). We were unable to use Female ID as a random effect since these models failed to converge ( $N = 69$  trials and 62 individuals). Additionally, because aggression and persistence were significantly lower for one of the SNI playback files that had the lowest chip rate, we conservatively eliminated trials in which that file was used from further analyses ( $N = 21$ ). Thus, when two trials were completed for the same female in the first (fledged prior to June 18<sup>th</sup>) and second (fledged after June 18<sup>th</sup>) clutches ( $N = 8$  females), we randomly selected one of the two trials for inclusion. This resulted in a total sample size of 40 independent trials across the two sites and clutches. SNI playback file and Decoy ID were then excluded from future analyses because they were not significant predictors of aggression or persistence (all  $p > 0.118$ ). Females that experienced a flush ( $N = 26$ ) did not react differently than those that did not ( $N = 14$ ), and for

individuals that experienced a flush, a hard or soft flush was not significant (all  $p > 0.176$ ), thus flush was similarly excluded from future analyses. Incubation stage (Early = Days 3-6, Late = Days 7-10) and trial date (Julian) also did not significantly influence aggression or persistence (all  $p > 0.137$ ) and were excluded from future analyses. The potential impact of male presence was not assessed because the male of the pair was present and visible for  $\geq 1$  minute in 36/40 trials. Female chip rate (per minute) was not correlated with aggression or persistence (all  $p > 0.142$ ) and was not examined further. For these zero-inflated models, a pseudo- $R^2$  was calculated as  $1 - (\text{var}(\text{residuals}(\text{model})) / \text{var}(\text{model response}))$ .

#### *Tradeoffs of aggression/persistence and ornamentation*

We used either aggression or persistence as a predictor in separate linear models with provisioning rate, the number of young fledged, mean nestling BCI, and ornamentation measures as response variables (Table 2). We are primarily interested in the influence of female aggression on these response variables and whether its influence is context dependent. To assess whether the costs or benefits of aggression are context-dependent, we included either an aggression by site interaction or an aggression by local density (# active nests within 60 m) interaction. Site and local density were not included within the same model because they were marginally related (Welch's  $t = 2.04$ ,  $df = 20.29$ ,  $p = 0.055$ ). However, before we could address these hypotheses of interest, we had to determine whether additional known biological factors were predictors of our response variables. These potential co-variables included female age (number of years breeding = 1 (SY), 2 (TY), and 3+ (ATY)) and clutch (1 = fledged prior to June 18<sup>th</sup>, 2 = fledged after June 18<sup>th</sup>). If one or more of these biological factors performed better than the null (intercept only model), then it was also included as a co-variate in the models with aggression/persistence, local density/site, and an interaction between these focal variables. All model sets evaluating

ornamentation and female fitness in the framework of aggression were compared using Akaike's Information Criterion adjusted for small sample size (AICc) and were developed and compared using the stats (R Core Team 2019) and MuMIn (Barton 2019) packages (Burnham and Anderson 2002). Values reported are means  $\pm$  SE, and for fixed effects,  $\beta$  (regression coefficient) and 95% CIs (confidence intervals) are reported.

## Results

We were unable to calculate within-clutch repeatability due to the small sample size ( $N = 3$ ). Because clutch was not a significant predictor of either aggression ( $t_{38} = 0.185$   $p = 0.854$ ) or persistence ( $t_{38} = 0.422$   $p = 0.675$ ), we calculated repeatability by combining trials for females tested twice within ( $N = 3$ ) and across ( $N = 8$ ) clutches. Aggression was repeatable (ICC = 0.665, 95% CI = 0.171, 0.896;  $N = 11$ ) while persistence was not (ICC = 0.126, 95% CI = -0.465, 0.650;  $N = 11$ ). To obtain repeatability comparable with studies using a similar aggression assay ( $r = 0.79$ , Rosvall 2008) with a 95% CI width of 0.4, 15 individuals would need to be tested twice within the same clutch (ICC package; Wolak 2011). Though clutch was not a predictor of either aggression metric, aggression decreases across a breeding attempt in other species (Araya-Ajoy and Dingemanse 2017, Bentz et al. 2019); because Prothonotary Warblers double brood, assessing within clutch repeatability would be the most conservative approach.

### *Predictors of Aggression/Persistence*

The top model assessing predictors of female aggression only included site ( $\beta = 1.244$ , 95% CI = 0.245, 2.242), where females nesting at RRC were more aggressive (Table 3). The second-best performing model ( $dAICc = 0.084$ ) only included local density ( $\beta = -0.742$ , 95% CI = -1.415, -0.069), where females with fewer neighbors were more aggressive (Figure 5). The top

model assessing predictors of female persistence included female age, but the parameter estimate CIs included zero (TY  $\beta = 0.361$ , 95% CI = -0.076, 0.798; ATY  $\beta = -0.222$ , 95% CI = -0.795, 0.351); the second-best model was the null model (Table 4).

#### *Tradeoffs of Aggression/Persistence – Provisioning Effort*

Our sample size of nests with provisioning data was 32 because 5 failed and 3 were removed from analysis: one was in the process of fledging during the video, another was the latest initiated and the female visited  $>1.5$  chick<sup>-1</sup> hour<sup>-1</sup> more than any other female, and the third experienced multiple intrusions by a different pair during the video. The latter two nests were also the only samples with no male provisioning visits. We were unable to examine site as a predictor because there were only 6 RRC nests left in this subset of the data. Female age was the only biological factor that predicted provisioning effort (both female and total) better than the null model and so was included in models with our focal predictors (aggression/persistence and site/local density). The top model for female provisioning included local density ( $\beta = 0.189$ , 95% CI = 0.041, 0.338) and female age (Table 5), where females nesting in a high-density environment provisioned more often (Figure 6). The top model for total provisioning effort included persistence and female age; pairs with more persistent females provisioned less often ( $\beta = -0.015$ , 95% CI = -0.026, -0.003; Figure 7). The second-best model (dAIC<sub>c</sub> = 0.402) included aggression and female age; pairs with aggressive females had lower total provisioning effort ( $\beta = -0.022$ , 95% CI = -0.040, -0.004; Table 6).

#### *Tradeoffs of Aggression/Persistence – Female Reproductive Success*

Since density changes over the course of the breeding season and we used the total number of young fledged over the entire breeding season (adjusted for nest initiation date of the first clutch) as a measure of reproductive success, density was not examined in these models.

The null model was the top model; all other models had parameter estimates with 95% CIs that included zero, suggesting that female age, aggression, persistence, and site were not predictors of the number of young fledged over the course of the breeding season (N = 40).

The top model for predictors of mean nestling BCI only included clutch ( $\beta = -0.510$ , 95% CI = -0.941, -0.079; Figure 8; N = 32), where nestling BCI was lower in later nests. The null model was the second-best model (dAICc = 2.8).

### *Ornamentation*

For breast yellow intensity, the top model only included aggression as a predictor (Table 9, Figure 9, N = 40), and indicated that more aggressive females were less ornamented ( $\beta = -0.231$ , 95% CI = -0.421, -0.041). The null model received the most support for crown yellow intensity, indicating that aggression, persistence, site, local density, and female age were not important predictors.

Female age and an interaction between persistence and local density were predictors in the top model for breast VB chroma (Table 10, N = 40); to examine this interaction, density was grouped into low (0-1 neighbors) and high (2-3 neighbors). In a high-density environment, more persistent females had higher breast carotenoid content (lower breast VB chroma), while in a low-density environment there was no relationship between persistence and breast carotenoid content (Figure 10). For crown VB chroma, the best supported model included site as the only predictor ( $\beta = 0.017$ , 95% CI = -0.005, 0.040), but the 95% CI included 0, and the null model was the second-best model (dAICc = 0.1, N = 40).

The top model for predictors of the amount of white in the tail only included female age; older females had more tail white than first year breeding females (Figure 11, N = 38).

Aggression, persistence, site, and local density were not predictors of tail white amount as the 95% CIs for all other models included zero ( $dAICc > 2.0$ ).

## **Discussion**

In two populations of Prothonotary Warblers experiencing varying local and historical (site-level) densities, we examined the relationships between female aggression and measures of reproductive fitness as well as the relationships between female aggression and ornamentation. We found that females nesting in boxes with higher densities were less aggressive and provisioned their young more often. Additionally, total provisioning effort (males and females) was lower in pairs with more aggressive or persistent females. However, more direct measures of fitness (mean nestling BCI and the number of young fledged) were not related to female aggression. We also found that female breast ornamentation may serve as a signal for aggressiveness, though one metric of ornamentation (yellow intensity) was negatively associated with aggression while another (carotenoid content) was positively associated with aggression. Collectively, these results suggest that female ornaments may function in conspecific competitive interactions, and that the tradeoffs of female aggression are context-dependent; local breeding density, a proxy for resource availability, may mediate the impacts of female aggressive interactions with conspecifics.

### *Aggression and Density*

Contrary to social selection theory and studies of the influence of breeding density on aggression in males, which have found that individuals in higher-density sites were more aggressive (Yoon et al. 2012, Araya-Ajoy and Dingemanse 2017), we found that individuals nesting at lower densities (site and local density) were more aggressive. This difference in the



effect of breeding density on intra-sexual aggression may be because males compete for access to mating opportunities with neighboring females while females compete for other resources such as limited nest sites (Clutton-Brock 2009, Lyon and Montgomerie 2012, Cain and Rosvall 2014). Resource selection theory may provide a better framework than social selection theory in this context, whereby the benefits of aggression outweigh the costs when resources are less available and/or have a clumped distribution (Emlen and Oring 1977, Grant 1993, Grant et al. 2000). Thus, the benefits and expression of aggression may be lower at DBP since the resource (nest box) is more abundant and evenly distributed even though there are a high number of competitors. We observe mean annual box occupancy rates of 75% at DBP and RRC such that there are always available boxes, but habitat quality at each box may not be the same.

In many systems, breeding density is indicative of habitat quality, as individuals will aggregate in and compete for high-quality areas (Bock and Jones 2004, Donahue 2006). Though we examined breeding density instead of resource availability per se, breeding density and nest box density are highly correlated in box nesting species. Our finding that females nesting in lower densities were more aggressive is also similar to Cain and Langmore's (2016) finding that females in lower quality, patchier habitat were more aggressive. We expected fewer competitive interactions among neighbors at RRC due to the availability of fewer and more spread out nest boxes. However, the limited number of nest boxes at RRC may be creating a more competitive environment compared to DBP, resulting in more intense resource defense (higher levels of aggression) at RRC. Additionally, when fewer nesting sites are available, females encountering an intruder may respond more aggressively to keep their nest box while also experiencing less of an energetic cost because they encounter fewer conspecifics (Smith and Parker 1976, Grant 2000, Cain and Langmore 2016). Because Prothonotary Warblers prefer nest boxes over natural

cavities in our study system and our breeding density metric is directly related to nest box availability, breeding density may be synonymous with habitat quality. However, as stated previously, our sites always have unoccupied boxes, and other factors such as food availability likely contribute to habitat quality as well.

Another explanation for the observed differences in female aggression between our sites is the potential influence of neighboring heterospecific competitors. At our sites, other species such as Carolina Chickadees (*Poecile carolinensis*) and Tree Swallows use the nest boxes as well. Carolina Chickadees are resident species and initiate nests before Prothonotary Warblers return to the breeding grounds, while Tree Swallows are migratory and begin to establish nests at the same time as Prothonotary Warblers. In both 2018 and 2019 at RRC, we observed 2 instances in which Tree Swallows usurped boxes that had been occupied by Prothonotary Warblers. Studies examining aggression to conspecific and heterospecific competitors have found that individuals respond equally aggressively to both conspecific and heterospecific intruders (Edworthy 2015, Freeman 2015), especially when there is a high degree of resource overlap (Peiman and Robinson 2010). For cavity nesting passerines, the presence of heterospecific competitors results in increased competition for a necessary and limited reproductive resource (cavity nesting sites), affecting the expression and tradeoffs of aggression. For instance, Western Bluebird (*Sialia mexicana*) pairs responded more aggressively to a heterospecific intruder when there is a cavity-nesting neighbor nearby (Bhardawj et al. 2015), and Eastern Bluebird (*Sialia sialis*) pairs that were most behaviorally similar (extremely aggressive/non-aggressive) had higher quality nestlings when nesting in areas of high interspecific competition with Tree Swallows (Harris and Siefferman 2014). Thus, the higher proportion of conspecifics (i.e., Carolina Chickadees and Tree Swallows) at RRC (On May 13<sup>th</sup>, 9/25 boxes, compared to 8/65

boxes at DBP) may be contributing to the higher level of aggression observed at that site.

Finally, although we only studied populations occupying artificial nest boxes, our results are likely conservative, as interspecific competition in populations of other cavity-nesting species using natural cavities is more intense than in populations using nest boxes (Robertson and Rendell 1990); interspecific competition in Prothonotary Warbler populations using natural cavities may be higher as well.

#### *Aggression vs. Parental Care & Reproductive Success*

Our finding that local density is also correlated to female provisioning rate further supports the idea that while local density may be an accurate proxy for habitat quality, other resources such as food may also be limiting. Females occupying higher-quality territories with an abundance of food can provision their young more often. Previous research in this system has found that the number of female provisioning visits is highly correlated with the amount of food being provided to the nestlings ( $r = 0.82$ ), and that there are differences between sites in the amount of food brought while the number of visits is the same (Dodson et al. 2016). Though we were unable to examine site in our provisioning models due to the small sample size, Dodson et al. (2016) observed within-site differences in food resource availability at DBP. Our two study sites (DBP and RRC) are more similar in terms of prey types than those used in Dodson et al. (2016), suggesting that within-site variability in habitat quality may be related to local density.

Although our female aggression metrics were not predictors of female provisioning effort, both aggression and persistence were negatively associated with total provisioning effort by both parents. Because female aggression is not correlated with female provisioning, this suggests that male provisioning effort varies as a function of female aggression where males paired with more aggressive females provision less. Previous studies have shown that more

aggressive males provision less (Duckworth 2006, Barnett et al. 2012), but in some species male reproductive success was not negatively impacted because their mates compensated with increased provisioning effort (Mutzel et al. 2013). Similarly, aggressive House Wren (*Troglodytes aedon*) females had mates that provisioned more often, and these females also experienced other fitness benefits such as decreased egg loss due to attempted nest take-overs (Krieg and Getty 2020). Male Prothonotary Warblers may be provisioning less when paired with aggressive (potentially lower-quality) females because they are evaluating tradeoffs between current and future (next breeding season or second clutch) reproductive output and investing less in parental effort when mated with a below-average individual (differential allocation; Burley 1986, Sheldon 2000). Additionally, because females may be competing for access to ecological resources besides mates, the increased expression of competitive traits such as aggression may not always have clear tradeoffs with parental care (Stiver and Alonzo 2009, Cain and Ketterson 2013); when there are tradeoffs, they are likely to vary by population (Rosvall 2011), habitat quality (Cain and Langmore 2016), or breeding conditions such as predation pressure (Cain and Ketterson 2013). We also did not examine incubation effort as a metric of female-specific parental care, and previous studies have found a negative relationship between aggression and incubation (Rosvall 2013, Cain and Ketterson 2013).

If the benefits of female aggression outweighed the costs in a higher breeding density (more competitive) environment as predicted by social selection theory, we would have observed higher reproductive success at higher breeding densities (increased number of young fledged or higher mean nestling BCI). However, we found no differences in total number of young fledged related to site and no differences in mean nestling BCI related to site or local density. Also, though there are instances of conspecific brood parasitism in our system, there seem to be no

long-term costs, suggesting that the predicted benefits of aggression (fending off conspecific parasites) at a higher-density site may be minimal (Tucker et al. 2016, Tucker and Bulluck 2018). The only significant predictor of mean nestling BCI was clutch, with lower mean nestling BCI in the second clutch, when food availability is likely lower (Goodbred and Holmes 1996). Our results differ from previous studies indicating relationships between female aggression and reproductive success; either that more aggressive females have lower quality (lighter) offspring (Rosvall 2011, Cain and Ketterson 2013) or higher quality (heavier) offspring (Krieg and Getty 2020). As with provisioning, the relationships between female aggression and reproductive success also change due to habitat quality or other environmental factors such as predation pressure (Cain and Ketterson 2013, Cain and Langmore 2016). In this system, the timing of nest initiation is the primary factor explaining variation in female reproductive success; females that initiate nests earlier in the season tend to have larger clutches and a higher probability of double brooding (Bulluck et al. 2013). Therefore, potential relationships between female aggression and measures of reproductive success may need to be examined for each clutch separately, which we were unable to do due to our small sample size (First Clutch N = 17, Second Clutch N = 15).

#### *Aggression vs. Ornamentation*

Like female ornaments in other species (Griggio et al. 2010; Midamegbe et al. 2011, Enbody et al. 2018), Prothonotary Warbler female breast ornamentation seems to serve as a signal in agonistic encounters; females with lower breast yellow intensity were more aggressive. Though previous research has not found relationships between yellow intensity and measures of reproductive success in this species (Beck 2013, Bulluck et al. 2017), if these drabber females are lower-quality (or less attractive) individuals, then they may respond more aggressively

against intruders to defend their nest/maximize their reproductive fitness. However, feather carotenoid content in this species is related to individual reproductive quality/parental care (Beck 2013, Bulluck et al. 2017). In this same study population (DBP), crown feather carotenoid content was positively related to the number of young fledged, and females with higher breast carotenoid content compensated for mates that provisioned less, while less ornamented females did not (Bulluck et al. 2017). We found that more persistent individuals had higher breast carotenoid content (lower breast VB chroma), but only in higher-density (2-3 neighbors) environments. Our persistence metric may represent individuals who express an intermediate level of aggression; if persistence is an important competitive trait, then the relationship between persistence and breast carotenoid content provides additional support for the signaling function of breast carotenoid content as a metric of individual quality, but specifically in high-density environments. The lack of this relationship in low-density environments is not surprising, as other studies have also found ornamentation to interact with factors such as breeding density (Estep et al 2005) or intruder identity (Midamegbe et al. 2011, Young et al 2016, Leitão et al. 2019). Like carotenoid-based ornaments in males of other species (Griggio et al. 2007, Leitão et al. 2015), female Prothonotary Warbler ornaments communicate both individual quality and aggression. VB chroma (carotenoid content) and yellow intensity are likely providing different signals because one (carotenoid content) is derived from diet, while the other (yellow intensity) is based on feather structure (Shawkey and Hill 2005).

### *Conclusion/Future Directions*

We acknowledge that our conclusions are limited by the low sample size and lack of repeatability related to persistence, and the need to further examine the potential effects of changes in environmental conditions such as breeding density within and across breeding

seasons (Cain and Ketterson 2013, Cain and Rosvall 2014). Especially because breeding density varies across and within breeding seasons, double-brooding species in particular may experience differing intra- and inter- seasonal tradeoffs (Plard et al. 2018) related to aggression. First broods tend to be highly synchronous such that access to nest boxes is more limited earlier in the season. And, though we found that breeding density influences female behavior including aggression and provisioning, this is a scale dependent metric; the relationships between female behavior and breeding density at other scales may be different. To our knowledge, few studies use metrics of breeding density at different scales; those that do have found that relationships between breeding density and measures of reproductive success do not change at different local scales (50 m, 200 m, 300 m; McKellar 2014), but that local and landscape (population) scales of density affect fecundity differently (Rodenhouse et al. 2003). The results presented here highlight that breeding density is an important metric to consider in studies of female aggression; future studies should explicitly consider the tradeoffs of female aggression related to the distribution of resources, such as breeding territories, at different spatial scales to further improve our understanding of how and why female competitive traits are expressed.

## Tables and Figures

**Table 1.** Ethogram used in SNI trials and modified from Rosvall (2008). Behaviors with an \* are considered aggressive.

<b>Behavior</b>	<b>Definition/Modifier</b>
<i>Flyby</i>	Flies in front of decoy with approximate distance from decoy noted ( $\leq 1$ m = Aggressive) *
<i>Peck*</i>	Physical contact of beak with decoy
<i>Hover*</i>	Sustained flight right next to the decoy, at least for 1 sec
<i>Tail fan</i>	Tail is spread open
<i>On decoy*</i>	Perched on the decoy
<i>On box*</i>	Perched on top of nest box next to decoy (as opposed to the sides or front of the box)
<i>In box</i> ____	Note whether the bird is visible (head out vs. in box and cannot see)
<i>On</i> ____	Describe where bird is perched and estimated distance from box (branch 3m away, etc.)
<i>Preening</i>	Bird running bill through feather
<i>Away</i>	Specify whether bird is away from the box and location if possible (e.g., “away, foraging in forest” or “away, out of sight”)
<i>Chipping</i>	Short notes made by female (or male), distinguished with observation in-the-field and the Tascam recording



**Table 2.** Predictor and response variables for model sets.

<b>Model Parameters</b>	<b>Description</b>
<b>Predictor Variables</b>	
Aggression	Number of 5-second intervals when an aggressive behavior occurred
Persistence	Number of 5-second intervals when an aggressive behavior occurred or focal individual was perched $\leq 3$ m
Local Density	Number of active nests within 60m
Site	Deep Bottom Park (high-density) or Rice Rivers Center (low-density)
Clutch	First (Julian Completed $\leq 169$ ) or second (Julian Completed $> 169$ )
Female Age	Number of years breeding = 1 (SY), 2 (TY), and 3+ (ATY)
Aggression * Site	Aggression and site interaction to examine potential site effects
Aggression * Local Density	Aggression and local density interaction to examine potential density effects
Persistence * Site	Persistence and site interaction to examine potential density effects
Persistence * Local Density	Persistence and local density interaction to examine potential density effects
<b>Response Variables</b>	
Ornamentation	Crown/breast yellow intensity/violet blue chroma or amount of tail white
Provisioning Rate	Number of visits with food made by the focal individual, standardized per chick per hour
Number of Young Fledged	Residuals from a generalized linear model (Poisson distribution and log link) of the number of young fledged and first nest initiation date
Mean Nestling Body Condition Index (BCI)	Residuals from a linear regression of mass and log (nestling age in days)

**Table 3.** Model selection results for all zero-inflated (negative binomial 1 fit) generalized linear models predicting female aggression (N = 40) where the models are ranked from left to right (best to worst). K is the number of estimable parameters, dAICc is the difference in second-order Akaike's Information Criterion compared with the top model,  $w_1$  is the AICc model weight, or relative likelihood of each model, and LL is the log-likelihood of each model.  $\beta$  and 95% CIs are reported. Pseudo  $R^2_{adj}$  is calculated as  $1 - var(residuals(model))/var(response(model))$ .

Model Parameters	Site	Local Density	Null	Incubation Stage	Clutch	Female Age
Site	1.244* 0.245; 2.242]					
Local Density		-0.742* [-1.415; -0.069]				
Incubation Stage				-0.640 [-1.802; 0.521]		
Clutch					0.130 [-0.791; 1.050]	
Female Age (TY)						0.214 [-0.842; 1.269]
Female Age (ATY)						0.144 [-1.072; 1.360]
K	4	4	3	4	4	5
dAICc	0.000 <sup>a</sup>	0.084	0.744	1.694	3.151	5.675
$w_1$	0.299	0.287	0.206	0.128	0.062	0.018
LL	-101.626	-101.668	-103.326	-102.473	-103.202	-103.153
Pseudo $R^2_{adj}$	0.164	0.147	-	0.0176	-0.00452	0.0130

\* 0 outside the confidence interval

<sup>a</sup> AICc = 212.395

**Table 4.** Model selection results for all zero-inflated (negative binomial 1 fit) generalized linear models predicting female persistence (N = 40) where the models are ranked from top to bottom (best to worst). K is the number of estimable parameters, dAICc is the difference in second-order Akaike’s Information Criterion compared with the top model,  $w_1$  is the AICc model weight, or relative likelihood of each model, and LL is the log-likelihood of each model. Pseudo- $R^2$  adjusted was calculated as  $1-(var(residuals(model))/var(model\ response))$ .

<b>Model Parameters</b>	<b>K</b>	<b>dAICc</b>	<b><math>w_1</math></b>	<b>LL</b>	<b>Pseudo <math>R^2</math> adj</b>
Female Age (SY/TY/ATY)	5	0.000 <sup>a</sup>	0.277	-139.419	0.001
1.00	3	0.288	0.240	-142.112	-
Incubation Stage	4	0.576	0.208	-141.017	0.0576
Site	4	1.511	0.130	-141.485	-0.0561
Clutch	4	2.566	0.0767	-142.013	0.00445
Local Density	4	2.764	0.0695	-142.112	0

<sup>a</sup> AICc = 290.602

**Table 5.** Model selection results for all aggression and biologically relevant linear models for female provisioning effort (N = 32) where the models are ranked from left to right (best to worst). K is the number of estimable parameters, dAICc is the difference in second-order Akaike's Information Criterion compared with the top model,  $w_1$  is the AICc model weight, or relative likelihood of each model, and LL is the log-likelihood of each model.  $\beta$  and 95% CIs are reported. An \* represents an interaction between the two variables. LD is Local Density.

	LD	LD * Aggr	Null	Female Age	Aggr	Pers	LD * Pers
Local Density	0.189* [0.041; 0.338]	0.137 [-0.030; 0.303]					0.118 [-0.089; 0.326]
Female Age (TY)	-0.175 [-0.485; 0.135]	-0.192 [-0.497; 0.113]		-0.222 [-0.557; 0.112]	-0.221 [-0.549; 0.107]	-0.236 [-0.567; 0.094]	-0.222 [-0.547; 0.103]
Female Age (ATY)	-0.328 [-0.691; 0.035]	-0.337 [-0.696; 0.021]		-0.423* [-0.809; -0.037]	-0.425* [-0.804; -0.047]	-0.473* [-0.861; -0.086]	-0.405* [-0.791; -0.018]
Aggression		-0.008 [-0.021; 0.005]			-0.009 [-0.021; 0.003]		
Local Density * Aggression		0.019 [-0.003; 0.042]					
Persistence						-0.005 [-0.013; 0.002]	-0.007 [-0.019; 0.005]
Persistence * Local Density							0.003 [-0.004; 0.010]
K	5	7	2	4	5	5	7
dAICc	0.000 <sup>a</sup>	2.734	3.299	3.644	4.076	4.411	4.557
$w_1$	0.512	0.131	0.098	0.083	0.067	0.056	0.052
R <sup>2</sup> adj	0.220	0.250	-	0.0777	0.114	0.104	0.206
LL	-10.811	-8.999	-16.408	-14.046	-12.849	-13.017	-9.910

\* 0 outside the confidence interval

<sup>a</sup> AICc = 33.930

**Table 6.** Model selection results for all aggression and biologically relevant linear models predicting total (female + male) provisioning effort (N = 32) where the models are ranked from left to right (best to worst). K is the number of estimable parameters, dAICc is the difference in second-order Akaike's Information Criterion compared with the top model,  $w_1$  is the AICc model weight, or relative likelihood of each model, and LL is the log-likelihood of each model.  $\beta$  and 95% CIs are reported. LD is Local Density.

	Pers	Aggr	LD	LD * Pers	Female Age	Null	LD * Aggr
Persistence	-0.015* [-0.026; -0.003]			-0.019* [-0.038; -0.001]			
Female Age (TY)	-0.292 [-0.784; 0.201]	-0.251 [-0.746; 0.243]	-0.194 [-0.710; 0.322]	-0.297 [-0.802; 0.209]	-0.254 [-0.789; 0.281]		-0.232 [-0.729; 0.265]
Female Age (ATY)	-0.840* [-1.418; -0.262]	-0.707* [-1.278; -0.136]	-0.581 [-1.185; 0.023]	-0.788* [-1.389; -0.188]	-0.701* [-1.319; -0.083]		-0.637* [-1.220; -0.053]
Aggression		-0.022* [-0.040; -0.004]					-0.023* [-0.045; -0.001]
Local Density			0.240 [-0.006; 0.487]	0.092 [-0.231; 0.415]			0.098 [-0.174; 0.370]
Local Density * Persistence				0.005 [-0.007; 0.016]			
Aggression * Local Density							0.021 [-0.015; 0.058]
K	5	5	5	7	4	2	7
dAICc	0.000 <sup>a</sup>	0.402	2.655	2.854	3.748	3.897	4.038
$w_1$	0.363	0.297	0.096	0.087	0.056	0.052	0.048
LL	-25.788	-25.989	-27.115	-24.035	-29.075	-31.683	-24.627
R <sup>2</sup> adj	0.234	0.224	0.168	0.233	0.0918	-	0.233

\* 0 outside the confidence interval

<sup>a</sup> AICc = 63.883

**Table 7.** Model selection results for the top 7 aggression and environment-related linear models predicting female breast yellow intensity (N = 40) where the models are ranked from left to right (best to worst). K is the number of estimable parameters, dAICc is the difference in second-order Akaike's Information Criterion compared with the top model,  $w_1$  is the AICc model weight, or relative likelihood of each model, and LL is the log-likelihood of each model.  $\beta$  and 95% CIs are reported. An \* represents an interaction between the two variables. LD is local density.

	<b>Aggr</b>	<b>LD</b>	<b>LD * Aggr</b>	<b>Null</b>	<b>Site * Aggr</b>	<b>Pers</b>	<b>Site</b>
Aggression	-0.231* [-0.421; -0.040]		-0.219 [-0.461; 0.022]		-0.096 [-0.412; 0.220]		
Local Density		2.412* [0.057; 4.767]	1.374 [-1.507; 4.255]				
Aggression * Local Density			0.049 [-0.163; 0.261]				
Aggression * Site					1.700 [-4.746; 8.146]		-2.628 [-7.580; 2.323]
Persistence					-0.232 [-0.656; 0.192]		
Site						-0.077 [-0.206; 0.051]	
K	3	3	5	2	5	3	3
dAICc	0.000 <sup>a</sup>	1.491	2.743	3.179	3.819	4.089	4.398
$w_1$	0.431	0.204	0.109	0.088	0.064	0.056	0.048
LL	-132.129	-132.875	-130.952	-134.890	-131.490	-134.174	-134.329
R <sup>2</sup> adj	0.106	0.072	0.110	-	0.086	0.010	0.002

\* 0 outside the confidence interval

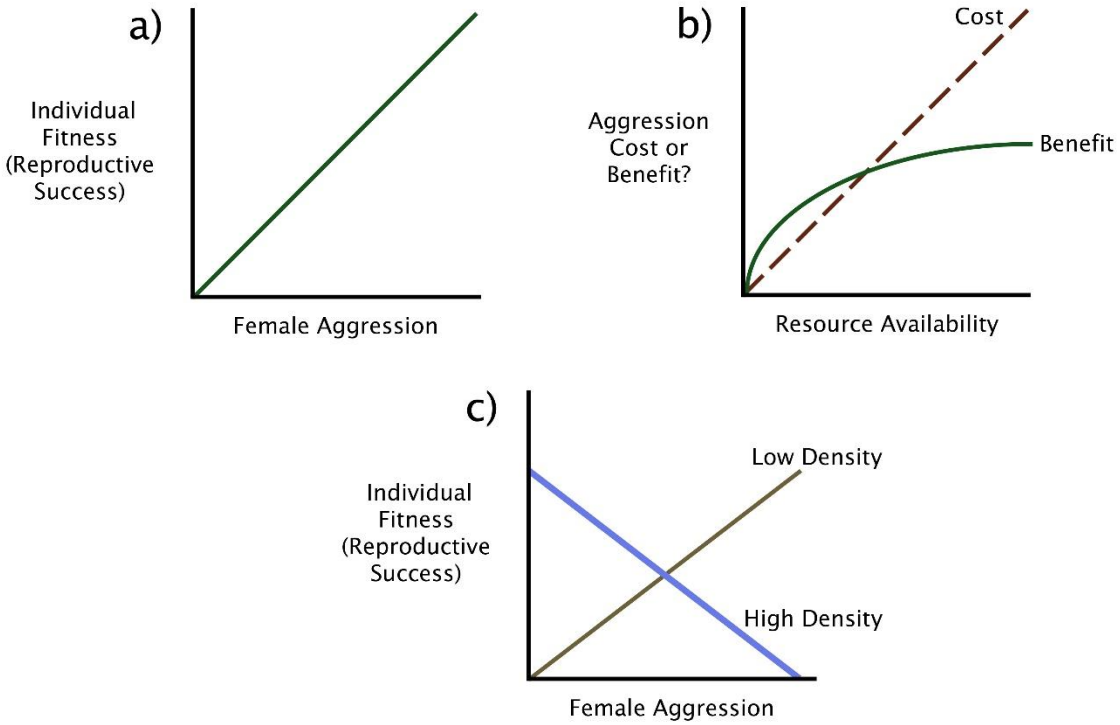
<sup>a</sup> AICc = 270.926

**Table 8.** Model selection results for the top 7 aggression and environment-related linear models predicting female breast VB chroma (N = 40). Female age is included as the only biologically relevant predictor. K is the number of estimable parameters, dAICc is the difference in second-order Akaike's Information Criterion compared with the top model,  $w_1$  is the AICc model weight, or relative likelihood of each model, and LL is the log-likelihood of each model.  $\beta$  and 95% CIs are reported. An \* represents an interaction between the two variables. LD is local density.

	LD * Pers	Female Age	Pers	Site * Pers	Null	Site	LD
Persistence	0.000 [-0.000; 0.001]		-0.000 [-0.001; 0.000]	-0.001* [-0.001; -0.000]			
Female Age (TY)	-0.010 [-0.026; 0.007]	-0.016 [-0.033; 0.001]	-0.016 [-0.032; 0.001]	-0.019* [-0.036; -0.002]		-0.018* [-0.036; -0.001]	-0.016 [-0.033; 0.001]
Female Age (ATY)	-0.020 [-0.040; 0.000]	-0.024* [-0.044; -0.004]	-0.026* [-0.046; -0.006]	-0.025* [-0.045; -0.006]		-0.024* [-0.044; -0.004]	-0.022* [-0.043; -0.002]
Local Density	0.013* [0.001; 0.025]						0.004 [-0.005; 0.012]
Persistence * Local Density	-0.000* [-0.001; -0.000]						
Site				-0.030* [-0.059; -0.000]		-0.008 [-0.025; 0.010]	
Persistence * Site				0.001* [0.000; 0.002]			
K	7	4	5	7	1	5	5
dAICc	0.000	0.356	0.373	1.256	1.790	2.170	2.228
$w_1$	0.234	0.196	0.194	0.125	0.096	0.076	0.077
LL	98.952	94.595	95.898	98.324	91.469	95.000	94.971
R <sup>2</sup> adj	0.211	0.0985	0.132	0.186	-	0.0920	0.0907

\* 0 outside the confidence interval

<sup>a</sup> AICc = 180.404

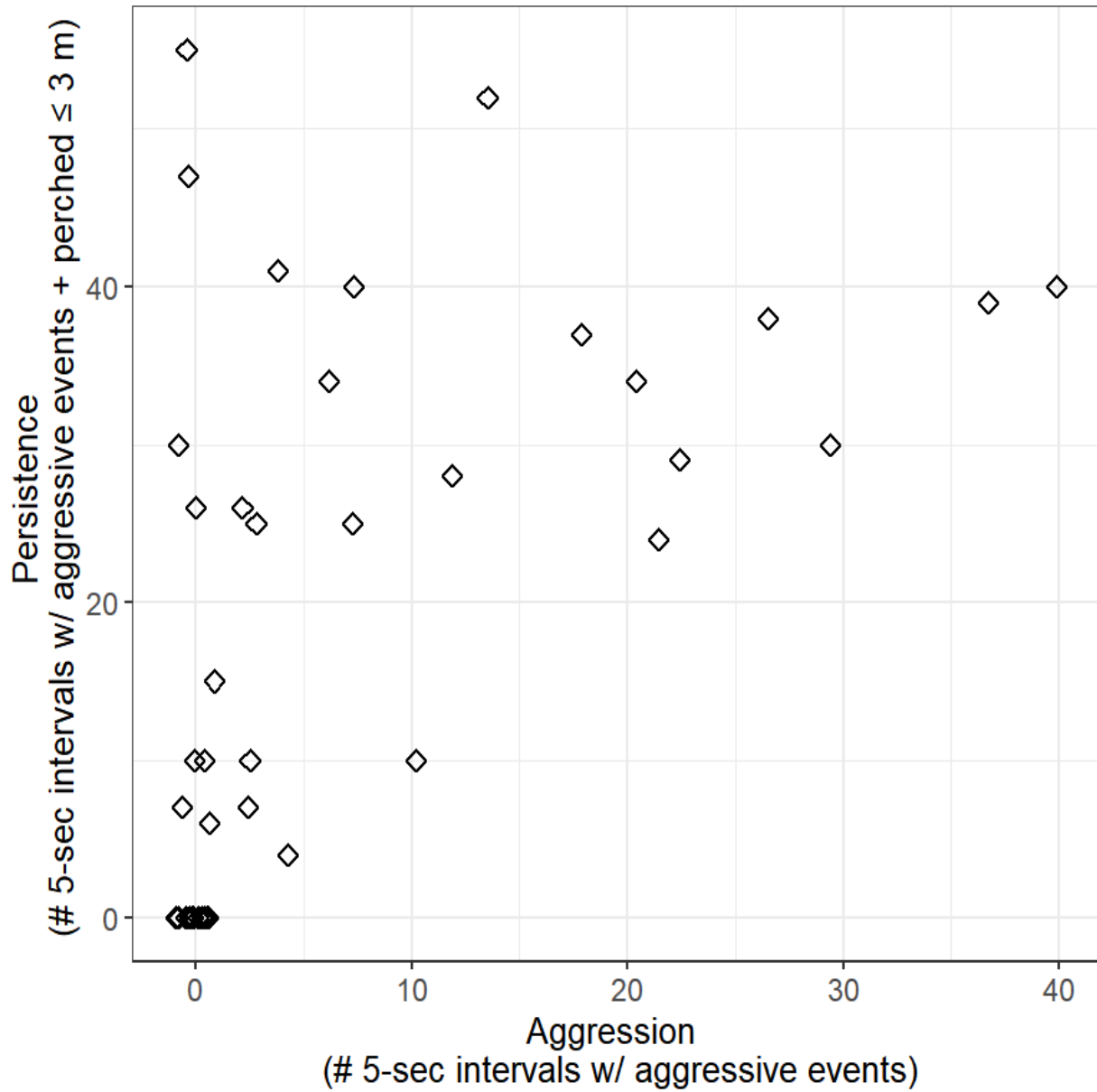


**Figure 1.** Expected cost-benefits (tradeoffs) for female aggression under a) social selection theory where the benefits outweigh the costs for high quality individuals in a competitive environment, and b) resource defense theory, where the benefits outweigh the costs only when resource availability is low/unevenly distributed. These predictions are then applied in c) the context of breeding density, where at low densities (i.e., low box availability), more aggressive individuals will experience benefits, while at high densities (i.e., high box availability), more aggressive individuals will experience costs.

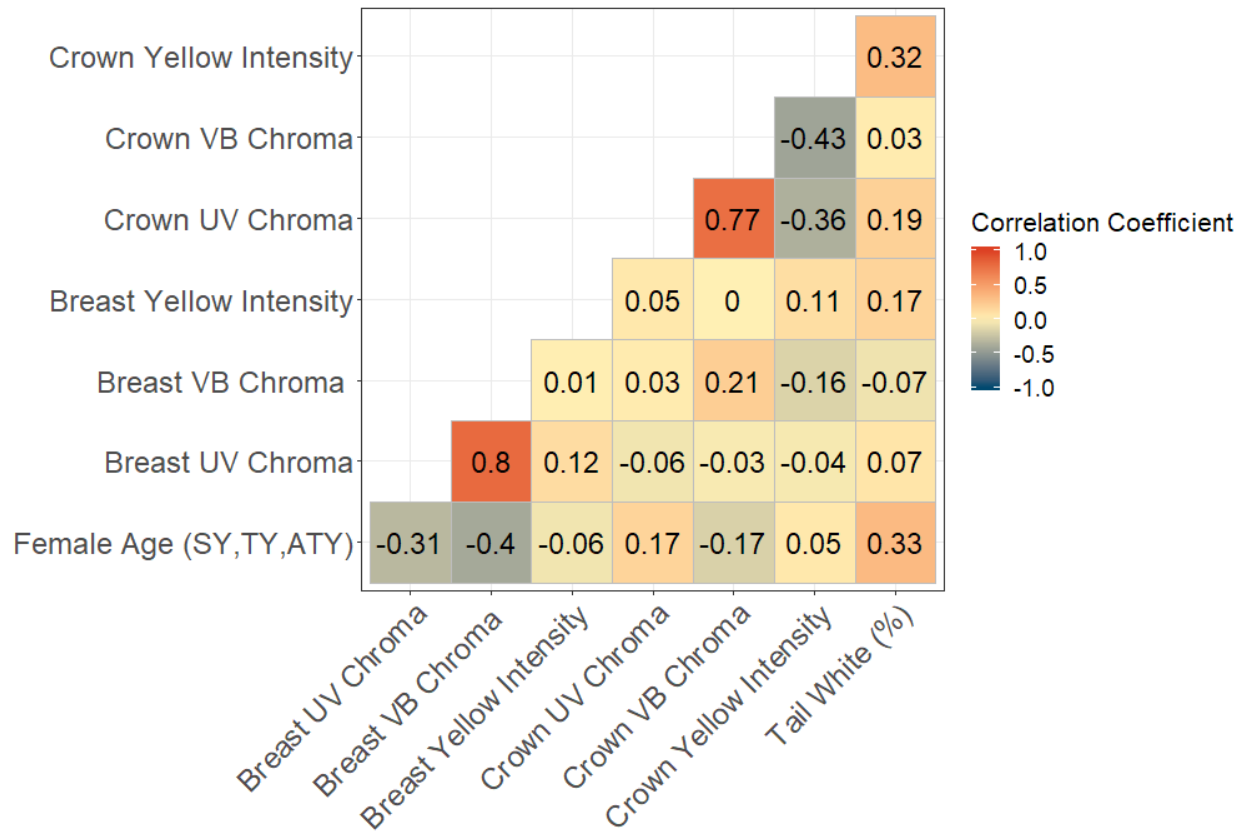




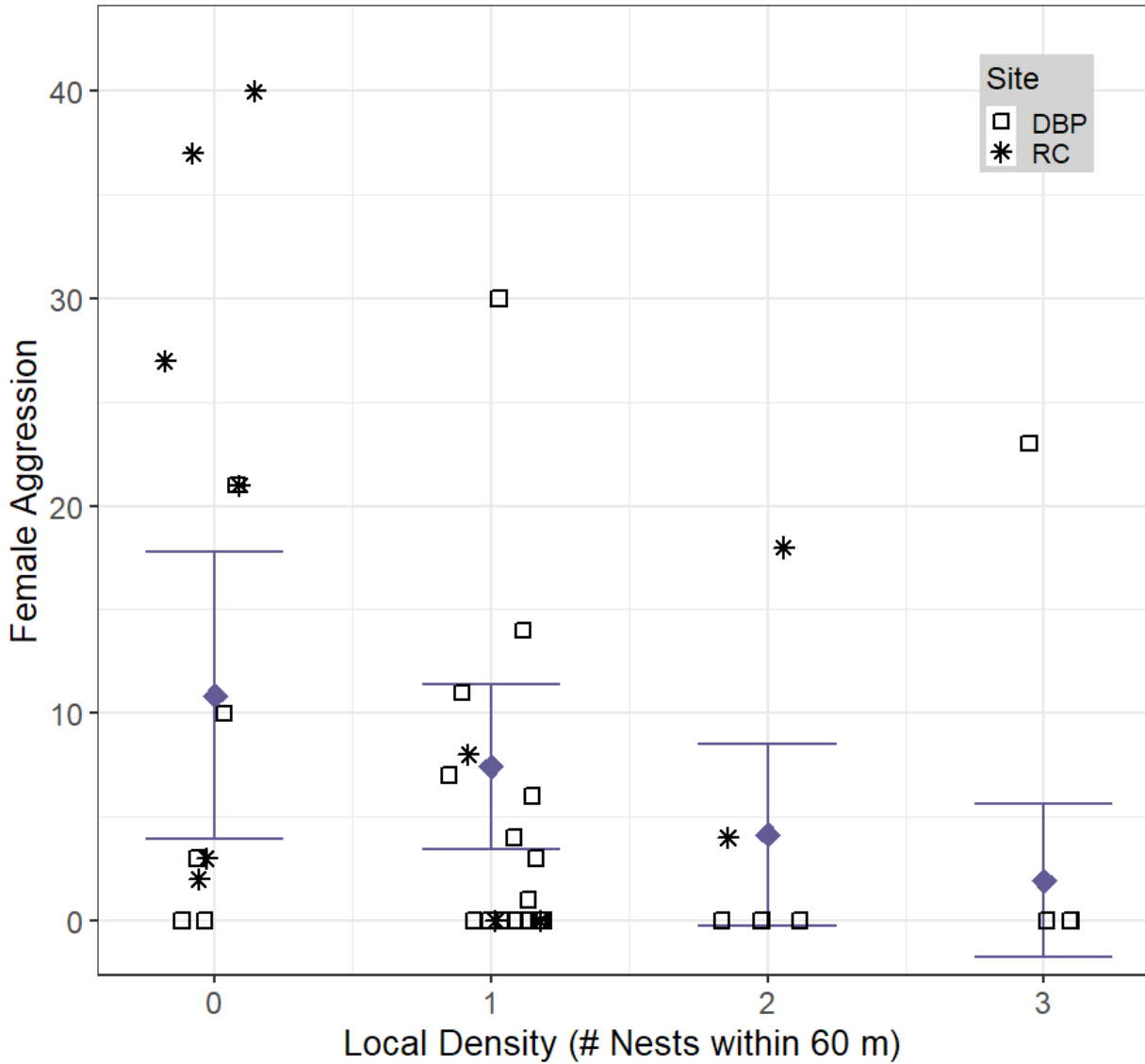
**Figure 2.** Staged Nest Intruder set-up in the field. A Tascam DR-05 recorder and Altec Lansing Mini H20 2 Bluetooth Speaker are looped around the nest box pole.



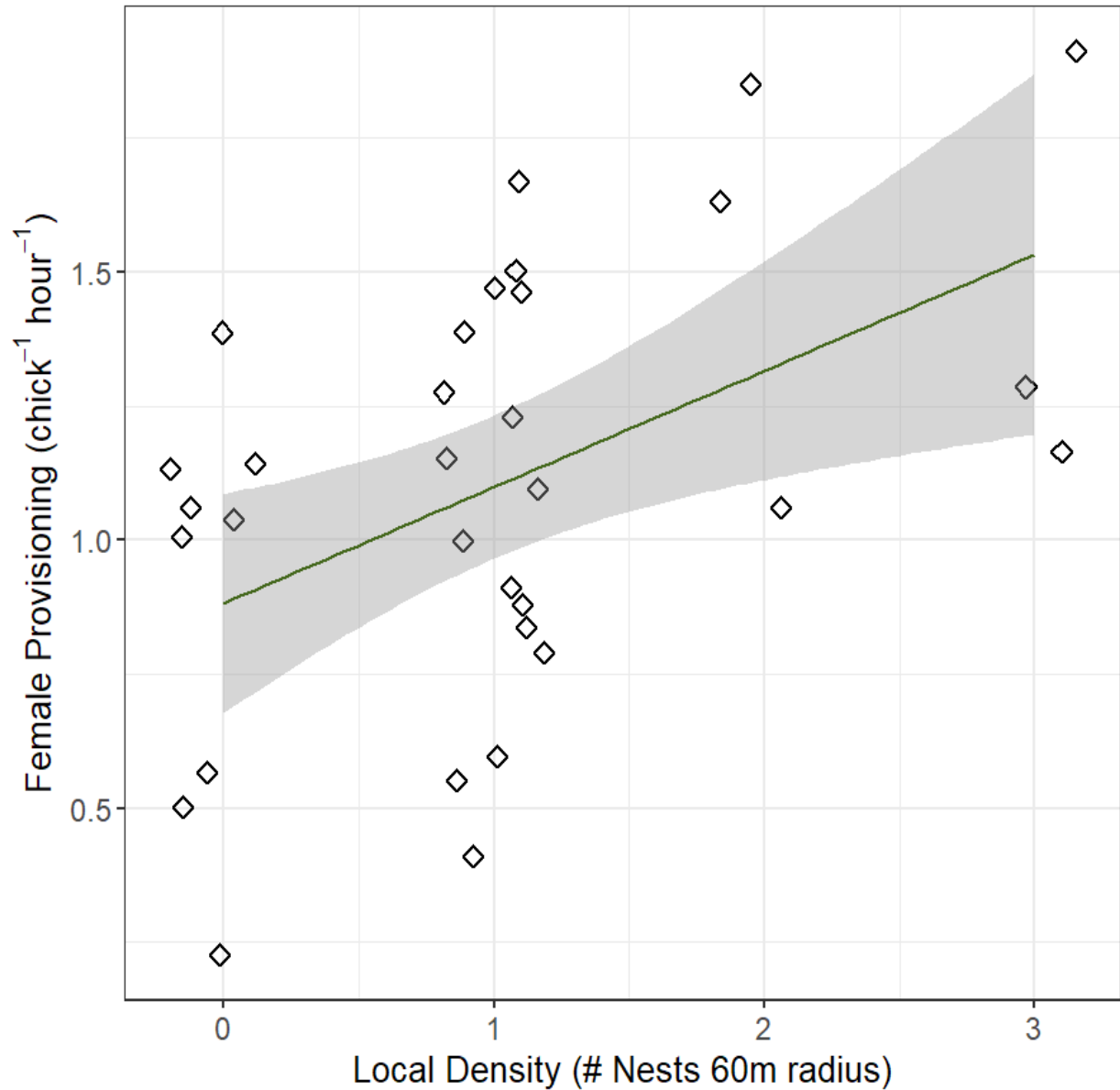
**Figure 3.** Aggression and persistence scores across all females sampled ( $N = 40$ ) demonstrating the variety of responses observed: individuals that were aggressive and persistent, individuals that were only persistent, and individuals that were never aggressive. Points are jittered for clarity.



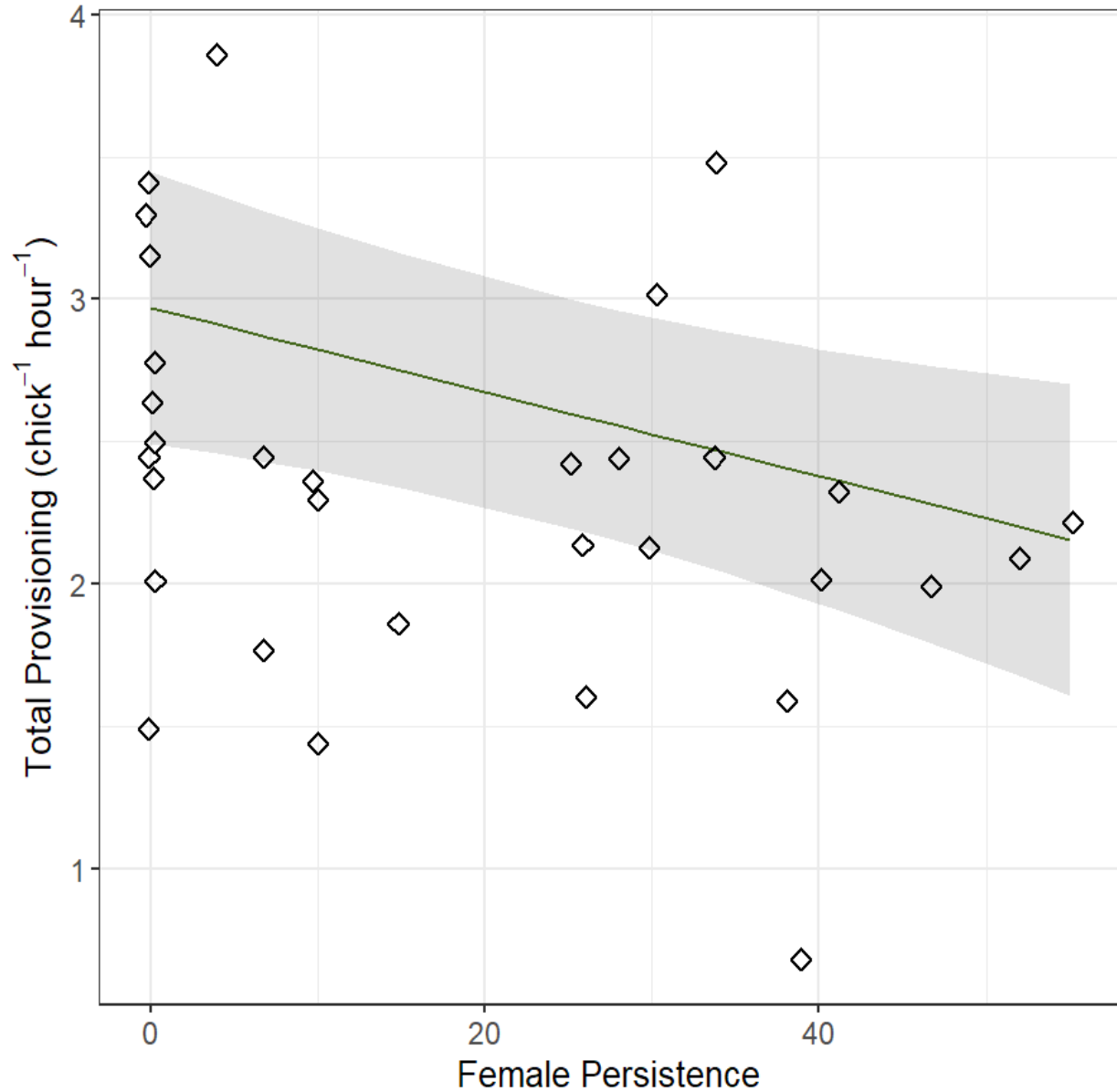
**Figure 4.** Correlation matrix for ornamentation measures and female age (N = 38). VB (violet-blue) chroma is inversely related to feather carotenoid content in both breast and crown feathers.



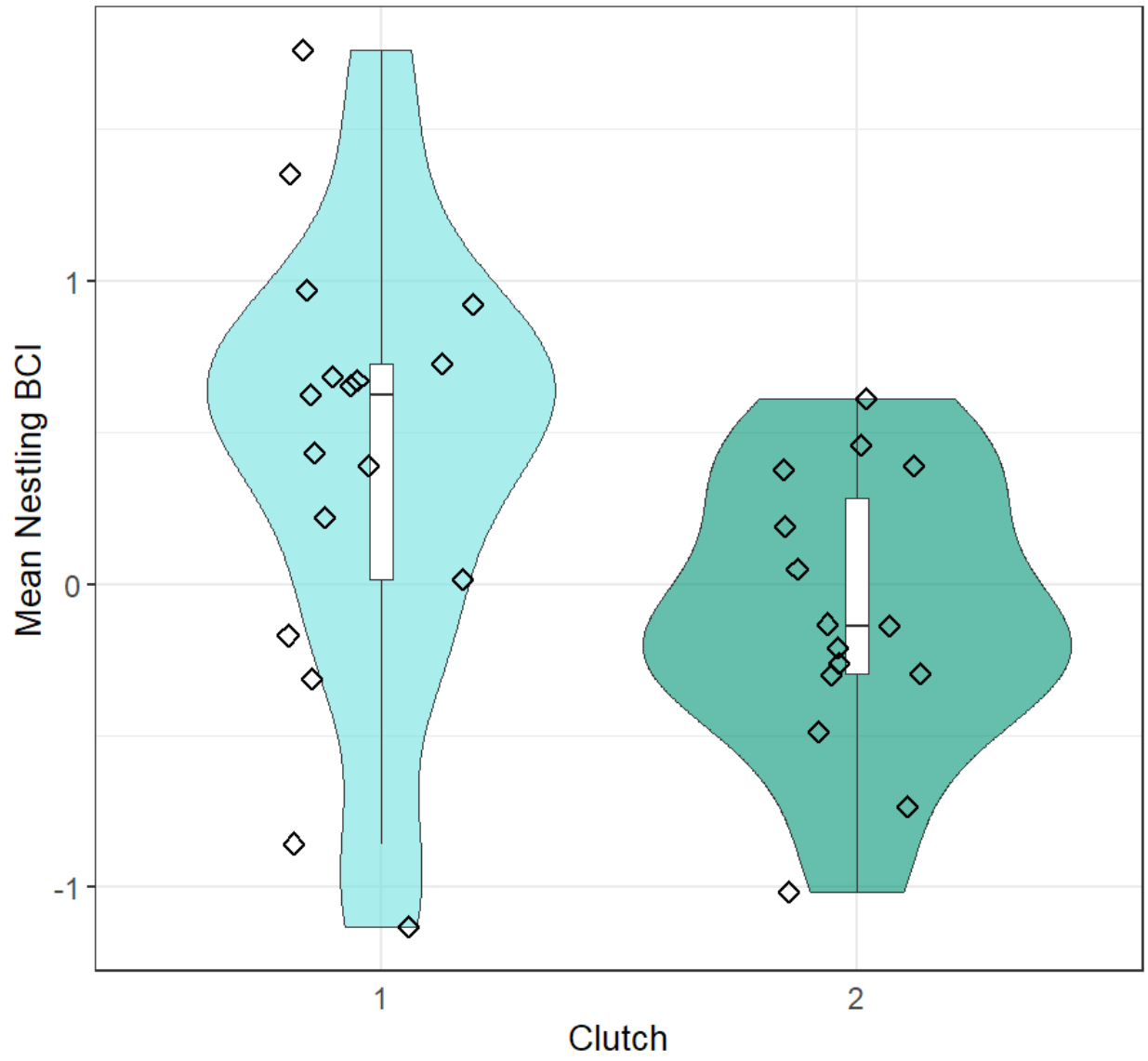
**Figure 5.** Diamonds indicate predicted female aggression as a function of local density with 95% confidence intervals. Raw aggression values are jittered with site indicated by shape (N = 40). The top model examining predictors of female aggression included only site ( $\beta = 1.244$ ,  $p = 0.0146$ ) and suggested that females nesting at Rice Rivers Center were more aggressive (pseudo- $R^2_{adj} = 0.164$ ). The second-best model ( $dAICc = 0.084$ ) included only local density ( $\beta = -0.788$ ,  $p = 0.0177$ ) and suggested that females nesting in higher-density environments were less aggressive (pseudo- $R^2_{adj} = 0.147$ ). Pseudo- $R^2_{adj}$  was calculated as  $1 - (var(residuals(model))/var(response))$ .



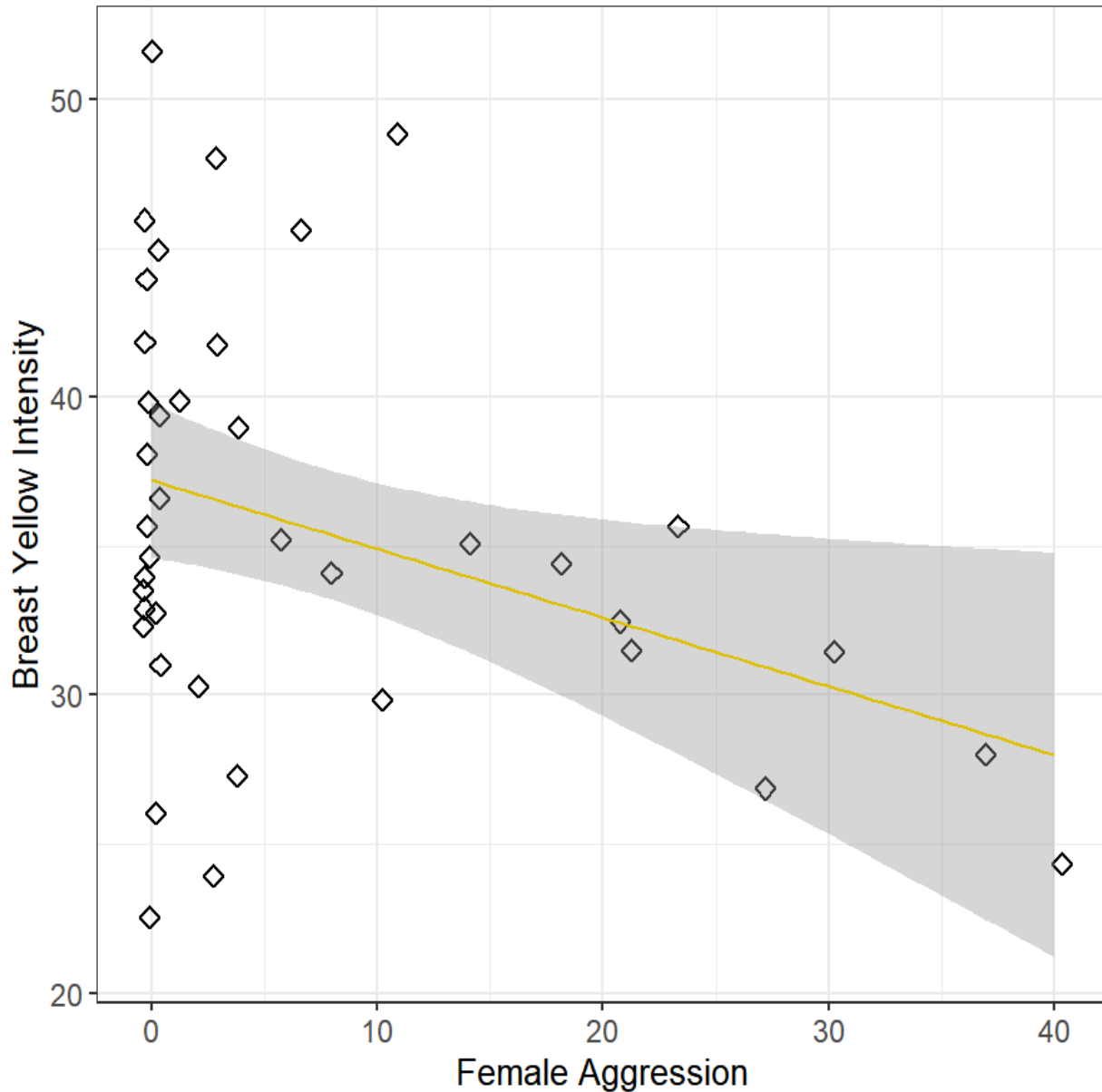
**Figure 6.** Female provisioning (number of visits with food per chick per hour) as a function of local density ( $N = 32$ ). In higher-density nesting sites, females provisioned their young more often ( $R^2_{\text{adj}} = 0.19$ ,  $p = 0.007$ ). Error bars represent 95% confidence intervals and raw data points are jittered for clarity.



**Figure 7.** Total provisioning (number of visits with food per chick per hour) as a function of female persistence adjusted for female age ( $N = 32$ ). Pairs with more persistent females provisioned their young less often ( $R^2_{\text{adj}} = 0.234$ ,  $p = 0.0148$ ). Error bars represent 95% confidence intervals and raw data points are jittered for clarity.

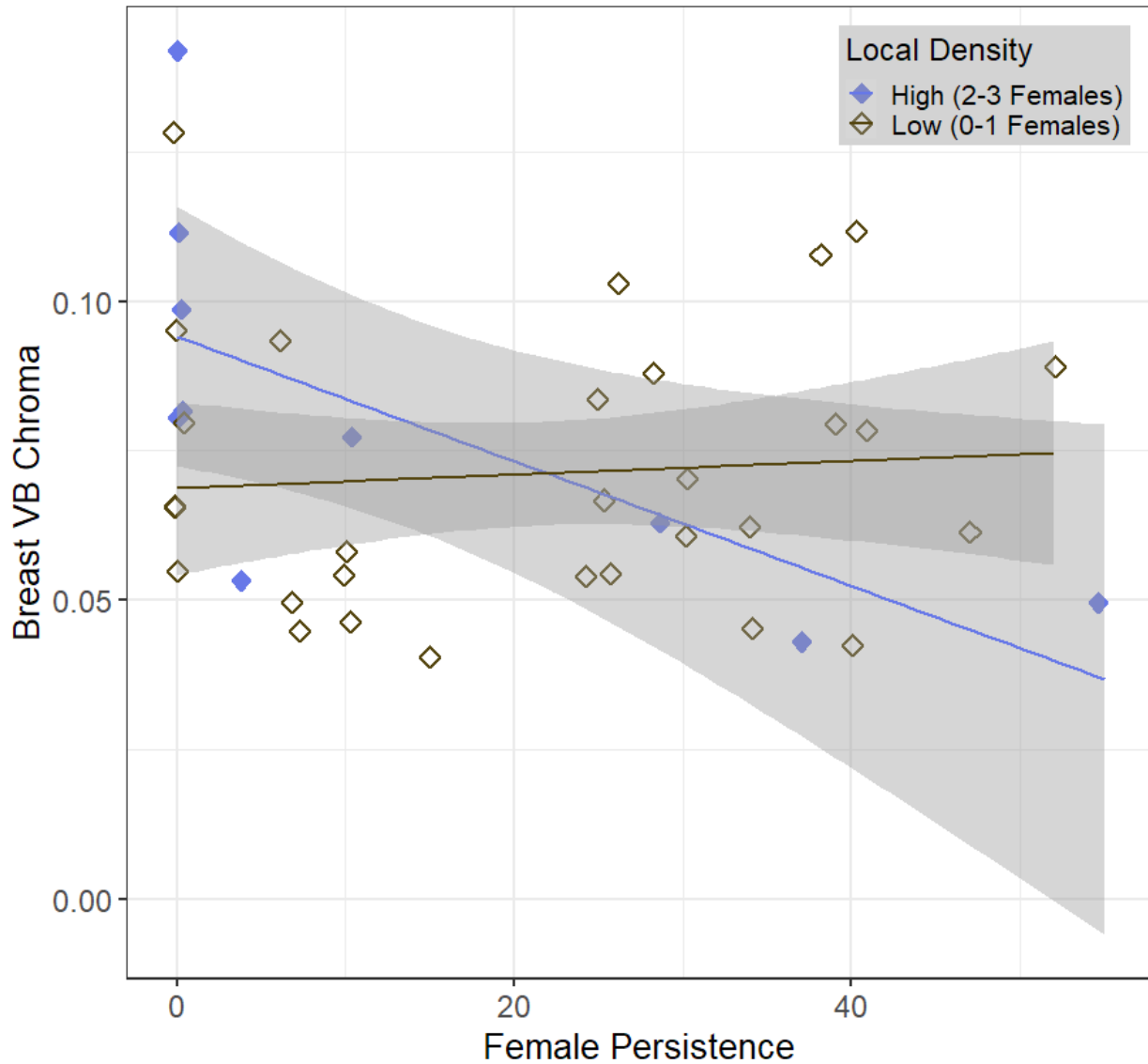


**Figure 8.** Mean Nestling BCI (body condition index) by clutch (N = 32). In the second clutch (fledged after June 18<sup>th</sup>), mean nestling BCI was lower ( $t_{58.0} = 8.80, p < 0.001$ ). Whiskers represent 95% confidence intervals and raw data points are jittered for clarity.

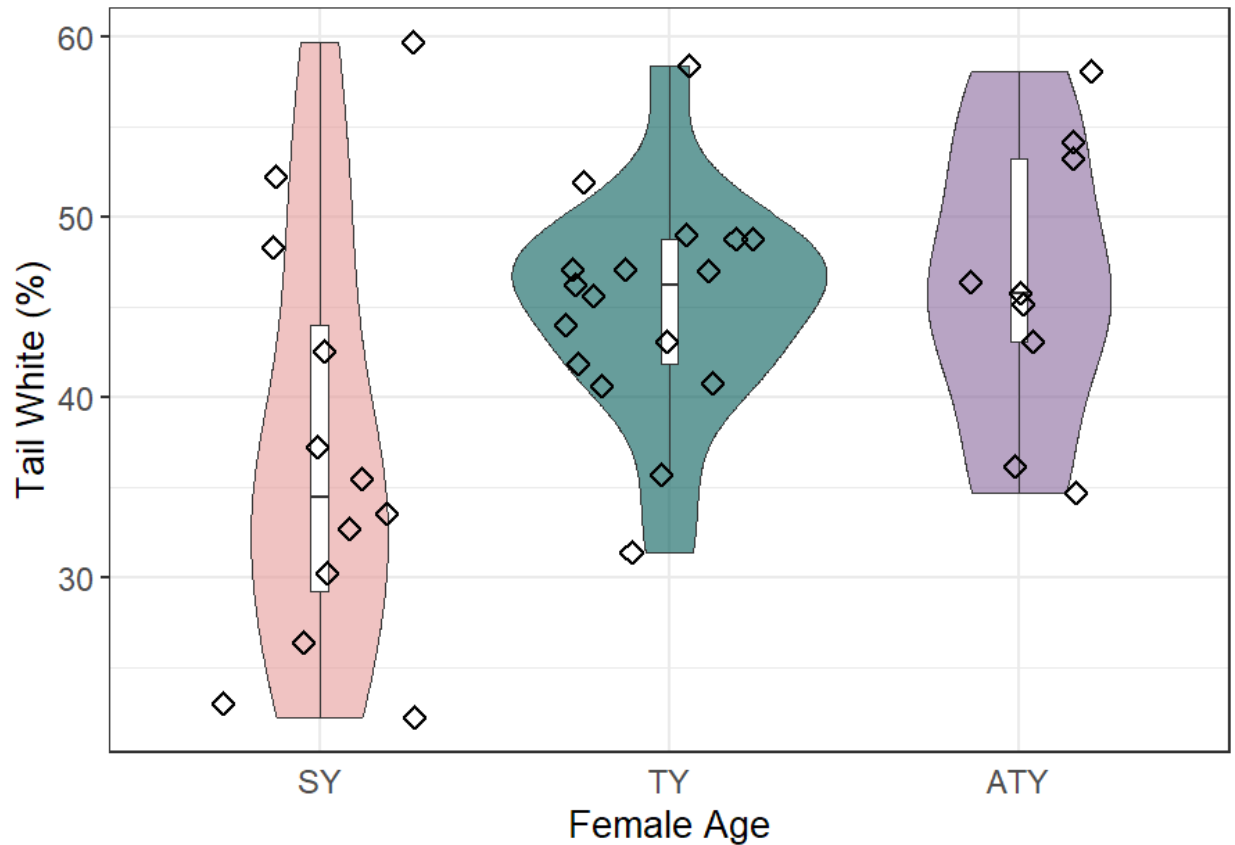


**Figure 9.** Female aggression as a predictor of breast yellow intensity ( $N = 40$ ). The linear model with the most support suggested that aggressive females had lower breast yellow intensity ( $R^2_{\text{adj}} = 0.106$ ,  $p = 0.0229$ ). Error bars represent 95% confidence intervals and raw data points are jittered for clarity.





**Figure 10.** Local density and female persistence as predictors of breast VB chroma (N = 40). The top model for predictors of breast VB chroma included female age (number of years breeding), local density, persistence, and persistence \* local density. In a high-density environment, more persistent females had lower breast violet blue chroma, or a higher carotenoid content ( $R^2_{adj} = 0.38$ ,  $p = 0.034$ ,  $N = 10$ ), while in a low-density environment there was no relationship between persistence and breast carotenoid content ( $R^2_{adj} = -0.033$ ,  $p = 0.777$ ,  $N = 30$ ). Error bars represent 95% confidence intervals and raw data points are jittered for clarity.



**Figure 11.** Female age (SY = first year breeding, TY = second year breeding, ATY = third+ year breeding) as a predictor of the amount of tail white (N = 38). The top model for amount of tail white indicated that SY females had tails with less white than TY ( $p = 0.0442$ ) and ATY ( $p = 0.0504$ ) females, but that TY and ATY females' tails did not differ in the amount of white ( $p = 0.943$ ). Whiskers represent 95% confidence intervals and raw data points are jittered for clarity.

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## **Vita**

Elsa B. Chen was born on August 4<sup>th</sup>, 1993 in Queens, NY. She graduated in 2015 from Skidmore College with a Bachelor of Arts in Biology, where she conducted undergraduate research on betta fish gill flaring and avian flight. Before joining the Bulluck Avian Ecology Lab, she spent several field seasons working on a variety of projects chasing passerines such as Cerulean Warblers and also spent some time working in wildlife rehab.