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Individual Variation in Response to Environmental Stressors in a Cavity-Nesting Bird

By

ALICIA KIMBERLY BIRD  
DISSERTATION

Submitted in partial satisfaction of the requirements for the degree of

DOCTOR OF PHILOSOPHY

in

Ecology

in the

OFFICE OF GRADUATE STUDIES

of the

UNIVERSITY OF CALIFORNIA

DAVIS

Approved:

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## **Dedication**

For my two wonderful daughters, Adelaide and Evangeline. You may not have been why I started, but I finished because of you. May you always pursue your dreams and go wherever your curiosity takes you.

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## DISSERTATION ABSTRACT

With increased development and expanding urbanization, there has been a rise in anthropogenic noise pollution. This alteration to the natural acoustic environment has significant impacts on a wide variety of species. However, not all species—nor individuals within a species—respond to noise pollution in the same way. Intrinsic factors such as sex, age, and behavioral tendency all contribute to intraspecific variation to responsiveness to environmental disturbances, including noise. Here, I explored how individual differences contribute to variation in response to noise during the breeding season. I did this by exposing nest boxes settled by established populations of tree swallows (*Tachycineta bicolor*) to experimental playbacks of traffic noise. First, I sought to determine whether relative differences in aggressive tendency of mated pairs explained differences in reproductive success under noise exposure. I found that in nest boxes exposed to low noise levels, pairs that were more similar in aggressiveness raised slightly larger nestlings than pairs that were more different in their aggressive tendencies, but under high noise, pairs that were more similar in aggressiveness exhibited a significant reduction in nestling size. I examined parental care to find a mechanism for this effect, but I found that noise exposure did not affect incubation, provisioning rate, nor vigilance behavior while at the nest box. However, I did find that aggressive tendency explained male provisioning rate, with a decrease in provisioning observed in highly aggressive males, but no effect in females.

Upon observing an effect of mate pair similarity on reproductive success in the context of noise, I examined whether individual aggressiveness, sex and quality played a role in settlement decisions, and could potentially impact mate assortment, and thus reproductive success. In a second experiment, I began noise exposure at the breeding grounds prior to territory establishment. I found that for both males and females, aggressiveness significantly explained nest box choice in regard to noise exposure. Highly aggressive individuals avoided settling in

boxes exposed to high noise levels. This resulted in positive assortative mating by aggressive tendency, with pairs in lower amplitude boxes exhibiting higher average aggressiveness than pairs in higher amplitude boxes. I found no relationship between noise and measures of adult quality (body condition, breast feather brightness, mantle feather saturation), and no measures of quality were correlated within mate pairs.

Lastly, during the height of breeding of the settlement study, the tree swallow populations were exposed to an unprecedented spring cold snap, with temperatures dipping to approximately 15°C (59°F) during the day and 6.67°C (44°F) at night, resulting in high nestling mortality and nest failure. Therefore, my last chapter explored the effects this severe weather event on reproductive success in the context of noise. I evaluated what factors influenced nest failure, how mates rebounded after the storm, and whether noise exposure potentially exacerbated consequences to breeding. I found that nestling age played a large role in nest success, with most mortality observed in the mid-age nestlings, rather than the recently hatched nestlings, or nestlings close to fledging. We also saw impacts to time to fledging and growth from the cold snap, though we did not find evidence that exposure to noise exacerbated the effects from the cold snap. Nestlings that lived through the storm, exhibited a similar response to noise as found in prior studies, with nestling mass decreasing with exposure to noise. However, for nestlings that hatched later in the season, after the cold snap, we see no such effect of noise. Additionally, adults varied in their response to the cold snap. Second year females were the most likely adults to cease breeding after the cold snap, and females with brighter breast feathers re-nested after the cold snap the soonest. Overall, intrinsic differences between nestlings as well as adults explained variation in how our population of tree swallows coped with a sudden extreme weather event.

# CHAPTER 1

## **Mate assortment by aggressiveness explains variation in reproductive success under noise pollution**

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## ABSTRACT

Individual behavioral tendencies are known to explain variation in response to environmental change. However, less is understood about how an individual's behavioral tendency relative to their mate's behavioral tendency affects reproductive success in changing environments. Here we use tree swallows (*Tachycineta bicolor*) to explore how mate assortment by aggressiveness affects reproductive success (as measured by nestling size) when faced with anthropogenic noise, by experimentally exposing established nesting territories and mated pairs to noise playbacks during the incubation and provisioning period of breeding. We show that pairs with more similar aggressive tendencies during nest defense have larger nestlings under conditions of low noise. However, as noise amplitude increases, these pairs exhibit a reduction in reproductive success (i.e. smaller nestlings), and pairs that are more dissimilar in aggressiveness exhibit an increase in reproductive success. This pattern emerged regardless of which sex was more aggressive within a pair. We found no effect of noise on provisioning or incubation. However, we did find that aggressiveness in males, but not females, is negatively associated with provisioning rate. These results demonstrate that it is important to focus both on individual differences and intra-pair differences in order to understand the impacts of anthropogenic disturbances like noise.

## INTRODUCTION

Widespread anthropogenic noise pollution from transportation networks, industrial activities, and urbanization alters the natural acoustic environment and may negatively impact wildlife (Ortega 2012b, Francis and Barber 2013, Shannon et al. 2016). There is strong evidence that noise pollution can interfere with communication (Patricelli and Blickley 2006), thus altering parental care (McIntyre et al. 2013, Leonard et al. 2015), mating (Swaddle et al. 2006), territory defense (Kleist et al. 2016), and predator avoidance (Rabin et al. 2006). There are also impacts to physiological processes in some species, which may indicate that noise serves as a stressor in some species (Blickley et al. 2012a, Injaian et al. 2018c, Kleist et al. 2018).

Additionally, many species may avoid otherwise suitable habitat due to noise (Francis et al. 2009, Blickley et al. 2012a, Luo et al. 2015, Ware et al. 2015, Halfwerk et al. 2016), causing effective habitat loss. Species may also exhibit increased vigilance in the presence of noise, at the expense of other behaviors like foraging (Shannon et al. 2014, Lynch et al. 2015, Klett-Mingo et al. 2016). These impacts can reduce reproductive success (Habib et al. 2007, Injaian et al. 2018a, Mulholland et al. 2018) and even shift community dynamics by reducing species diversity (Francis et al. 2011a, Shannon et al. 2016).

While the negative effects of noise on wildlife are increasingly well documented, there is wide variation in the behavioral, physiological and reproductive consequences of noise across species (see review Shannon et al. 2015). Some species appear to show no effects from noise, and others actually benefit from increased mating opportunities, reduced predation pressure, and lower competition (Sun and Narins 2005, Francis et al. 2009, 2011b).

Just as species differ in response to noise, individuals within a species are also likely to vary in how they cope with noise. Individuals often exhibit consistent and predictable differences in their behavioral tendencies, such as being more bold, aggressive, or exploratory, in a given

context (mating, foraging, anti-predator behaviors, etc.; Turkheimer 2000; Gosling 2001). When such individual tendencies are consistent across multiple contexts they are sometimes referred to as an individual's "personality" or "behavioral type" (Sih et al. 2004). The costs and benefits of behavioral tendencies or types are dependent, in part, on context, such as the level of competition, risk or available resources (Dall et al. 2004, Sih et al. 2004, Stamps 2007, Biro and Stamps 2008). Human activities can alter these contexts, for example, through changes in population density, predation pressure, and resources. Studies show that behavioral tendency can explain differences in response to anthropogenic disturbance (Martin and Réale 2008, Tuomainen and Candolin 2011, Sih 2013, Wong and Candolin 2015). For example, chipmunks (*Tamias striatus*) with more exploratory and docile tendencies are more likely to build burrows in areas frequented by humans than individuals with less exploratory and docile tendencies (Martin and Réale 2008). Such results could mean that novel stimuli like noise are driving selection in areas of high human activity.

While an individual's behavioral tendency can affect fitness, patterns of mate assortment by behavioral tendency may also have consequences for reproductive success (Spoon et al. 2006, Schuett et al. 2011). Studies on great tits (*Parus major*) show that males and females of the same behavioral tendency consistently exhibit opposite impacts regarding the number of offspring surviving to breed. Additionally, this selection on behavioral tendency by sex varies across years. In a given year, females with more exploratory tendencies may have higher reproductive success than more exploratory males, and in the following year the opposite may be true (Dingemanse et al. 2004). The combination of behavioral tendencies of mates may be particularly important for species that exhibit biparental care, where the behavior of both the mother and the father have direct impacts on offspring development. Mates with similar behavioral tendencies are thought to be better at coordinating parental care, and often exhibit higher reproductive success than

dissimilar mates (Schuett et al. 2011, Harris and Siefferman 2014, Burtka and Grindstaff 2015). For example, male great tits have been shown to increase provisioning rate when paired with a female of similar exploratory tendency, as compared to males in dissimilar partnerships (David et al. 2015). However, mates that are highly similar do not always exhibit higher reproductive success, and the advantage of such pairings varies depending on environmental conditions (Dingemanse et al. 2004, Both et al. 2005, Gabriel and Black 2012). In some contexts, there may be an adaptive advantage to disassortative mating by behavior (Schuett et al. 2010, Martin-Wintle et al. 2017) and dissimilar mates may bring complementary strengths to the partnership (Scherer et al. 2017).

There is evidence to suggest that differences by sex and behavioral tendency may be important in evaluating response to anthropogenic disturbances, like noise. In house sparrows (*Passer domesticus*), high quality males show a slight preference for noise-exposed nesting sites, but females do not differ in preference. Additionally, female house sparrows exposed to noise significantly reduce provisioning rates and produce smaller nestlings, whereas males provision at consistent rates regardless of noise exposure (Schroeder et al. 2012). There are also often interaction effects of sex and behavioral tendency. For example, in yellow-eyed penguins (*Megadyptes antipodes*), male recovery time after being handled by a researcher was not affected by aggressive tendency, but timid females showed significantly slower recovery than aggressive females (Ellenberg et al. 2009). In great tits, bold males and shy females adapt and learn better under novel environmental circumstances, and exhibit higher provisioning rates than their shy male and bold female counterparts (Titulaer et al. 2012, Naguib et al. 2013). Therefore, evaluating how individuals differ in response to novel stimuli, like anthropogenic noise, will help us better understand what may be facilitating or hampering how individuals adjust and populations adapt to a rapidly changing world.

Here, we used tree swallows (*Tachycineta bicolor*) as a study system to focus on how relative aggressive tendency of mated pairs influences reproductive success in the context of noise pollution. Within a breeding season, individual aggressiveness is consistent and repeatable in female tree swallows exposed to a conspecific in their territory (Rosvall 2008). In other studies that took repeated measures across years of both sexes, aggressiveness during nest defense against a human observer was also highly repeatable within and across years (Betini and Norris 2012). Additionally, studies have shown that noise pollution negatively impacts tree swallows in multiple ways. White noise is associated with changes in nestling vocal development (Leonard and Horn 2005) and adversely impacts communication between parents and offspring, which could result in increased predation risk and reduced provisioning (Leonard and Horn 2012, McIntyre et al. 2013, Leonard et al. 2015), though those studies did not find an effect on offspring growth or fledging success (Leonard and Horn 2005). Previous research on our study population found that traffic noise playbacks reduce body condition and alter levels of corticosterone, a hormone that can be associated with stress responses, in nestlings and adult females (Injaian, Taff, Pearson, et al. 2018; Injaian, Taff, and Patricelli 2018).

Other studies show that the degree of similarity in aggressive tendency of tree swallow mate pairs affects reproductive success. Though tree swallows do not exhibit assortative mating by aggressiveness (i.e. they do not pair with like or unlike individuals more than expected by chance, referred to as “disassortative”), studies have found that mates that are dissimilar in aggressiveness have larger broods than those with similar aggressiveness (Rosvall 2010). Since mates of similar aggressiveness have lower reproductive success than dissimilar mates, this disadvantage may be exacerbated under noisy conditions.

Past studies on tree swallows found that in the absence of artificially high noise levels, dissimilar mate pairs of tree swallows have higher reproductive success (larger brood size and



heavier eggs) regardless of which sex is more aggressive (Rosvall 2010). However, this might not be the case in the context of noise if males and females and/or individuals of different behavioral tendencies vary in response to a stressor like noise. Injaian, Poon, et al. (2018) found that female tree swallows are more likely to avoid settling in noise-exposed territories than males, suggesting a sex difference in noise response. Furthermore, one study found aggressiveness in female tree swallows is associated with lower nestling condition (Rosvall 2011). However, this may not hold true under anthropogenic disturbance. Individuals from populations adapted to urban environments often exhibit more aggressive tendencies than their rural counterparts (Miranda et al. 2013), indicating aggressiveness may have an adaptive advantage under disturbance.

In this study we conducted repeated measures within and across years to confirm individual aggressiveness in tree swallows is consistent, and then used that measure of behavior to answer two primary questions focused on the interaction between aggressive tendencies, mate assortment, noise and reproductive success. First, we asked: to what degree does the similarity/dissimilarity in aggressiveness of mated pairs affect reproductive success under noisy conditions? To answer this question, we tested two alternative hypotheses. One hypothesis is that noise exacerbates the difference in reproductive success between pairs that vary in similarity. Specifically, given prior results finding that disassortative pairs do better under ambient conditions, we predicted that pairs with more similar mates would exhibit even lower reproductive success than dissimilar pairs when exposed to noise. However, given that assortative mating is often advantageous, our alternative hypothesis was that pairs of similar aggressiveness may be better able to cope with noise than disassortative pairs, and therefore we may observe less variation in reproductive success across such pairs under noisy conditions.

Secondly, we asked: how might the sex of the more aggressive mate explain variation in reproductive success among pairs? While previous research has shown the sex of the more aggressive mate to be insignificant under normal conditions (Rosvall 2010), other studies have shown that female tree swallows are more sensitive to noise (Injaian et al. 2018a). Therefore, we tested two alternative hypotheses focused on how female aggressiveness relative to her mate's aggressiveness may affect reproductive success under noise. One hypothesis is that reproductive costs of female aggressiveness will be exacerbated under noise. Therefore, we would predict that pairs with a more aggressive female and a more passive male may exhibit lower reproductive success at high noise levels than their counterpart pairs. Alternatively, the reverse hypothesis could be true, that passive females are more sensitive to noise than aggressive females, and therefore we would observe pairs with a passive female and aggressive male suffering greater reproductive consequences under high noise.

Furthermore, to test for a possible mechanism to explain why the interaction between behavioral tendency and sex may influence reproductive success we measured effects on parental care behavior. We hypothesized that noise would differentially affect provisioning based on the sex and behavioral tendency of each parent, as well as the amount of time females spend incubating, though we did not make a priori predictions on which direction we expected a relationship.

To test our hypotheses, we exposed wild breeding tree swallows to experimental playbacks of vehicular traffic noise near nest boxes, which began prior to egg-laying but after boxes were settled by a mated pair and territories were established. This allowed us to test for the effects of noise on reproductive success, without noise levels affecting nest box selection and, thus, mate assortment. We tracked nestling growth throughout the provisioning period and recorded parental feeding rate, as well as time spent incubating. We also assayed male and

female tree swallows to score their aggressive tendencies (hereafter “aggressiveness”). This allowed us to determine, in the context of noise pollution, whether variation in nestling size and other measures of reproductive success could be explained by the difference in aggressiveness and parental care of mated pairs.

## **METHODS**

### **Study Species and Site**

Field experiments were conducted from April to June in 2017 and 2018, at two field sites in Yolo County, CA: Putah Creek Reserve (PCR) and South Fork Preserve (SFP). PCR is private land used for grazing and research. SFP is a riparian, mixed woodland habitat preserve managed by the City of Davis. Both field sites are adjacent to Putah Creek, a source of aerial insect emergence.

This study was conducted on tree swallows, a rural cavity nesting bird. Tree swallows exhibit nest defense by both males and females (Leffelaar and Robertson 1985) seasonal social monogamy (Leffelaar and Robertson 1986), and biparental care of nestlings (Leffelaar and Robertson 1986).

Each field site is equipped with artificial nest boxes (2017: PCR had n=37 nest boxes, SFP n=28; 2018: PCR n=42, SFP n=44) that are predominately settled by tree swallows annually (~82% during our study). During the two years of this study, some boxes were also settled by western bluebirds (*Sialia mexicana*, n=23) and ash-throated flycatchers (*Myiarchus cinerascens*, n=3).

## Playback Design

To avoid affecting mate assortment, playback experiments began after nest boxes were settled by a pair, determined by the presence of nest building in the boxes, but prior to egg laying. Nest boxes were arranged in clusters made up of four nest boxes each. Within a cluster, boxes were spaced 20 m apart. Clusters were spaced a minimum of 40 m apart and rows of clusters were spaced a minimum of 80 m apart (Supplemental Figure 1.1). In the center of every other cluster, we placed an outdoor speaker (Model TFS14, TIC Corp., City of Industry, CA, U.S.A.) and played pre-recorded vehicular traffic noise. See Injaian et al. 2018a for methodology on compilation of traffic noise files and playback setup. Ambient noise levels, measured when no noise was playing at the field sites, were  $43.55 \pm 1.98$  dBA at PCR and  $38.9 \pm 0.56$  dBA at SFP (Injaian et al. 2018b). We calibrated the speakers such that boxes within clusters where speakers were placed (i.e. boxes closest to the speakers) were exposed to noise levels 10-15 dBA higher than ambient noise levels. Playbacks could be faintly heard from some boxes in clusters without speakers and there was variation in noise levels among boxes in the same cluster. Therefore, noise exposure at each box was treated as a continuous variable. Noise levels were measured in dBA using a sound pressure level (SPL) meter (Model 824, Larson-Davis, Inc., Depew, NY, U.S.A.). The SPL meter was held adjacent to the nest box at the height of the entrance hole; we recorded the average  $L_{eq}$  (equivalent continuous sound level) across a 60-second interval. Noise was played 6 hours per day, from the hours of 0800-1400 in 2017 and 0700-1300 in 2018, which overlaps with the most active foraging period for tree swallows. The time shift between the two years was made for logistical reasons. Noise was turned on and off each day automatically using a timer (Model CN101, Favolcano, Edwardsville, IL, U.S.A.).

## **Nest Box Monitoring & Processing Adult & Nestling Tree Swallows**

We alternated which site we visited daily. Therefore, nest boxes were checked every other day to record the progress of nest building, clutch initiation date, clutch size, hatch date (when at least one egg had hatched), and brood size.

Adult tree swallows were captured in the nest box by pulling a wooden flap shut after they entered. Occasionally, incubating females were opportunistically caught by hand during nest box checks. All females (n=103) were caught during the incubation period, but most males (n=83) did not enter the boxes and therefore could not be caught until the provisioning period. Unbanded birds were issued a standard US Geological Service aluminum band. We took morphological measurements of adults during capture: mass was taken to the nearest 0.1g using a pocket scale (Model AWS-600, American Weigh Scales, Cumming, GA, U.S.A.); wing chord and tail length were measured to the nearest 0.5 mm using a standard ruler; and tarsus was measured to the nearest 0.1 mm using a digital caliper (Neiko 01407A, Grace Marketing Company, Los Angeles, CA, U.S.A.). Because male and female tree swallows do not have sexually dimorphic plumage we determined sex upon capture by the presence of a brood patch, which is only present for females. Before release, we marked birds on their tail with non-toxic paint to identify individuals.

Nestlings (n=396) were measured on days 4, 8, and 12 post-hatch, for a total of 3 morphological measurements per nestling. We measured mass, wing chord and tail length of nestlings using the same methods used for adults. Nestlings were banded on day 10 or 12 post-hatch depending on size. Prior to banding, nestlings were marked with nail polish on the nails of one foot to track individuals starting at day 4.

## **Adult Aggression Assays**

To assess aggression during nest defense against a human intruder, we adapted assays from previous studies on tree swallows (Betini and Norris 2012). An observer stood adjacent to the side of the nest box for 5 minutes, beginning when the male or female entered the territory. On a given day, assays were conducted prior to any handling of adults or nestlings at the nest box to avoid affecting response to the assay. Because not all males were caught and therefore not color marked prior to assays, unmarked birds responding to the assay were assumed to be the male of the nesting pair. We had high confidence such males were of the original pair, as personal observations showed that when a new male or female took over a box, this resulted in a new nest being built on top of the old nest, which we could determine during nest box checks. We recorded time until the bird made their first dive (fast, direct movement toward the observer), total number of dives, presence of alarm calling, distance of closest approach (<1 m, <5 m, 5-10m, >10m), and duration of response (includes circling, alarm calling, and diving). Alarm calls were easily identifiable as a repeated series of low-pitched calls in quick succession (Sharman et al. 1994). If the first dive was made while the observer was approaching the box, the time was recorded as 0:00. We attempted to perform this assay twice in 2017 approximately 3 weeks apart (once during incubation and once during provisioning) and three times in 2018 (once during incubation and twice during provisioning). All aggression assay observations were performed by a single observer for consistency. In 2017, we found males exhibited very low responsiveness during incubation, therefore behavioral data were only collected from females during that stage of the breeding season in 2018. During the provisioning period, we found it was very rare for only one mate to respond to an assay. Therefore, we collected individual data on both the male and female simultaneously. While individual behavior may be influenced by the presence of one's mate, we do have strong evidence that individual tree swallow behavior in this context is

highly repeatable within and across seasons (see Statistical Analyses below). Additionally, our questions are focused on understanding impacts to reproductive success based on the most natural behavioral responses of the pairs.

## **Parental Care**

To test whether noise affected parental care behavior, we collected video data on incubation and provisioning. Incubation data were collected in 2016 as part of a different study which used the same experimental noise setup, but did not assess adult aggressiveness (Injaian et al. 2019). Provisioning data were collected in 2018, as part of the study presented here.

In 2016, we recorded nest boxes (n=31) 1-6 times during the incubation period in order to measure adult visitation rates and behavior. We mounted digital video cameras (Model HMX-F90, Samsung, Ridgefield Park, NJ, U.S.A) approximately 5 meters in front of the box and recorded for approximately 2 hours each day. Birds were flushed at the start of recording to ensure birds were not already present in the box.

During data transcription, recordings were muted to ensure observers scoring the videos were blind to each box's treatment status to eliminate any recorder bias. As focal bird behavior may have been altered due to the setup of the camera, we discarded the first 20 minutes of each recording. We collected data on the number and duration of visits to the nest box. A "nest visit" started when a bird entered the frame and interacted with the box (landed, entered, etc.), and ended when the bird exited the frame. This excluded any birds that only passed the camera frame or briefly flew around the box without stopping. For each nest visit, we scored the duration of time each bird spent vigilant, non-vigilant and inside the nest. Birds were considered vigilant when they were visible outside the box and alert, with their head up scanning the area or otherwise not distracted. Birds were considered non-vigilant when they were visible outside of

the box but not vigilant. This included behaviors such as preening, looking into the box, interactions with other birds, etc. Time spent in the nest was considered to be when a bird was inside the nest box and completely hidden from view. This was used as a proxy for time spent incubating (Lombardo et al. 1995). In 2016, adults were not color marked, so we could not distinguish males from females. Therefore, behavior was summed for both individuals at the box. To ensure that all time budgets were from complete nest box visits, we excluded all visits where a bird was at the nest box at the start or end of the day's recording, where recordings were incomplete.

Using the same field methods, in 2018 we recorded behavior at nest boxes ( $n=45$ ) during the provisioning period when nestlings were 8 days old. This age was chosen in order to avoid recording on a day when nestlings were measured, when parental care may have been influenced by our presence at the nest box. Videos were later transcribed by observers blind to noise treatment and sex. Observers recorded the number and length of nest visits, number of times a bird entered the nest box (which we considered a proxy for provisioning), the duration of time spent inside the nest box, and whether an individual removed a nestling fecal sac upon exiting the box. Individuals were tracked based on the paint color marking their tail covert feathers, which allowed us to distinguish males and females during analyses.

### **Statistical Analyses**

To get an aggression score for each individual ( $n = 141$ ) we conducted a principle component analysis using the 5 behavioral measures from the adult aggression assays. Temporal data (time of first dive, duration of alarm calling, and duration of response) was binned into 15-second increments. Additionally, we multiplied the values for time of first dive and distance of closest approach by -1, so that for all behaviors larger values represented greater aggressiveness.



We found that the first principle coordinate (PC1) accounted for 55.6% of the variation across individuals and all five behaviors had negative loadings for this PC (Supplemental Table 1.1 and Supplemental Figure 1.2). We used the values from PC1 as our aggressiveness scores in all subsequent analyses. We performed a linear regression of aggressiveness scores with the fixed effect of sampling period (early or late in the provisioning period) and a random effect of bird identity (ID).

To verify that individual aggressiveness scores are consistent and repeatable across years, we combined the data from this two-year study with another experiment from 2019, which differed in that noise playbacks were started before settlement but used the same behavioral assays during the provisioning period to assess aggressiveness. We ran a linear mixed-effects model (lme4, R package) that included the fixed effects of dBA, year, site, sex, and period of the breeding season (incubation, early provisioning, or late provisioning), and the random effect of individual band number, and calculated repeatability using the rptR package in R (Stoffel et al. 2017). Individual aggressiveness had a high and statistically significant adjusted repeatability of 0.453 (CI = 0.346, 0.577,  $p < 0.0001$ ), which is consistent with what has been found for other populations of this species (Betini & Norris 2012).

For this study, we used the aggressiveness score from the first assay conducted during the provisioning period to maximize our sample size (we were unable to get repeated measures for all individuals due to logistical constraints). We performed a Spearman rank correlation test of male and female aggressiveness by nest box to determine if mates paired assortatively by aggressiveness. For each pair ( $n=81$ ), we subtracted male aggressiveness score from female aggressiveness score to get an aggression-difference score (Ag-Dif), where higher Ag-Dif scores represented pairs with a more aggressive female and lower Ag-Dif scores represented pairs with a more aggressive male. We also took the absolute value of the Ag-Dif score to get an absolute

aggression-difference score (Abs-Ag-Dif), with higher Abs-Ag-Dif scores representing more dissimilar mate pairs, and lower Abs-Ag-Dif scores representing more similar mate pairs. By using these two measures (adapted from Rosvall 2010), we were able to test whether the sex of the more aggressive mate matters (Ag-Dif) or if simply the overall difference in aggressiveness (Abs-Ag-Dif) is what explains difference in reproductive success across pairs (see details below).

We constructed linear mixed-effects models (lme4, R package) to test the effects of various predictors on nestling morphological measures (mass, wing chord, and tail length). We scaled continuous predictor variables using the *scale* function in the *base* package in R. We used the *dredge* function from the *MuMIn* package to calculate Akaike information criterion corrected for small sample size (AICc) and compare different candidate models (Hurvich and Tsai 1989, Burnham and Anderson 2001). Models with  $\Delta AICc < 2$  were considered to have highest model support (Burnham and Anderson 2001). Where applicable, all full candidate models included nestling age, female body condition, site, and year, however, female body condition did not improve model fit so it was dropped from the final candidate models. For models of mass and wing, the quadratic effect of age was included. Random effects included: nest, nestling ID and female ID. We originally included playback speaker cluster as a random effect, to account for similarities of boxes in close proximity, however it did not account for significant variation and was dropped from the final candidate models. For each nest and nestling, we also accounted for random slopes by age. Because some females were present in both years, including female ID allowed us to account for similarities in those females' clutches. Male ID and body condition were not included since not all males were caught and including those variables would significantly reduce our sample size.

We created candidate models that varied by the possible combinations of the following fixed effects: dBA (i.e. noise amplitude), Ag-Dif, Abs-Ag-Dif, and the interactions of dBA with age, dBA with Ag-Dif, and dBA with Abs-Ag-Dif. Note that models could contain either Ag-Dif or Abs-Ag-Dif, but not both, in order to test alternative hypotheses of interest. If Abs-Ag-Dif was present in top models this was considered support for the hypothesis that relative aggressiveness of mate pairs affects the response variable. If Ag-Dif was present in the top models this was considered support for the hypothesis that relative aggressiveness of mate pairs affects the response variable, and it matters which sex within a pair is more aggressive.

We also looked at whether noise, difference in mate aggressiveness (Ag-Dif or Abs-Ag-Dif), and/or their interactions influenced direct metrics of parental care including brood size, clutch size, hatch success, time spent incubating or provisioning rate. We originally ran generalized linear mixed-effects models of clutch size and brood size. However, we found that our random effects of cluster and female ID explained zero variance for both response variables. Therefore, we dropped the random effects and proceeded using generalized linear models for brood size and clutch size, as well as hatch success, which was fitted with a binomial distribution. All nest level candidate models included site and year. Decreased female body condition is associated with lower clutch size and longer incubation periods, but not hatch success, in tree swallows (Nooker et al. 2005), so we included it in models of clutch size and brood size, but not hatch success.

In our first set of analyses we could not distinguish differences between mate pairs that have high similarity in contrasting ways (i.e. both aggressive or both passive). Therefore, we conducted post-hoc analyses to examine whether average mate aggressiveness (“AvAg”) of a mate pair influenced nestling size (mass, wing chord, tail length). This allowed us to examine differences in reproductive success between pairs with similar aggressiveness (i.e. pairs with low

Abs-Ag-Dif scores) that differ in their overall aggressiveness. For these analyses we used a reduced model set, maintaining any variables that were present in the top models of mass, wing chord, and tail length in the original analyses of nestling size (with the exception of Ag-Dif and Abs-Ag-Dif which were excluded from this analysis).

We ran a generalized linear mixed-effects model of adult provisioning rate fitted to a poisson distribution, with number of visits, weighted by time recorded, as the response variable. Nest box was included as a random effect. All candidate models included the fixed effects of brood size and site. Candidate models varied by the following fixed effects: dBA, sex, Ag-Dif or Abs-Ag-Dif, as well as their possible interactions.

To analyze the effects of noise on parental time budgets during the incubation period, we ran linear mixed effects models of the percent time spent incubating (time spent inside nest box divided by duration of nest visits) and the percent time spent being vigilant (time spent vigilant divided by duration of nest visits). For each response variable (incubation and vigilance) we compared two candidate models, which varied by whether or not they contained the fixed effect of dBA. Both candidate models of incubation included the fixed effects of clutch size, day of incubation, and site. For both candidate models of vigilance, we included the fixed effect of site. All models contained the random effect of nest box.

### **Ethics Statement**

This research was conducted with approval from the University of California, Davis Institutional Animal Care and Use Committee (protocol no. 19805), the California Department of Fish and Wildlife (permit no. SC-012919), the US Fish and Wildlife Service (permit no. MB72334C), and the USGS Bird Banding Laboratory (permit no. 22712). We sought to reduce disturbance to birds by only visiting sites every other day and approaching nest boxes only when

necessary for data collection. When animal handling was necessary for measuring and marking individuals, we aimed to handle each bird for no longer than 10 minutes and immediately released them once processed.

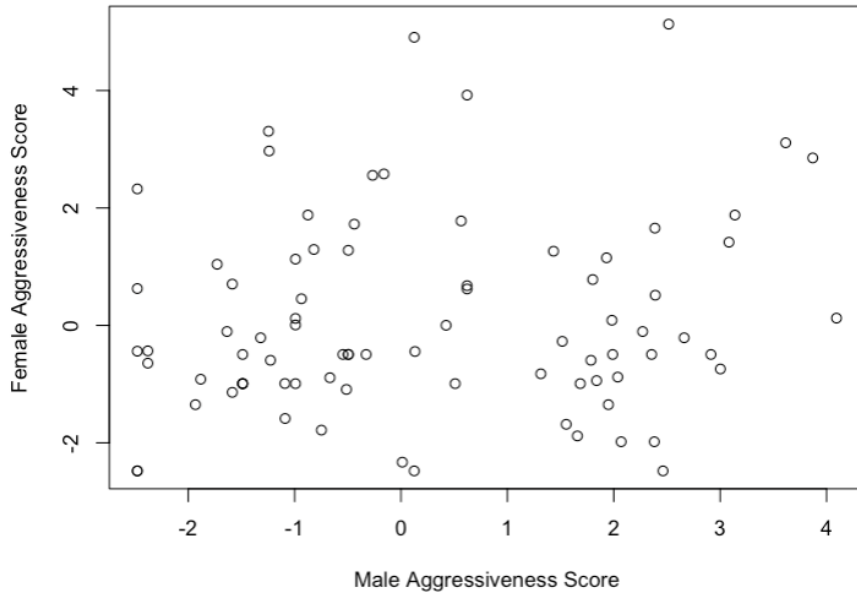
## **RESULTS**

We found no evidence that either sex was more aggressive on average (Students t-test,  $p=0.546$ ). We also found no evidence that males and females mate assortatively by aggressiveness (Spearman's rank correlation,  $r = -0.14$ ,  $p = 0.208$ , Figure 1.1). However, we found a relationship between the difference in aggressiveness of individuals within a pair and reproductive success in the context of noise, as detailed below.

### **Nestling Size**

We found strong support for the effect of noise amplitude (dBA) and the absolute difference in aggressiveness of mate pairs (Abs-Ag-Dif) on nestling growth. The top models for nestling mass ( $w_i = 0.792$ ), wing chord ( $w_i = 0.47$ ) and tail length ( $w_i = 0.396$ ) included Abs-Ag-Dif, dBA and the interaction between those two variables (Table 1.1). Top models of mass and tail length also included the interaction effect of age and dBA. The second highest model of wing chord included all the variables present in the top model, as well as the interaction effect of dBA and age ( $\Delta AICc = 1.87$ ,  $w_i = 0.185$ ; Table 1.1).

**Figure 1.1.** Male and female aggressiveness is not correlated (Spearman’s rank correlation,  $r = -0.14$ ,  $p = 0.208$ ).



**Table 1.1.** Top candidate models ( $\Delta AICc < 2$ ) of nestling mass, wing chord, and tail length. Note, variables that are present in all models (site, year, age, and brood size) not listed for brevity. Colons designate an interaction effect and \* designates both terms are present as well as their interaction. See Supplemental Tables 1.2-1.4 for full sets of candidate models.

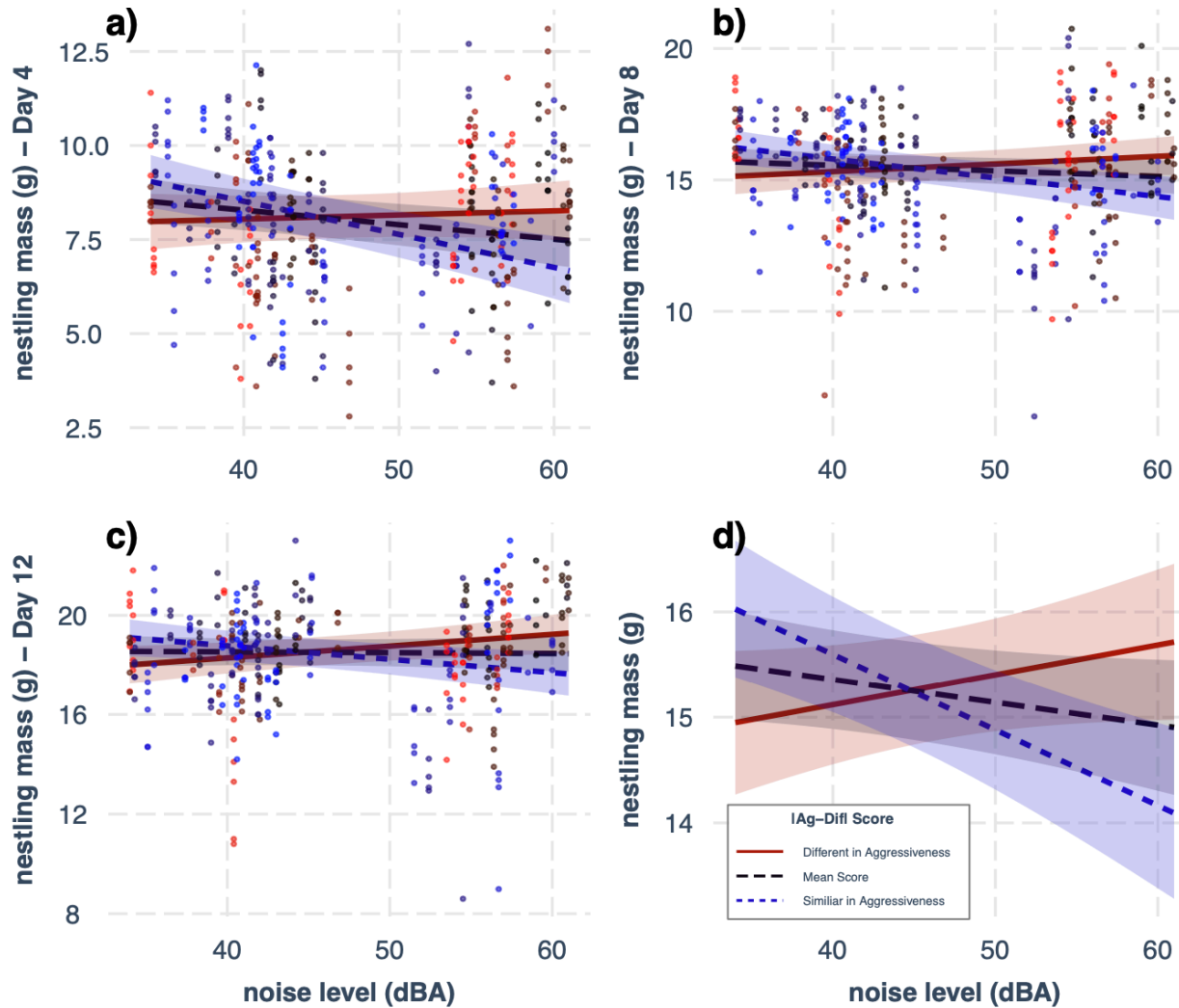
Candidate Model	k	AICc	$\Delta AICc$	$w_i$
<i>Nestling mass</i>				
mass ~ Abs-Ag-Dif * dBA + dBA:age	18	4270.7	0	0.792
<i>Nestling wing</i>				
wing ~ Abs-Ag-Dif * dBA	15	5551.3	0	0.47
wing ~ Abs-Ag-Dif * dBA + dBA:age	16	5553.2	1.87	0.185
<i>Nestling tail</i>				
tail ~ Abs-Ag-Dif * dBA + dBA:age	16	3224.3	0	0.396

Nearly all variables in the top models of mass, wing chord, and tail length had 95% CIs that did not overlap zero (Table 1.2, Supplemental Table 1.5). One notable exception was the dBA variable in the top model of tail length, which had 95% CIs that did overlap zero; all interaction effects with dBA in the model of tail length, however, were significant, with 95% CIs not overlapping zero (Supplemental Table 1.5). In the top models of nestling mass, wing chord, and tail length, Abs-Ag-Dif and dBA had a negative relationship with nestling size (Table 1.2). Nestlings were smaller on average when dBA was higher, or when mate pairs were more different in their aggressiveness. However, when considering the interaction effect of dBA and Abs-Ag-Diff, we found that mate pairs that are more similar in aggressiveness have smaller nestlings as noise amplitude increases (Figure 1.2, Supplemental Figure 1.3).

**Table 1.2.**  $\beta$  estimates and 95% confidence intervals (CI) for fixed effects in top model of nestling mass. Variables with confidence intervals that do not overlap zero considered to have strong support. See Supplemental Table 1.5 for  $\beta$  estimates and confidence intervals of variables that were included in all possible models. Italicized variables had confidence intervals that overlapped zero and not considered to have strong support.

<b>Response Variable</b>	<b>Fixed Effect</b>	<b><math>\beta</math> estimate</b>	<b>95% CI</b>
Nestling mass	(Intercept)	4.716	2.011,7.42
	Abs-Ag-Dif	-3.82	-6.014,-1.626
	dBA	-0.126	-0.178,-0.073
	Abs-Ag-Dif:dBA	0.085	0.039,0.131
	dBA:age	0.004	0.001,0.008
Nestling wing chord	<i>(Intercept)</i>	<i>3.403</i>	<i>-0.599,7.404</i>
	Abs-Ag-Dif	-6.095	-10.057,-2.134
	dBA	-0.132	-0.209,-0.055
	Abs-Ag-Dif:dBA	0.124	0.042,0.206
Nestling tail length	(Intercept)	-17.954	-22.258,-13.649
	Abs-Ag-Dif	-3.661	-6.404,-0.918
	<i>dBA</i>	<i>-0.009</i>	<i>-0.092,0.075</i>
	Abs-Ag-Dif:dBA	0.079	0.021,0.136
	dBA:age	-0.01	-0.018,-0.001

**Figure 1.2.** Top model outputs for predicted values of nestling mass at day 4 (a), day 8 (b) and day 12 (c) post hatch across noise levels (dBA). (d) is the overall model output with all data. The legend applies to all four panels. Solid red line is +1SD above the mean Abs-Ag-Dif score (the absolute difference in the aggressiveness of the mate pair), representing mate pairs more different in aggressiveness. Large black dash is mean Abs-Ag-Dif score. Dotted blue line is -1SD below mean Abs-Ag-Dif Score, representing mate pairs more similar in aggressiveness. Colors of points on a gradient from blue to black to red, representing Abs-Ag-Dif score of parent pair.



Overall, average aggressiveness of the mate pair had a significant impact on nestling size in the context of noise. The interaction effect of AvAg and dBA was present in the top models for mass and wing chord, and the confidence intervals for the interaction effect in both models did not overlap zero (Supplemental Tables 1.6 and 1.7). This interaction effect suggests a



disadvantage for pairs with lower average aggressiveness as noise amplitude increased, particularly for younger nestlings (Supplemental Figure 1.4, Supplemental Table 1.7).

We also found that average aggressiveness of the mate pairs was positively correlated with the Abs-Ag-Dif score (Spearman's rank correlation,  $p < 0.001$ , Supplemental Figure 1.5), such that the higher average aggressiveness of a pair, the greater absolute difference in their aggressiveness. To determine which variable, the similarity between mates (Abs-Ag-Dif) or the average aggressiveness of the pair (AvAg), was more important, we performed post-hoc tests to assess which of these scores better explained variation in nestling size. We compared the top models from both analyses of nestling size, which varied by whether they had fixed effect of the AvAg score or the fixed effect of the Abs-Ag-Dif score. The model with the Abs-Ag-Dif score had a lower AIC score and considerably more model weight ( $AICc = 4270.7$ ,  $w_i = 0.825$ ) than the model with the Av-Ag score ( $AICc = 4274.5$ ,  $\Delta AICc = 3.87$ ,  $w_i = 0.126$ ).

### **Nest Level Effects**

Nest level analyses found no effects of noise on clutch size, brood size, nor hatch success (Table 1.3, Supplemental Tables 1.8 and 1.9). The null models ranked highest for all nest level variables. The second-best models for brood size and hatch success gave some support ( $\Delta AIC < 2$ ) that the Ag-Dif score may have some impact, with a slight decrease in the number of nestlings that hatch the more aggressive a female is relative to her mate. However, in both these cases, the second-best models had less than half the model weight of the top models and the confidence intervals of all variables except the intercept overlapped zero.

**Table 1.3.** Top candidate models ( $\Delta\text{AICc} < 2$ ) of clutch size, brood size, and hatch success. Note, variables that are present in all models (see Methods) not listed for brevity. See Supplemental Table 1.8 for full set of candidate models.

<b>Candidate Model</b>	<b>k</b>	<b>AICc</b>	<b><math>\Delta\text{AICc}</math></b>	<b><math>w_i</math></b>
<i>Clutch Size</i>				
null	4	298.1	0	0.439
<i>Brood Size</i>				
null	4	298.3	0	0.419
Brood Size ~ Ag-Dif	5	300.1	1.84	0.167
<i>Hatch Success</i>				
null	3	180.7	0	0.339
Hatch Success ~ Ag-Dif	4	181.9	1.26	0.18

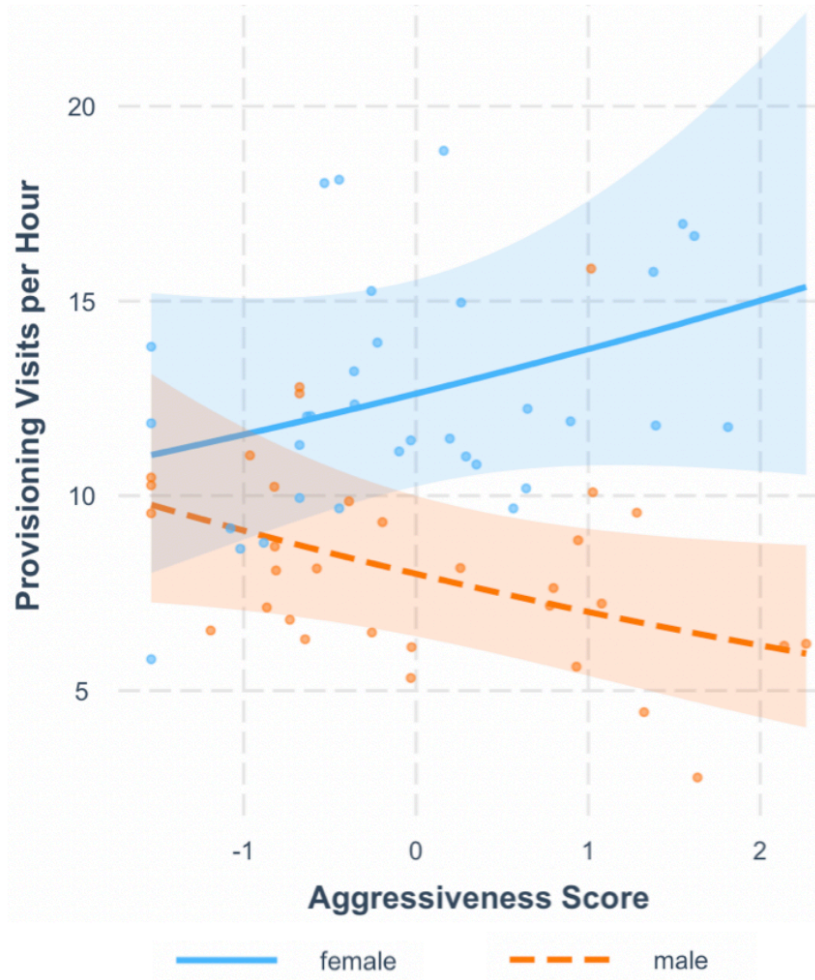
## Parental Care

The top model for provisioning rate had high support ( $w_i = 0.559$ ) and contained the significant interaction effect of individual aggressiveness and sex (Table 1.4). Our results suggest that females provisioned more than males and that this became more pronounced as individuals increased in aggressiveness, with highly aggressive males provisioning less than highly aggressive females (Figure 1.3). The second highest model of provisioning rate had moderate support ( $\Delta\text{AICc} = 1.57$ ,  $w_i = 0.255$ ) and contained all the same variables as the top model, plus the additional fixed effect of dBA, however, the 95% CI for dBA overlapped zero (-0.245, 0.077). When testing whether mate similarity mattered for overall provisioning rate at a given nest box we found that the Ag-Dif score, rather than the Abs-Ag-Dif score, was present in the top model of overall provisioning rate at a nest box, with pairs that have a male that is more aggressive than his mate having the lowest rates of provisioning and pairs with a male that is less aggressive than his mate having the highest rates of provisioning (Tables 1.4 and 1.5, Figure 1.4).

We found no effect of noise on parental behavior during the incubation period, with dBA absent from top models of percent time spent incubating and percent time spent vigilant (Table

1.4). The second ranked model of percent time spent incubating, which contained the variable dBA, had some support ( $\Delta AICc = 1.55$ ,  $w_i = 0.316$ ), however the confidence intervals for dBA overlapped zero (-0.221, 0.562).

**Figure 1.3.** Top model output of individual provisioning rate shows females provision more than males, and as individuals increase in aggressiveness males decrease provisioning.



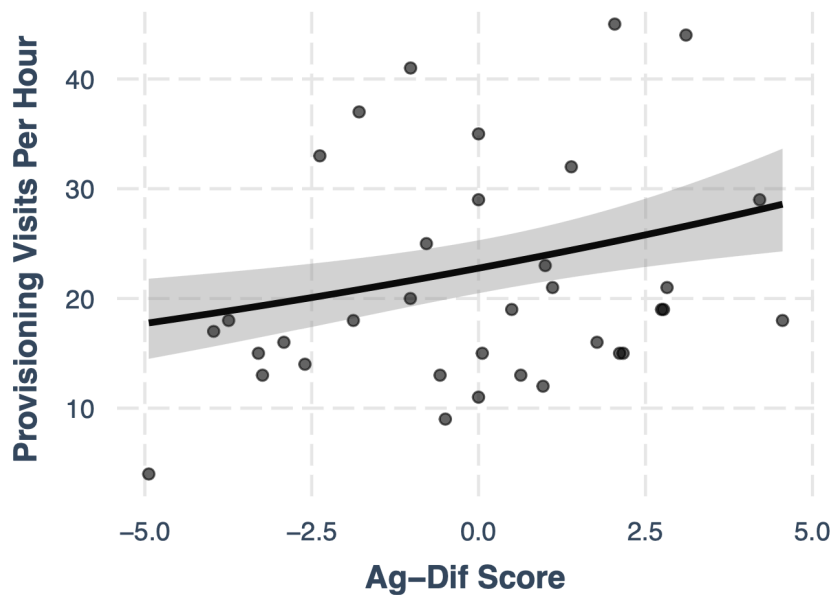
**Table 1.4.** Top 3 candidate models of individual provisioning rate and total provisioning rate of a given mate pair, as well as all candidate models of incubation and vigilance during incubation period. Note, variables that are present in all models (see Methods) not listed for brevity.

<b>Candidate Model</b>	<b>k</b>	<b>AICc</b>	<b><math>\Delta</math>AICc</b>	<b>w<sub>i</sub></b>
<i>Individual Provisioning Rate</i>				
visits ~ Agg*Sex	7	866.7	0	0.559
visits ~ Agg*Sex + dBA	8	868.3	1.57	0.255
visits ~ Agg*Sex + dBA*Sex	9	870.5	3.75	0.086
<i>Mate Pair Provisioning Rate</i>				
visits ~ Ag-Dif	4	309.2	0	0.628
visits ~ Ag-Dif + dBA	5	311.9	2.74	0.160
visits ~ Ag-Dif*dBA	6	311.9	2.75	0.159
<i>Incubation</i>				
null	6	916.0	0	0.684
incubation ~ dBA	7	917.5	1.55	0.316
<i>Vigilance</i>				
null	4	880.3	0	0.735
vigilance ~ dBA	5	882.4	2.04	0.265

**Table 1.5.**  $\beta$  estimates and 95% confidence intervals for fixed effects in top models of provisioning rate, percent time spent incubating, and percent time spent being vigilant during the incubation period. Variables with confidence intervals that do not overlap zero considered to have strong support. Italicized variables had confidence intervals that overlapped zero.

Response Variable	Fixed Effect	$\beta$ estimate	95% CI
Individual Provisioning Rate	(Intercept)	3.132	2.326, 3.939
	<i>Agg</i>	<i>0.018</i>	<i>-0.031, 0.068</i>
	Sexmale	-0.464	-0.542, -0.385
	<i>BroodSize.8</i>	<i>0.022</i>	<i>-0.130, 0.174</i>
	<i>SiteSFP</i>	<i>-0.230</i>	<i>-0.579, 0.119</i>
	Agg:Sexmale	-0.105	-0.163, -0.046
Mate Pair Provisioning Rate	(Intercept)	2.853	2.471, 3.227
	MAD	0.050	0.020, 0.081
	<i>BroodSize.8</i>	<i>0.058</i>	<i>-0.012, 0.129</i>
	<i>SiteSFP</i>	<i>-0.172</i>	<i>-0.330, -0.014</i>
% Time Incubating	(Intercept)	34.82	8.873, 60.989
	Clutch Size	4.803	0.316, 9.232
	<i>Day of Incubation</i>	<i>0.569</i>	<i>-0.150, 1.287</i>
	<i>SiteSFP</i>	<i>11.439</i>	<i>5.661, 17.218</i>
% Time Vigilant	(Intercept)	28.313	23.434, 33.289
	<i>SiteSFP</i>	<i>-13.296</i>	<i>-20.259, -6.461</i>

**Figure 1.4.** Top model output of overall provisioning rate by both parents shows a positive relationship between the mate aggression difference (Ag-Dif) score and provisioning rate. Mate pairs with low Ag-Dif scores (male aggressiveness > female aggressiveness) have lower provisioning rates than pairs with high Ag-Dif scores (male aggressiveness < female aggressiveness).



## DISCUSSION

### Nestling Growth

Previous studies have found that noise pollution negatively affects reproductive success in many species of birds (Halfwerk et al. 2011, Kight et al. 2012, Potvin and MacDougall-Shackleton 2015, Huet des Aunay et al. 2017, Zollinger et al. 2019), including tree swallows (Injaian et al. 2018a, 2018b). Here we show the magnitude of those effects may be influenced, in part, by the relative behavioral tendencies of mates.

The interaction effect of absolute difference in aggressiveness of individuals within a social pair and noise (Abs-Ag-Dif \*dBA) was present in all top models of nestling size (Table 1.1), which is an important indicator of post-fledging success in this species (Gebhardt-Henrich and Richner 1998, McCarty 2001). While nestling size generally decreased the more dissimilar mate pairs were in aggressiveness, the negative effect of mate dissimilarity was not present when birds experienced high noise levels at nesting sites. Rather, at high noise levels, nestling size of similar pairs decreased and nestling size for dissimilar pairs slightly increased (Figure 1.2, Supplemental Figure 1.3). The results are in partial agreement with other studies on tree swallows which found that pairs more dissimilar in aggressive tendency exhibit higher reproductive success (Rosvall 2010). Those results were found under normal conditions where noise levels were not manipulated, whereas our study only saw this association under high noise levels. This may be explained by unknown differences in the breeding sites of these populations used in these two studies. If populations vary in exposure to environmental stressors such as food availability, competition for nesting sites, etc. we might expect population-level differences regarding which mate pairs do better overall. The advantages of having a similar mate vs. dissimilar mate may be largely context dependent, which may explain why we do not see assortative mating by aggressiveness in tree swallows here (Figure 1.1) or in other populations

(Rosvall 2010). Further studies are needed to examine causes of population-level differences in how assortment by behavioral tendency affects reproductive outcomes.

Thus far, most of the research done on assortative mating focuses on morphology rather than behavior. A meta-analysis found that assortative mating based on morphological traits is generally more adaptive than non-assortative or disassortative mating, however they were unable to make conclusions based on behavioral traits, as such studies are much less represented in the literature (Jiang et al. 2013). While there are some studies that suggest similar behavioral tendency between mates is associated with increased reproductive success (Both et al. 2005, Schuett et al. 2011, Gabriel and Black 2012, Laubu et al. 2016), we still do sometimes observe disassortative mating by behavioral tendency (Laubu et al. 2017, Martin-Wintle et al. 2017, Scherer et al. 2017). This could be because the adaptability of mate pairings by behavioral tendency vary depending on the changing selective pressures in the environment (Schuett et al. 2010). For example, in blue tits (*Cyanistes caeruleus*), there is evidence that environmental heterogeneity is associated with population level differences in personality (Dubuc-Messier et al. 2017). Additionally, variation in environmental conditions is related to changes in adult survival by behavioral tendency in great tits (Dingemanse et al. 2004). Therefore, factors related to reproductive success that may be disrupted by noise, such as parent-offspring communication in tree swallows (McIntyre et al. 2013, Leonard et al. 2015), might be related to behavioral tendency and explain why disassortative pairs exhibit an advantage in more stressful or distracting environments. Further research is needed to determine why similar pairs exhibit a reproductive disadvantage under noise, and what aspects of dissimilar pairs might allow them to better mitigate the stressors associated with exposure to anthropogenic noise pollution. In particular, our study demonstrates the importance of considering how mate similarity by behavioral tendency may influence response to a novel stressor. Another factor worth

considering is the role of behavioral plasticity. We found strong evidence of consistent individual differences in aggressiveness across years with high repeatability (see Methods), however, some individuals may also be better able to adjust their behavior to enhance coordination of duties with their mate.

While we found support for our hypothesis that similar pairs will respond worse to noise than dissimilar pairs (as exhibited by their lower reproductive success), we found no significant effect of the sex of the more aggressive partner. We hypothesized two alternative scenarios: 1) female aggression would result in greater reproductive costs under noise, or 2) passive females would be more sensitive to noise. Neither of these hypotheses regarding female aggressiveness within dissimilar pairs explained reproductive success – we found that absolute difference in aggressiveness between pairmates (Abs-Ag-Dif) rather than the difference in aggressiveness between pairmates (Ag-Dif) was a better predictor of nestling size; absolute difference scores do not reflect which sex was more aggressive, whereas the aggressiveness difference score does. Or put more simply, an individual's sex and aggressiveness is less indicative of reproductive success than an individual's aggressiveness relative to their mate's. This may suggest that mates are able to compensate for one another in ways that we were not able to capture in this study.

In addition to the effects of mate similarity, we found evidence that overall aggressiveness of the pair influences reproductive success under noise. For pairs of high average aggressiveness, we see little change in nestling size as noise levels increase. In contrast, pairs with low average aggressiveness have larger nestlings in quiet conditions, and significantly smaller nestlings in noisy conditions (Supplemental Figure 1.4). Though overall aggressiveness of parents is likely playing a role in reproductive success, when we compared models that accounted for mate similarity (Abs-Ag-Dif) to those with overall aggressiveness, we found that



the former was much stronger at predicting nestling size, indicating that mate similarity may be a more important factor to consider than the effects of aggressiveness alone.

### **Clutch Size, Brood Size & Hatch Success**

We did not find strong evidence that noise or relative aggressiveness of mates impacted clutch size, brood size, or hatch success. This contrasts somewhat with previous studies from this population, which also found no impacts of noise on brood size or hatch success, but did find reduced clutch size with noise exposure (Injaian et al. 2018a). Initiation of noise exposure in this study began just prior to egg laying, whereas Injaian, Poon, et al. (2018) began playbacks earlier in the breeding season. Therefore, noise exposure in this study may have been too short to impact egg laying and therefore clutch size.

### **Parental Care**

We found no evidence that noise impacted the parental care behaviors that were measured in this study. Birds did not vary across noise levels in the amount of time spent vigilant or time spent incubating. Additionally, noise did not affect provisioning rate by either sex regardless of behavioral tendency, which confirms previous results that also found no effect of noise on provisioning (Injaian et al. 2018c).

However, we did find significant effects of mate similarity and aggressiveness on provisioning. The more aggressive the male, the fewer visits he made to provision the nestlings; whereas females exhibited no difference in provisioning by aggressiveness (Figure 1.3). This was further demonstrated by the fact we found the difference in aggressiveness of mates strongly predicted overall provisioning rate, with lower provisioning observed in dissimilar pairs with highly aggressive males (Figure 1.4).

This effect of male aggressiveness on provisioning rate is surprising, given our results related to nestling size, which found that nestling size was significantly affected by noise and the absolute difference in aggressiveness within mated pairs, irrespective of which sex was more aggressive. Taken together, these contrasting results indicate that, while noise may not be directly affecting parental care, there may be other impacts on parents that are driving lower nestling size, such as physiological effects. Noise is known to affect corticosterone levels in both adult and nestling tree swallows (Injaian et al. 2018c) and other birds (Blickley et al. 2012b, Zollinger et al. 2019). Furthermore, levels of hormones that can be associated with stressors vary with behavioral tendencies in a variety of species (see review Carere et al. 2010). In wild populations of great tits, eggs produced from mates with similar behavioral tendencies, had lower levels of androgens (testosterone and androstenedione), as compared to those from mates in disassortative pairings (Ruuskanen et al. 2018). We know that yolk androgens affect nestling growth (Schwabl 1996, Eising et al. 2001, Pilz et al. 2004, Navara et al. 2005, 2006) and in tree swallows specifically, yolk testosterone is related to the amount of aggressive encounters the mother has around the time of egg laying (Whittingham and Schwabl 2002). Therefore, if such adult physiological response to noise varies with behavioral tendencies, these effects could explain differences we see in nestling size (particularly when nestlings are younger), despite no evidence of noise impacts on parental care. It is also important to note that we only measured provisioning rate when nestlings were 8 days old, and whether provisioning rates shift with nestling age requires further investigation. Additionally, given the sex of the more aggressive mate influenced provisioning but not overall nestling size, future studies should evaluate the potential trade-offs between certain behavioral tendencies by sex and environmental circumstances to better elucidate how each sex is responding to noise and potentially compensating for any negative effects on the other member of the pair.

## **Conclusion**

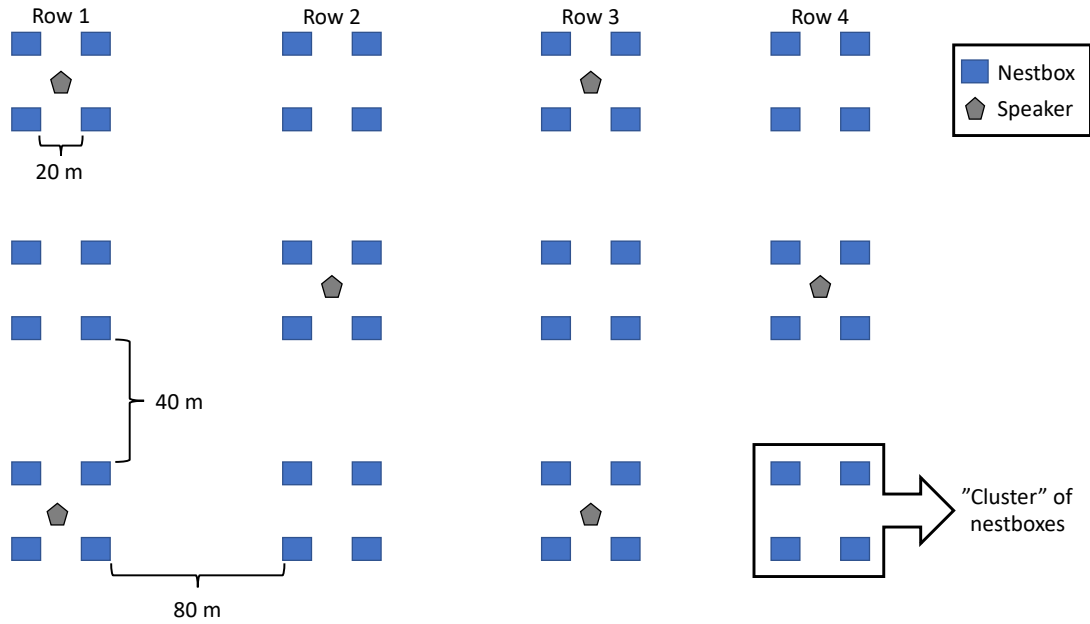
Here, we showed that pairs with more similar aggressive tendencies have larger nestlings under conditions of low noise. However, as noise amplitude increases, these more similar pairs exhibit a reduction in reproductive success (i.e. smaller nestlings), and pairs that are more dissimilar in aggressiveness exhibit an increase in reproductive success. This has important implications for how human activity may be driving selection on certain behavioral tendencies, and highlights the need to evaluate differences within mated pairs to fully understand how populations might respond to anthropogenic stressors.

## **ACKNOWLEDGEMENTS**

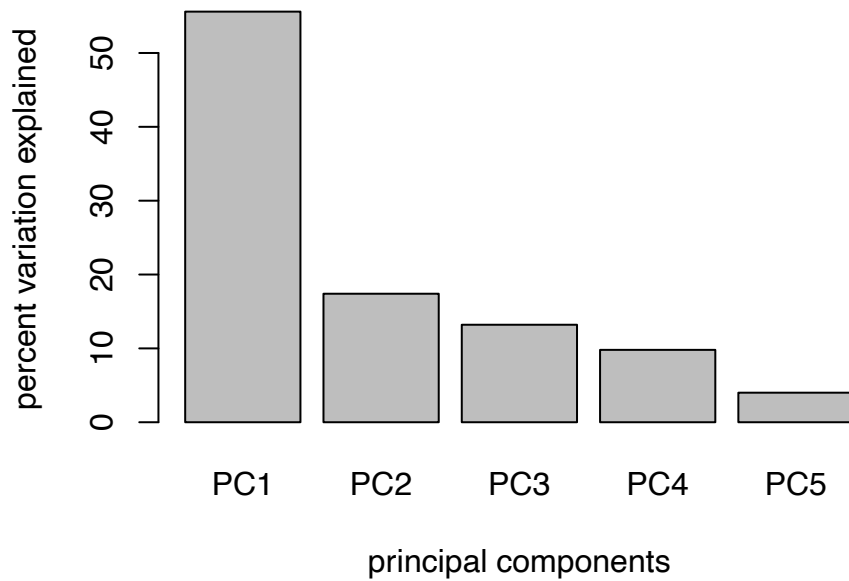
This work was supported by funds from the American Ornithological Society and student research grants from the UC Davis Graduate Group in Ecology awarded to AKB. AKB was also supported by a UC Davis Graduate Group in Ecology fellowship while conducting this study. We would like to thank members of the Patricelli lab for feedback on experimental design and Thomas Coombs-Hahn, Ryane Logsdon, and Sarah Jennings for comments on earlier versions of the manuscript. This work would not be possible without the help of our many undergraduate field assistants, as well as Michael Smith who assisted in setting up the experimental playbacks. Thank you to the City of Davis for permitting us to use the South Fork Preserve and UC Davis for the use of the Putah Creek Riparian Reserve.

## SUPPLEMENTAL MATERIALS

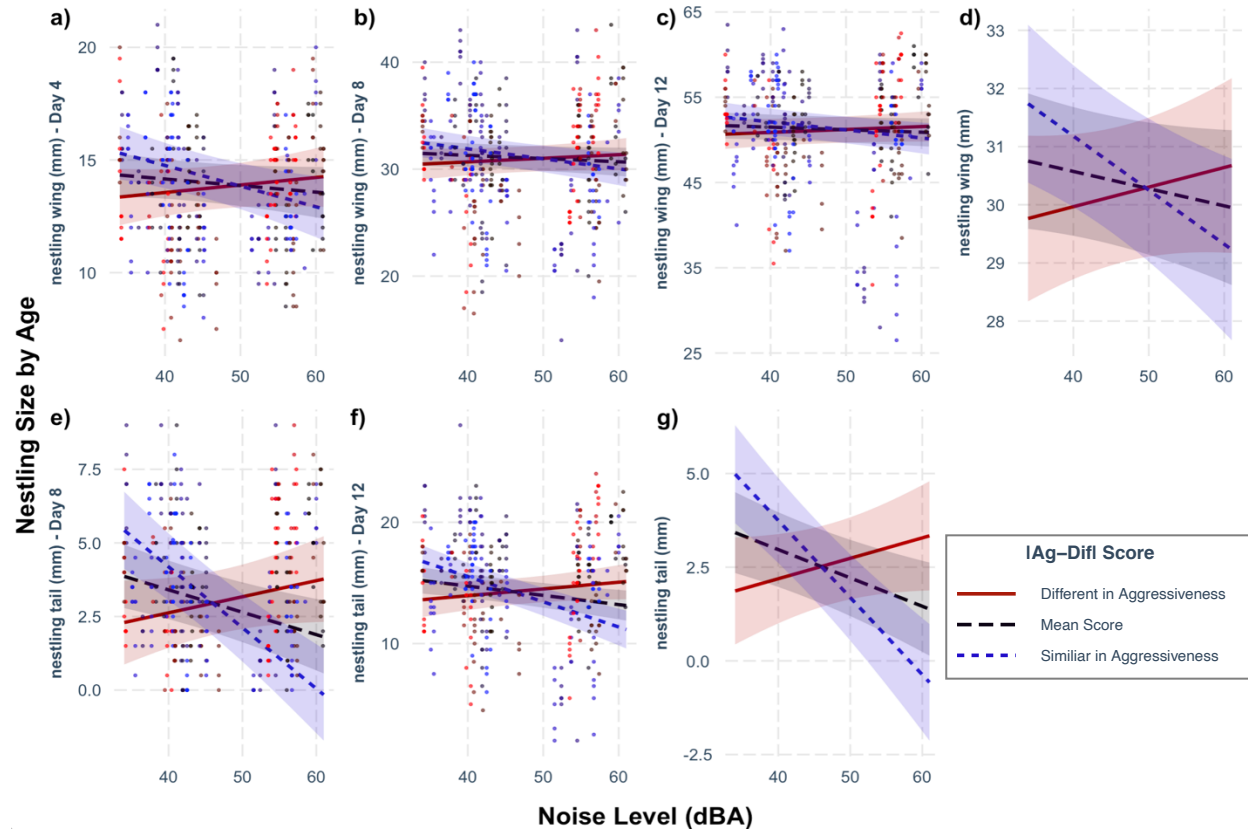
**Supplemental Figure 1.1.** Sample map of nest box setup



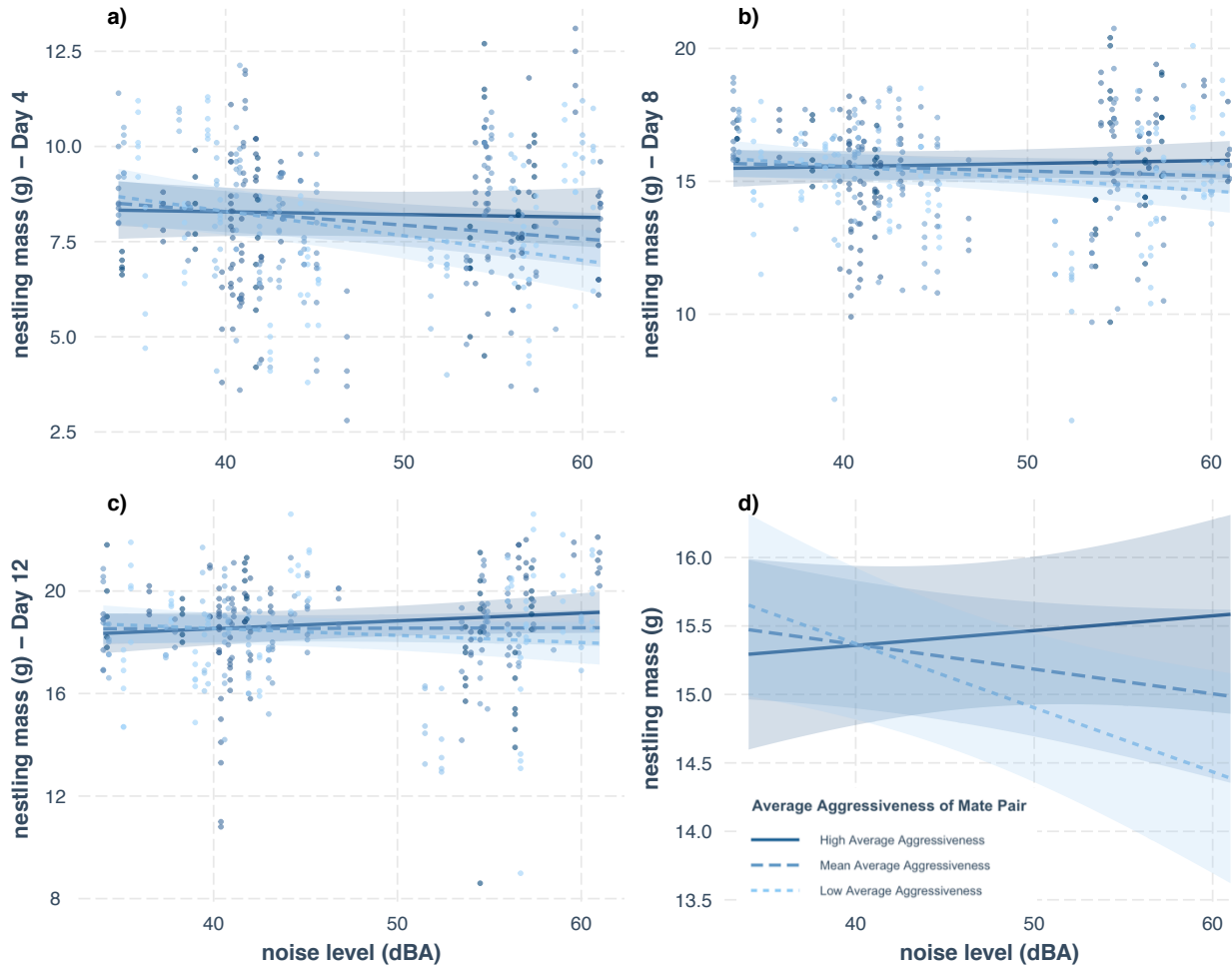
**Supplemental Figure 1.2.** Scree plot of percent variation of behavioral aggressiveness data explained by each principle component.



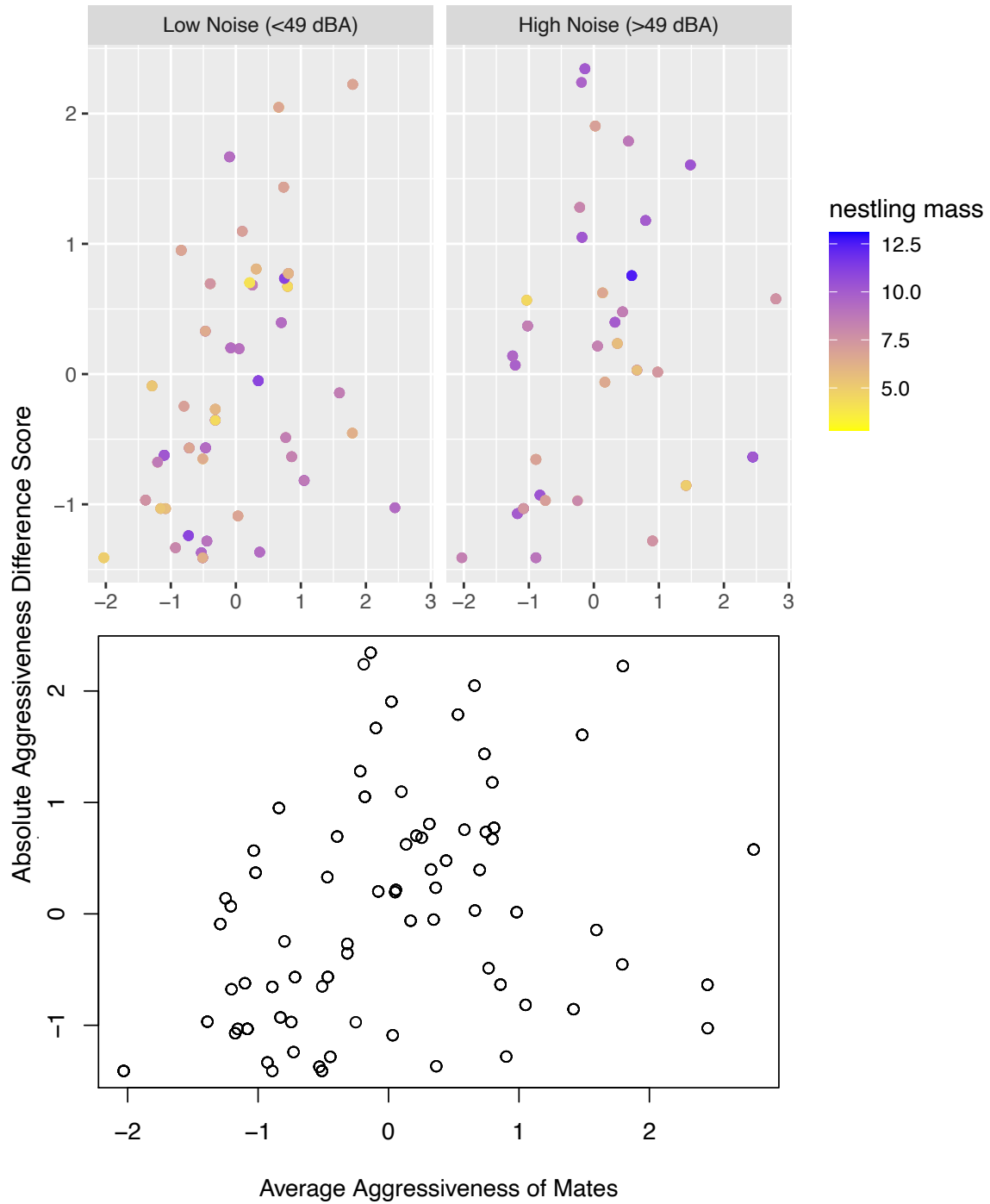
**Supplemental Figure 1.3.** Top model outputs for predicted values of nestling wing chord and tail length at day 4 (a), day 8 (b,e) and day 12 (c,f) post hatch across noise levels (dBA). (d,g) are the overall model outputs with all data. The legend applies to all panels. Solid red line is +1SD above the mean Abs-Ag-Dif score (the absolute difference in the aggressiveness of the mate pair), representing mate pairs more different in aggressiveness. Large black dash is mean Abs-Ag-Dif score. Dotted blue line is -1SD below mean Abs-Ag-Dif Score, representing mate pairs more similar in aggressiveness.



**Supplemental Figure 1.4.** Top model outputs for predicted values of nestling mass at day 4 (a), day 8 (b) and day 12 (c) post hatch across noise levels (dBA). (d) is the overall model output with all data. Solid line is +1SD above the mean AvAg score (the average aggressiveness score of a mate pair), representing mate pairs with higher overall aggressiveness. Large dash is mean AvAg score. Dotted line is -1SD below mean AvAg score, representing mate pairs with lower overall aggressiveness.



**Supplemental Figure 1.5.** Average aggressiveness (AvAg) and Absolute Aggressiveness Difference (Abs-Ag-Dif) score significantly correlated (Spearman's rank correlation,  $r = 0.398$ ,  $p < 0.001$ )



**Supplemental Table 1.1.** Loadings of each behavior by each principle component (percent variation explained in parentheses). All behaviors loaded negatively on PC1, which was used as our measure of aggressive tendency in all subsequent analyses

<b>Behavior</b>	<b>PC1 (55.6%)</b>	<b>PC2 (17.4%)</b>	<b>PC3 (13.2%)</b>	<b>PC4 (9.8%)</b>	<b>PC5 (4%)</b>
FirstDive	-0.5112081	0.37010369	-0.1786432	0.2559521	-0.7101159
NumDives	-0.4363177	0.41350413	0.3405645	-0.6967678	0.1927993
Approach	-0.5072041	0.08700048	-0.4697934	0.3175763	0.6431285
AlarmDur	-0.4020206	-0.3646148	0.7303536	0.4098803	0.06338112
RespTime	-0.359745	-0.742647	-0.3130177	-0.4244368	-0.2023174

**Supplemental Table 1.2.** Full set of candidate models of nestling mass. Note, parameters that are present in all models (site, year, age, and brood size) not listed for brevity. Colons designate an interaction effect and \* designates both terms are present as well as their interaction.

<b>Model</b>	<b>df</b>	<b>AICc</b>	<b>ΔAICc</b>	<b>w<sub>i</sub></b>
mass ~ Abs-Ag-Dif * dBA + dBA:age	18	4270.7	0	0.792
mass ~ Abs-Ag-Dif * dBA	17	4273.7	3.05	0.172
mass ~ dBA + dBA:age	16	4279.1	8.47	0.011
mass ~ Abs-Ag-Dif + dBA + dBA:age	17	4280.3	9.59	0.007
mass ~ dBA + Ag-Dif + dBA:age	17	4280.6	9.9	0.006
mass ~ dBA:age + dBA * Ag-Dif	18	4282.2	11.5	0.003
mass ~ dBA	15	4282.2	11.55	0.002
null	14	4282.3	11.67	0.002
mass ~ Abs-Ag-Dif + dBA	16	4283.4	12.76	0.001
mass ~ dBA + Ag-Dif	16	4283.6	12.91	0.001
mass ~ Ag-Dif	15	4283.8	13.15	0.001
mass ~ Abs-Ag-Dif	15	4284	13.3	0.001
mass ~ dBA * Ag-Dif	17	4285.3	14.64	0.001



**Supplemental Table 1.3.** Full set of candidate models of nestling wing chord. Note, parameters that are present in all models (site, year, age, and brood size) not listed for brevity. Colons designate an interaction effect and \* designates both terms are present as well as their interaction.

Candidate Model	k	AICc	$\Delta$ AICc	w <sub>i</sub>
wing ~ Abs-Ag-Dif * dBA	15	5551.3	0	0.47
wing ~ Abs-Ag-Dif * dBA + dBA:age	16	5553.2	1.87	0.185
wing ~ dBA	13	5555.4	4.04	0.062
null	12	5555.6	4.27	0.056
wing ~ dBA + Ag-Dif	14	5556	4.7	0.045
wing ~ Ag-Dif	13	5556.2	4.9	0.041
wing ~ Abs-Ag-Dif	13	5556.9	5.52	0.03
wing ~ Abs-Ag-Dif + dBA	14	5557	5.63	0.028
wing ~ dBA + dBA:age	14	5557.3	5.94	0.024
wing ~ dBA * Ag-Dif	15	5557.3	6	0.023
wing ~ dBA + Ag-Dif + dBA:age	15	5557.9	6.59	0.017
wing ~ Abs-Ag-Dif + dBA + dBA:age	15	5558.9	7.53	0.011
wing ~ dBA:age + dBA * Ag-Dif	16	5559.3	7.91	0.009

**Supplemental Table 1.4.** Full set of candidate models of nestling tail length. Note, parameters that are present in all models (site, year, age, and brood size) not listed for brevity. Colons designate an interaction effect and \* designates both terms are present as well as their interaction.

Candidate Model	k	AICc	$\Delta$ AICc	w <sub>i</sub>
tail ~ Abs-Ag-Dif * dBA + dBA:age	16	3224.3	0	0.396
tail ~ dBA + dBA:age	14	3226.4	2.08	0.14
tail ~ Abs-Ag-Dif * dBA	15	3227.5	3.13	0.083
tail ~ dBA + Ag-Dif + dBA:age	15	3227.6	3.32	0.076
tail ~ dBA:age + dBA * Ag-Dif	16	3227.8	3.43	0.071
tail ~ 1	12	3228.1	3.73	0.061
tail ~ Abs-Ag-Dif + dBA + dBA:age	15	3228.5	4.16	0.05
tail ~ Ag-Dif	13	3229.2	4.85	0.035
tail ~ dBA	13	3229.9	5.56	0.025
tail ~ Abs-Ag-Dif	13	3230.1	5.8	0.022
tail ~ dBA * Ag-Dif	15	3230.5	6.22	0.018
tail ~ dBA + Ag-Dif	14	3230.8	6.5	0.015
tail ~ Abs-Ag-Dif + dBA	14	3232	7.63	0.009

**Supplemental Table 1.5.**  $\beta$  estimates and 95% confidence intervals for fixed effects in top models of nestling mass, wing chord and tail length. Parameters with confidence intervals that do not overlap zero considered to have strong support. Italicized parameters had confidence intervals that overlapped zero.

<b>Response Variable</b>	<b>Fixed Effect</b>	<b><math>\beta</math> estimate</b>	<b>95% CI</b>
Nestling mass	(Intercept)	4.716	2.011,7.42
	Abs-Ag-Dif	-3.82	-6.014,-1.626
	dBA	-0.126	-0.178,-0.073
	age	3.231	2.993,3.468
	I(age <sup>2</sup> )	-0.134	-0.143,-0.126
	BroodSize	-0.489	-0.652,-0.326
	SiteS	-0.943	-1.527,-0.358
	YearAb18	0.589	0.196,0.982
	Abs-Ag-Dif:dBA	0.085	0.039,0.131
	dBA:age	0.004	0.001,0.008
Nestling wing chord	<i>(Intercept)</i>	<i>3.403</i>	<i>-0.599,7.404</i>
	Abs-Ag-Dif	-6.095	-10.057,-2.134
	dBA	-0.132	-0.209,-0.055
	age	3.104	2.901,3.307
	I(age <sup>2</sup> )	0.097	0.085,0.11
	BroodSize	0.582	0.314,0.851
	<i>SiteS</i>	<i>-0.353</i>	<i>-1.463,0.758</i>
	<i>YearAb18</i>	<i>-0.358</i>	<i>-0.985,0.269</i>
	Abs-Ag-Dif:dBA	0.124	0.042,0.206
	Nestling tail length	(Intercept)	-17.954
Abs-Ag-Dif		-3.661	-6.404,-0.918
<i>dBA</i>		<i>-0.009</i>	<i>-0.092,0.075</i>
age		3.272	2.869,3.674
<i>BroodSize</i>		<i>-0.143</i>	<i>-0.384,0.098</i>
<i>SiteS</i>		<i>-0.498</i>	<i>-1.148,0.153</i>
YearAb18		0.729	0.179,1.279
Abs-Ag-Dif:dBA		0.079	0.021,0.136
dBA:age		-0.01	-0.018,-0.001

**Supplemental Table 1.6.** Results of post-hoc analyses to test effect of overall mate pair aggressiveness on nestling size. Full sets of candidate models of nestling mass, wing chord and tail length. Note, fixed effects that are present in all models (site, year, age, interaction of age and dBA and brood size) and random effects (nestling band number, female band number and nestbox) not listed for brevity. Colons designate an interaction effect and \* designates both terms are present as well as their interaction.

<b>Candidate Model</b>	<b>k</b>	<b>AICc</b>	<b><math>\Delta</math>AICc</b>	<b>w<sub>i</sub></b>
<i>Nestling Mass</i>				
mass ~ AvAg + AvAg:dBA	18	4274.5	0	0.708
mass ~ AvAg	17	4276.9	2.33	0.221
null	16	4279.1	4.6	0.071
<i>Nestling Wing Chord</i>				
wing ~ AvAg + AvAg:dBA	13	5552.1	0	0.687
null	11	5554.5	2.38	0.209
wing ~ AvAg	12	5555.9	3.77	0.104
<i>Nestling Tail Length</i>				
tail ~ dBA	12	3223.5	0	0.417
tail ~ AvAg + dBA	13	3223.9	0.41	0.34
tail ~ AvAg * dBA	14	3224.5	1.08	0.243

**Supplemental Table 1.7.**  $\beta$  estimates and 95% confidence intervals for fixed effects in top model of nestling mass from the post-hoc analysis looking at the effect of average mate aggressiveness. Parameters with confidence intervals that do not overlap zero considered to have strong support. Italicized parameters had confidence intervals that overlapped zero.

<b>Response Variable</b>	<b>Fixed effect</b>	<b><math>\beta</math> estimate</b>	<b>95% CI</b>
Nestling mass	(Intercept)	1.541	-0.486,3.567
	<i>AvAg</i>	<i>-1.15</i>	<i>-2.451,0.151</i>
	age	3.227	2.989,3.464
	I(age <sup>2</sup> )	-0.135	-0.144,-0.126
	BroodSize	-0.494	-0.657,-0.33
	dBA	-0.054	-0.091,-0.017
	SiteS	-0.846	-1.424,-0.268
	YearAb18	0.533	0.135,0.932
	AvAg:dBA	0.029	0.002,0.055
	age:dBA	0.005	0.001,0.008
Nestling wing chord	(Intercept)	-1.37	-3.851,1.112
	<i>AvAg</i>	<i>-2.949</i>	<i>-5.085,-0.813</i>
	age	3.105	2.902,3.308
	I(age <sup>2</sup> )	0.097	0.085,0.11
	BroodSize	0.619	0.349,0.888
	dBA	-0.047	-0.086,-0.007
	AvAg:dBA	0.057	0.014,0.1
Nestling tail length	(Intercept)	-21.932	-25.069,-18.794
	<i>dBA</i>	<i>0.056</i>	<i>-0.009,0.122</i>
	age	3.288	2.89,3.685
	YearAb18	0.691	0.163,1.218
	dBA:age	-0.01	-0.018,-0.002

**Supplemental Table 1.8.** Full sets of candidate models of clutch size, brood size and hatch success. Note, parameters that are present in all models (site, year, age, and brood size where applicable) not listed for brevity. Colons designate an interaction effect and \* designates both terms are present as well as their interaction.

Candidate Model	k	AICc	$\Delta$ AICc	w <sub>i</sub>
<i>Clutch Size</i>				
null	4	298.1	0	0.439
Clutch Size ~ Ag-Dif	5	300.3	2.18	0.147
Clutch Size ~ Abs-Ag-Dif	5	300.3	2.2	0.146
Clutch Size ~ dBA	5	300.4	2.23	0.144
Clutch Size ~ dBA + Ag-Dif	6	302.6	4.44	0.048
Clutch Size ~ Abs-Ag-Dif + dBA	6	302.6	4.47	0.047
Clutch Size ~ dBA * Ag-Dif	7	304.9	6.8	0.015
Clutch Size ~ Abs-Ag-Dif * dBA	7	305	6.88	0.014
<i>Brood Size</i>				
null	4	298.3	0	0.419
Brood Size ~ Ag-Dif	5	300.1	1.84	0.167
Brood Size ~ Abs-Ag-Dif	5	300.3	2.09	0.147
Brood Size ~ dBA	5	300.5	2.27	0.135
Brood Size ~ dBA + Ag-Dif	6	302.4	4.13	0.053
Brood Size ~ Abs-Ag-Dif + dBA	6	302.7	4.41	0.046
Brood Size ~ dBA * Ag-Dif	7	304.7	6.44	0.017
Brood Size ~ Abs-Ag-Dif * dBA	7	304.9	6.65	0.015
<i>Hatch Success</i>				
null	3	180.7	0	0.339
Hatch Success ~ Ag-Dif	4	181.9	1.26	0.18
Hatch Success ~ Abs-Ag-Dif	4	182.7	2.02	0.123
Hatch Success ~ dBA	4	182.7	2.07	0.12
Hatch Success ~ Abs-Ag-Dif + Ag-Dif	5	184	3.39	0.062
Hatch Success ~ dBA + Ag-Dif	5	184.2	3.51	0.059
Hatch Success ~ Abs-Ag-Dif + dBA	5	184.9	4.2	0.042
Hatch Success ~ Abs-Ag-Dif * dBA	6	186.3	5.62	0.02
Hatch Success ~ Abs-Ag-Dif + dBA + Ag-Dif	6	186.4	5.72	0.019
Hatch Success ~ dBA * Ag-Dif	6	186.4	5.78	0.019
Hatch Success ~ Ag-Dif + Abs-Ag-Dif * dBA	7	188.1	7.49	0.008
Hatch Success ~ Abs-Ag-Dif + dBA * Ag-Dif	7	188.7	8.09	0.006
Hatch Success ~ Abs-Ag-Dif * dBA + dBA * Ag-Dif	8	190.6	9.93	0.002

**Supplemental Table 1.9.**  $\beta$  estimates and 95% confidence intervals for fixed effects in top models of clutch size, brood size, and hatch success. Parameters with confidence intervals that do not overlap zero considered to have strong support. Italicized parameters had confidence intervals that overlapped zero.

<b>Response Variable</b>	<b>Fixed Effect</b>	<b><math>\beta</math> estimate</b>	<b>95% CI</b>
Clutch Size	(Intercept)	1.773	1.601,1.938
	f.bci	-0.011	-0.108,0.087
	SiteS	-0.014	-0.203,0.176
	YearAb18	-0.044	-0.242,0.156
Brood Size	(Intercept)	1.646	1.463,1.821
	f.bci	-0.023	-0.126,0.082
	SiteS	-0.03	-0.232,0.172
	YearAb18	-0.031	-0.242,0.183
Hatch Success	(Intercept)	2.019	1.526,2.565
	<i>SiteS</i>	<i>-0.102</i>	<i>-0.679,0.47</i>
	YearAb18	0.046	-0.54,0.62

## **CHAPTER 2**

### **Presence of anthropogenic noise during the settlement period drives assortative mating by aggressiveness in a wild bird**

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## ABSTRACT

Many wildlife species are sensitive to anthropogenic noise pollution. However, intraspecific variation in response to noise is less well understood. Here we explored how individual differences in a consistent behavioral tendency – aggressiveness during nest defense against a human intruder – influences settlement decisions in tree swallows (*Tachycineta bicolor*) during the breeding season. We experimentally exposed artificial nest boxes to traffic noise playbacks beginning prior to territory establishment to determine whether noise level affects nest choice. We found that body condition and plumage characteristics indicative of quality (mantle saturation and breast brightness) did not drive nest box choice by noise amplitude. However, we found that both males and females who are more aggressive are more likely to settle in quieter boxes, and individuals who are less aggressive are more likely to settle in louder boxes. This resulted in positive assortative mating by aggressive tendency, and may have implications for reproductive success.



## INTRODUCTION

With human population growth and increases in urbanization, expansion of transportation networks and increased resource extraction, anthropogenic noise is causing substantial shifts in the acoustic environment, extending into even the most pristine habitats (Barber et al. 2010, Buxton et al. 2017). The impacts of anthropogenic noise are seen in a wide variety of taxa including: mammals (Rabin et al. 2006), birds (Ortega 2012), fish (Wysocki et al. 2006), amphibians (Sun and Narins 2005), and mollusks (Nedelec et al. 2014). These impacts include changes in physiology, behavior, and reproductive success, which may scale up to shift community dynamics (see reviews Barber et al. 2010; Shannon et al. 2016). However, a recent review found that few of these studies have explored how and why individuals within a species might differ in their response to noise (Harding et al. 2019).

Intraspecific variation is an important factor to consider if we want to understand how populations might be adapting to an increasingly human dominated world. Intrinsic characteristics like sex, behavioral tendencies, quality and age can all influence how sensitive an individual is to disturbances, and facilitate or hamper adaptation in the face of a stressor like anthropogenic noise. For example, male cichlids (*Neolamprologus pulcher*) change parental care behavior when exposed to anthropogenic noise, but females do not (Bruitjes and Radford 2013). In European eels (*Anguilla anguilla*), body condition affects whether or not anti-predatory behavior is altered under noisy conditions (Purser et al. 2016). And internal injuries due to exposure to noise from pile driving appears to affect larger individuals more than smaller individuals for one hybrid species of bass (white bass *Morone chrysops* x striped bass *Morone saxatilis*) (Casper et al. 2013). These are just a few examples of how nuanced the effects of noise pollution can be, and why it is important to evaluate what intraspecific traits might explain variation in how individuals cope with noise.

One important area to focus on regarding how intrinsic characteristics of individuals influence response to noise is habitat use. The phenotypic habitat-selection hypothesis posits that behavioral tendencies may affect habitat selection decisions. Supporting this hypothesis, studies have found that in areas with anthropogenic disturbance, individuals distribute non-randomly by behavioral tendency (Martin and Réale 2008, Carrete and Tella 2010). If intraspecific differences affect how individuals perceive a given habitat's quality, due to the presence of artificial noise, it may change how individuals distribute themselves within that habitat. In birds, we know there are many species that experience negative effects of noise pollution (see review Ortega 2012), including impacts to habitat use. One study found that during migratory stopovers approximately 30% of bird species community avoided suitable habitat that was exposed to noise (Ware et al. 2015). In sage grouse (*Centrocercus urophasianus*), male attendance is significantly lower at breeding grounds (leks) exposed to noise than compared to control leks (Blickley et al. 2012a). There is evidence that some cavity nesting species avoid artificial nest boxes exposed to higher noise levels (Halfwerk et al. 2016, Kleist et al. 2017, Injaian et al. 2018a, Plummer et al. 2021).

There is also research that suggests an interaction of sex and behavioral tendency that drives individual differences in response to environmental change in some circumstances (Van Oers et al. 2005, Ellenberg et al. 2009). Differential assessment of noise may alter patterns of mate assortment and, in turn, have repercussions for reproductive success. Previous studies on house sparrows (*Passer domesticus*) and tree swallows (*Tachycineta bicolor*) show that females are more averse to settling in noisy territories than males (Schroeder et al. 2012, Injaian et al. 2018a), and females who do settle in noisier territories are of lower quality (Injaian et al. 2018a).

In this study we sought to understand whether individual differences in behavior of wild breeding tree swallows influence territory choice in relation to noise exposure, and whether this might have implications for mate assortment and reproductive success. Tree swallows are an

appropriate study system to explore the interaction of sex and behavioral tendency, given the differences between males and females in response to noise and the role of aggressiveness in reproductive success. In a previous study on our population of tree swallows, both males and females exhibited a preference for quiet boxes, but this preference was stronger in females (Injaian et al. 2018a). Additionally, there was a positive relationship between noise amplitude and egg-laying date, which in tree swallows is correlated with heavier eggs (Ardia et al. 2006), larger clutch sizes (Winkler and Allen 1996) and better flight ability in females (Bowlin and Winkler 2004), suggesting that higher-quality females preferentially settled in the control treatment (Injaian et al. 2018a). This could mean that some high-quality males that settle in noisy boxes may miss out on high-quality female mates who more strongly avoid those boxes (Habib et al. 2007).

Aggressiveness during nest defense has been identified as a consistent behavioral tendency in tree swallows, both within and across breeding seasons (Chapter 1, Rosvall 2008, Betini and Norris 2012). While males and females do not pair assortatively by aggressiveness (Rosvall 2010, Chapter 1), mate assortment by this behavioral trait does have fitness implications in the context of noise. In a previous study, we found that under low noise levels, mate assortment by aggressiveness had marginal effects on nestling size, but under high noise, pairs that were more similar in aggressiveness (i.e. assortatively mated) saw a significant decrease in nestling size (Chapter 1).

Differences in sensitivity to noise by behavioral tendency has been demonstrated in multiple species, besides tree swallows. A study on great tits (*Parus major*) experimentally exposed to noise found that provisioning rate and latency to return to the nest varied with sex, age and exploratory tendency (Grunst et al. 2021). If sex and/or behavioral tendency results in individuals evaluating noisy nest sites using different criteria, this could result in changes in the

degree of assortative mating by aggressiveness and quality in tree swallows. This may ultimately impact reproductive success and have implications for adaptation and selection of certain attributes, by constraining diversity, under conditions of noise pollution.

In this study, we tested the hypothesis that intraspecific differences related to sex, quality and aggressiveness explains variation in sensitivity to noise during the territory settlement period of the breeding season. We used measures of body condition and plumage characteristics to assess individual quality. Based on results from Injaian, et al (2018a), we predicted a negative relationship between individual quality and the noise levels at their nest box, such that lower quality individuals would be more likely to settle onto territories exposed to high noise levels than higher quality individuals. Additionally, we expected that females would be more sensitive to noise and therefore this relationship would be stronger for females than for males. Based on Injaian, et al. (2018a) and our results presented in Chapter 1, we expected an interaction effect between sex and aggressiveness on nest site selection, with aggressiveness explaining variation in noise amplitude at the chosen nest box for females, but not males. We hypothesized two possible alternatives that may lead to such an interaction. First, if more aggressive females are less likely to avoid noisy boxes than less aggressive females, we expect a higher proportion of aggressive females in territories of higher noise levels. The alternative hypothesis is that if all females prefer quiet boxes, aggressive females may better compete for higher quality boxes and we might observe aggressive females settling in quieter territories. Either result would suggest that these intrinsic traits are explaining intraspecific differences in response to noise pollution during the breeding season. We also evaluated what effects noise and mate assortment may have on breeding and reproductive success by looking at clutch initiation, clutch size and nestling quality.

## **METHODS**

### **Field Site & Experimental Setup**

This study was conducted in Davis, CA at the UC Davis Putah Creek Riparian Reserve. The site consists of open pasture grassland directly adjacent to Putah Creek and has an established system of nest boxes that are readily settled by tree swallows and Western bluebirds (*Sialia mexicana*) each year. In early February 2019, prior to settlement by tree swallows, we rearranged the boxes (n=46) in 6 rows of 8-12 boxes. All boxes were a minimum of 20 m apart and were also at least 20 m from the location of any boxes from the prior year. This made it less likely that settlement decisions would be based on an individual's box selection in prior years.

Originally, when we began our experiment in February 2019, we included a second site at the South Fork Preserve in Davis, CA. However, due to an unprecedented rainy season, that field site experienced extreme flooding, making the site inaccessible for several weeks and damaging the experimental equipment. Therefore, that site was excluded from the experiment. Given these circumstances, we put up an additional 14 nest boxes at the Putah Creek Riparian Reserve site on March 8<sup>th</sup> in order to increase our sample size to 60 boxes. We observed 100% settlement of the nest boxes for this experiment by tree swallows (n=51) and Western bluebirds (n=9). Two of the boxes were settled by mated pairs that switched boxes, which had been previously unoccupied, after experiencing nest failure and their former boxes were not claimed by any other mated pairs.

Five noise playback systems were placed evenly amongst the rows of boxes. Individual playback systems were located in between 2 rows, within a cluster of 4 boxes. Playback systems consisted of a speaker (Model TFS14, TIC Corp., City of Industry, CA, U.S.A.) hooked up to a car amplifier, a timer, and an MP3 player, all of which were powered by a 12V lead-acid battery. The MP3 players contained two noise files that were played on a continuous loop and randomly shuffled. See Injaian et al. 2018b for methodology on compilation of traffic noise files. We

began playbacks of pre-recorded traffic noise on February 16<sup>th</sup>. We used an automatic timer (Model CN101, Favolcano, Edwardsville, IL, U.S.A.) to play noise daily from 0700-1300. Playbacks began in February, prior to territory establishment, and continued through the end of June.

Because the speakers could be heard to some degree from all boxes and because it is not possible to expose boxes to the exact same amplitude, we considered noise exposure a continuous variable, ranging from 37.1 dBA to 61.4 dBA. Noise levels were measured in dBA using a sound pressure level (SPL) meter (Model 824, Larson-Davis, Inc., Depew, NY, U.S.A.). The SPL meter was held adjacent to the nest box at the height of the entrance hole; we recorded the average Leq (equivalent continuous sound level) across a 60-second interval.

### **General Field Methods**

Nest boxes were checked daily beginning April 1 to record progress of nest building, initiation of egg laying, clutch size and hatch date of nestlings. Adults were caught in the nest box by pulling closed a wooden flap affixed to the front of the nest box immediately after they entered the box. Females were caught in the nest box 2-4 days after clutch completion during the incubation period. We measured wing chord, tail length, tarsus, and mass, and recorded their band number. Any unbanded birds were banded with a standard USGS aluminum band. We also uniquely marked birds with nontoxic paint on their undertail coverts in order to identify individuals. Males were caught, and females caught a second time, during the provisioning period. Males were measured and marked in the same manner as females. Additionally, we collected contour feathers from the center of the breast and back, as well as a blood sample during this period of the breeding season. We also took a second mass measurement for females.

Nestlings were measured for wing chord, tail length, and mass on days 4, 8 and 12 post-hatch. Each nestling was uniquely marked with paint on their toe nails to track individuals. On day 12 post-hatch, we also collected blood samples and measured tarsus length. Nestlings were banded on day 10 post-hatch.

On the night of May 19<sup>th</sup> to May 20<sup>th</sup> there was an unprecedented temperature drop (down to 44 degrees F) and heavy rain at the field site which resulted in high nestling mortality and nest failure. Therefore, we only included nestling morphological data that was collected prior to the extreme weather event.

### **Behavioral Assays**

In order to assess individual aggressiveness of adults we performed a human intruder assay adapted from Betini & Norris 2012. This consisted of an observer (AKB) standing adjacent to the side of the nest box for 5 minutes. The assay did not begin until the focal bird was present in the territory. We recorded the presence and duration of alarm calling, the number of dives made at the observer, the time of the first dive, the closest approach made toward the observer (<1 m, 1-5 m, 5-10m, >10m), the presence or absence of any circling around the observer, and the total duration of the response. We performed this assay for females during incubation after clutch completion, and for both males and females during the provisioning period on day 11 post-hatch.

For the assays done during provisioning, most pairs were assessed at the same time, though both birds were not always present at the start of the assay. Therefore, the start of the 5 minute observation period began for each bird when that particular individual arrived into the territory (e.g. if the female was present at the start and the male arrived 1 minute into the assay, observations for the female would start at time zero and end at 5 minutes, but we would continue

observing the male starting at 1 minute and until the 6 minute mark for a total of 5 minutes of observation time). If only one bird was present during the assay, which was rare, we attempted the assay again the next day.

We calculated an individual aggression score for each adult ( $n = 68$ ) from the 5 behaviors measured during the aggression assays using a principle component analysis. These methods were established in a previous study where we confirmed that this behavior was repeatable in individuals within a breeding season and across years (Chapter 1).

### **Plumage Measurements**

A spectrophotometer was used to measure the brightness of the tree swallow breast and mantle feathers of adults. Feathers were prepared by layering four feathers, either breast or mantle, on top of one another to simulate how they would have been layered on the individual, and secured on a white notecard with a piece of tape. Spectral analysis was completed using the same method described in (Bitton et al. 2007). This included the use of an Ocean Optics USB2000 spectrometer (Dunedin, FL, USA) and a bifurcated probe in a cylindrical PVC pipe to exclude ambient light and keep the probe a standard distance from the sample. The probe was held at a 90 degree angle against the feathers and four readings were taken of each set of feathers. We recorded brightness as a measure of percent reflectance between 300nm and 700nm wavelengths (Doucet 2002). Brightness, or our B2 value, was calculated as the mean relative reflectance over our entire spectral range, which is equivalent to taking the area under the curve made by the percent reflectance at each wavelength in our interval (Maia et al. 2013). The spectral curve readings were then averaged for each feather type of each individual to determine the average brightness of the mantle and breast feathers. Different techniques for analyzing the spectral data using the R package ‘pavo’ (version 2.4.0) were inspired by Maia et al. (2013) and



included the functions ‘getspec’ to upload our data, ‘aggspec’ to find the mean of the four feather samples for each feather type per individual, ‘prospec’ to smooth our data, and ‘aggplot’ to plot our spectral analysis by treatment.

## **Statistical Analyses**

To identify which factors influence whether a noisy box gets settled and by whom, we compared linear models of dBA. All candidate models included the fixed effects of timing (whether the box was put up in February or March), row (relative distance from the creek) and edge (proximity of the box to the edge of the grid of boxes). Candidate models varied in whether they included the fixed effects of sex, aggressiveness score and a measure of quality (body condition, breast feather brightness, or mantle feather saturation), as well as possible interaction effects of sex and aggressiveness and sex and quality. Mantle feather saturation was chosen as a measure of quality because it is associated with parental care in tree swallows (Dakin et al. 2016), as well as baseline corticosterone levels (Taff et al. 2019a). Plumage breast brightness explains hatching success and stress response (Taff 2019). During data exploration, one female outlier for aggressiveness (>1.5 interquartile range above the third quartile) was identified and removed from the analyses.

Because measures of quality are likely to be correlated we restricted our model set so that a given model could include only one of the three measures of quality. We compared the candidate models based on Akaike information criterion corrected for small sample size (AICc) and model weight (Hurvich and Tsai 1989, Burnham and Anderson 2001), which were calculated using the *dredge* function (MuMIn, R package). We considered any models with a  $\Delta\text{AICc}$  value less than 2 to have the strongest model support (Burnham and Anderson 2001).

We assessed whether noise and nest box traits influence relative aggressiveness attributes of the pair. The three aggressiveness attributes we tested were: aggression-difference score (“Ag-Dif”), absolute aggression-difference score (“Abs-Ag-Dif”), and average mate aggressiveness (“AvAg”). Aggression-difference score was calculated by subtracting the male aggressiveness score from female aggressiveness score so that higher Ag-Dif scores represented pairs with a more aggressive female and lower Ag-Dif scores represented pairs with a more aggressive male. The absolute aggression-difference score is simply the absolute value of the Ag-Dif score and reflects the overall difference in aggressiveness of the mates regardless of which sex is more aggressive. For each of these three mate level scores, we ran a separate linear model comparison. All models contained the fixed effects of Timing, Row and Edge to account for nest box traits that might influence settlement decisions. Models varied by whether they contained the fixed effect of dBA or not.

We also tested whether noise affects mate assortment of four adult traits (aggressiveness score, body condition, breast feather brightness, and mantle feather saturation) by completing four linear model comparisons (one for each trait). For each analysis, the response variable was the measure of the female trait. Original candidate models varied by whether they contained the following fixed effects: measure of the male trait, dBA, and the interaction of the male trait and dBA. However, dBA and male aggressiveness were colinear so we removed dBA from the analysis of female aggressiveness. Timing, Row, and Edge were originally included in the candidate models but did not significantly explain any female trait and were removed from all candidate models to improve model fit. For the analysis of breast feather brightness, one male was identified as an outlier and was removed from the analysis.

To test for effects on reproduction, we ran two linear model comparisons, one where the response variable was lay date (the date at which the first egg in a clutch was laid) and another

where the response variable was clutch size. For both analyses, the full candidate model included a three-way interaction of dBA, female aggressiveness, and male aggressiveness. We compared this model to all other possible models that varied by the presence of these effects and their possible interactions. All candidate models included the fixed effects of edge, timing and row. For the analysis of clutch size, all candidate models also included the fixed effect of lay date. We also ran linear models to test for effects on nestling mass and nestling wing chord. All candidate models included the fixed effects of age, the quadratic effect of age, and brood size. They also included the random effects of box and nestling ID. Candidate models of mass and wing chord varied by whether they included dBA or the interaction of dBA and age.

## RESULTS

### Settlement Patterns

Three models of nest box choice by dBA had high support ( $\Delta AICc < 2$ , model weight sum = 0.577, Table 2.1). All top models showed a significant effect of aggressiveness (95% CIs did not overlap zero) on nest box choice, with more aggressive birds being more likely to settle in quieter boxes (Figure 2.1, Tables 2.1 & 2.2). The top model had an  $R^2$  value of 0.427. We found no evidence of an effect of sex, body condition or feather attributes on nest box choice by dBA. The top model of nest box choice ( $w_i = 0.235$ ) included body condition and the third ranked model included mantle feather saturation, but in both cases the 95% CIs overlapped zero. The top model also showed a significant effect of Edge, Row and Timing (Table 2.2).

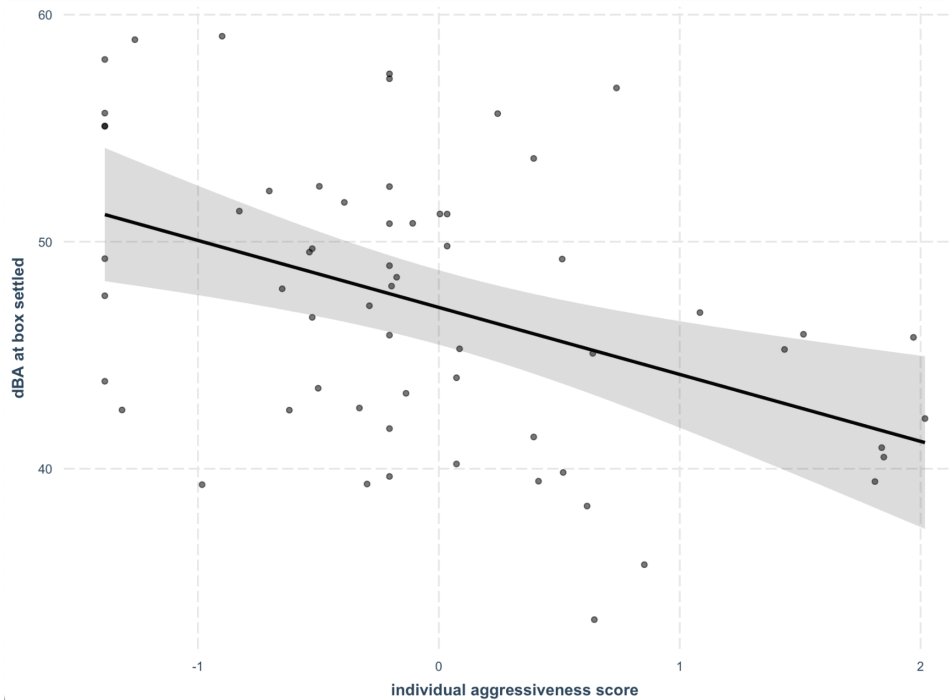
**Table 2.1** Top 3 candidate models of noise amplitude (dBA) of the chosen nest box that individuals settled in. Note, variables that are present in all models (Edge, Timing, Row) not listed for brevity.

Candidate Model	k	AICc	$\Delta$ AICc	w <sub>i</sub>
dBA ~ body condition + Aggressiveness	7	398.5	0	0.235
dBA ~ Aggressiveness	6	399	0.51	0.182
dBA ~ mantle saturation + Aggressiveness	7	399.2	0.77	0.16

**Table 2.2**  $\beta$  estimates and 95% confidence intervals for fixed effects in top model of dBA at the box settled. Variables with confidence intervals that do not overlap zero considered to have strong support. Italicized variables had confidence intervals that overlapped zero.

Fixed Effect	$\beta$ estimate	95% CI
(Intercept)	59.049	52.889, 65.21
<i>body condition</i>	-1.278	-2.797, 0.242
Aggressiveness	-2.951	-4.672, -1.23
Edge	-3.75	-5.944, -1.556
Row	-1.372	-2.344, -0.4
Timinglate	-5.622	-10.122, -1.123

**Figure 2.1** Partial residual plot with 95% CI calculated from the top model of dBA at the nest box, showing that as individuals increase in their aggressiveness score, they are more likely to choose quieter boxes to settle in.



## Impacts on Mate Assortment

We found that mates do exhibit positive assortment by aggressiveness when noise playbacks begin prior to settlement (Figure 2.2). The top model of female aggressiveness had greater support ( $w_i = 0.818$ ) than the null model ( $\Delta AICc = 3.01$ ,  $w_i = 0.182$ ) and included male aggressiveness ( $\beta = 0.404$ , 95% CI = 0.055, 0.753).

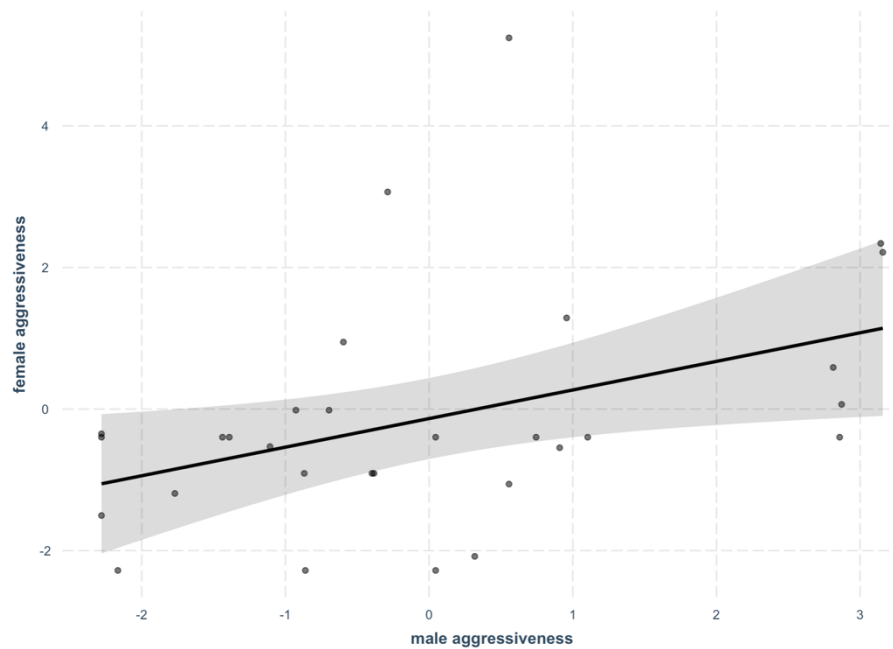
Mates did not assort by breast feather brightness, mantle feather saturation or body condition. The top model of female breast feather brightness ( $w_i = 0.777$ ) was the null model, which excluded male breast feather brightness. The top model of female mantle feather saturation ( $w_i = 0.660$ ) included the fixed effect of male mantle feather saturation, but the 95% CIs overlapped zero (-0.010, 0.380) and the null model had some support ( $\Delta AICc = 1.32$ ,  $w_i = 0.34$ ). For female body condition, the null model had the highest model support ( $w_i = 0.729$ ) and while the alternative model did have some support ( $\Delta AICc = 1.98$ ,  $w_i = 0.271$ ) the confidence intervals for male body condition overlapped zero (-0.259, 0.473).

We found that the degree of similarity in aggressiveness of mates did not vary with noise amplitude (i.e. birds that settled in quieter boxes were not more or less likely to be similar in aggressiveness than birds that settled in louder boxes). Noise amplitude was absent in the top model ( $w_i = 0.663$ ) of the aggressiveness difference score that accounts for which sex in a pair is more aggressive (AggDiff). The alternative model, which did contain dBA, had some support ( $\Delta AICc = 1.36$ ,  $w_i = 0.337$ ), but the 95% CIs for dBA overlapped zero (-0.044, 0.089).

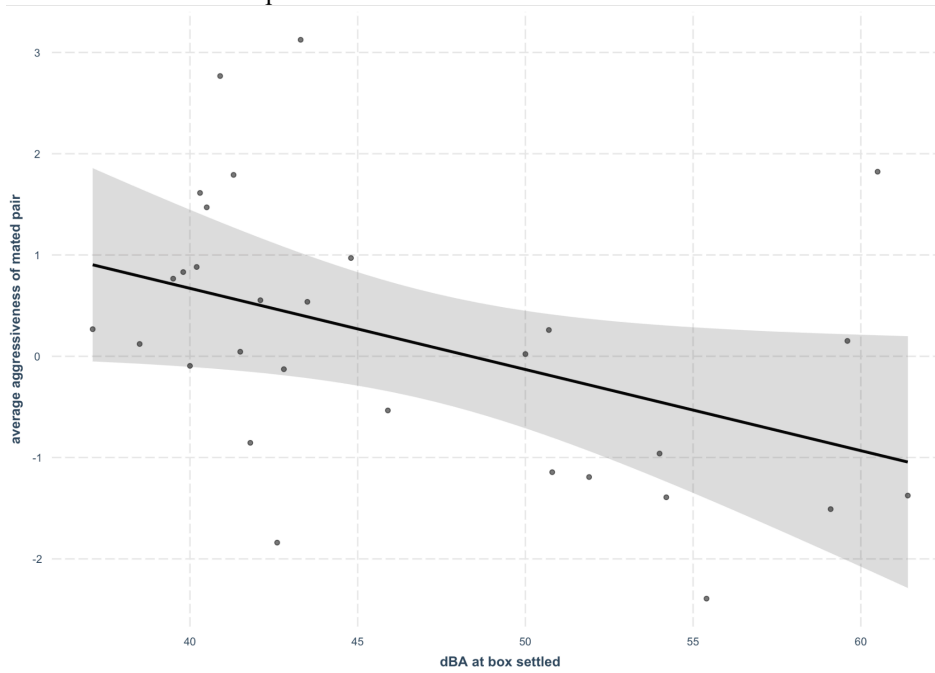
The top model ( $w_i = 0.784$ ) for the absolute difference in aggressiveness (Abs-Agg-Diff) also did not include dBA as a fixed effect. The alternative model of Abs-Agg-Diff, which did include dBA, had lower model support ( $\Delta AICc = 2.69$ ,  $w_i = 0.207$ ) and the 95% CIs for dBA overlapped zero (-0.044, 0.089).

Noise does have a significant relationship with average aggressiveness of a mated pair, with aggressive pairs settling in quiet boxes and more passive pairs settling in noisy boxes (Figure 2.3). The top model of average aggressiveness of mates ( $w_i = 0.702$ ), included dBA, with 95% CI intervals that did not overlap zero (Table 2.3). The alternative model, which only included the intercept, had some support ( $\Delta AICc = 1.71$ ), but much less model weight ( $w_i = 0.298$ ) than the top model.

**Figure 2.2** Males and females positively assort by individual aggressiveness. Line and 95% confidence intervals calculated from predicted values of top model. Points represent raw data.



**Figure 2.3** Partial residual plot with 95% CI of dBA on average aggressiveness of mated pair, after controlling for all other effects in the top model.



**Table 2.3**  $\beta$  estimates and 95% confidence intervals for fixed effects in top model of average aggressiveness of mated pairs. Variables with confidence intervals that do not overlap zero considered to have strong support. Italicized variables had confidence intervals that overlapped zero.

Response Variable	Fixed Effect	$\beta$ estimate	95% CI
Average Aggressiveness	(Intercept)	5.534	0.452,10.616
	dBA	-0.08	-0.159,-0.001
	<i>Edge</i>	-0.287	-1.023,0.448
	<i>Row</i>	-0.292	-0.629,0.045
	<i>Timinglate</i>	-1.272	-2.659,0.115

### Impacts on Measures of Reproductive Success

We found no effects of noise or parental aggressiveness on clutch initiation date or clutch size. The top model of clutch initiation date was the null model ( $w_i = 0.828$ ). The alternative model, which included dBA was much less supported ( $\Delta AIC = 3.15$ ,  $w_i = 0.172$ ). Timing and row did not affect clutch initiation date, but we did see an effect of edge ( $\beta = -3.995$ , CI: -7.026, -

0.964), with egg laying occurring earlier in boxes located more central in the community, than boxes located more on the periphery.

The top model of clutch size was the null model ( $w_i = 0.803$ ) and the CIs for clutch initiation date, edge, timing and row all overlapped zero (Supplemental Table 2.1). The alternative candidate models had  $\Delta AICc > 2$  (Supplemental Table 2.2).

We also found no effect of dBA or brood size on nestling size (mass and wing chord length) (Tables 2.5 & 2.6). The top models for both nestling mass and wing chord did not include dBA (Table 2.4). For candidate models with a  $\Delta AICc < 2$  that did include dBA, the confidence intervals overlapped zero.

**Table 2.4.** Candidate models for nestling mass and wing chord.

<b>Candidate Model</b>	<b>k</b>	<b>AICc</b>	<b><math>\Delta AICc</math></b>	<b><math>w_i</math></b>
<i>Nesting mass</i>				
mass ~ age + I(age <sup>2</sup> ) + Brood_Size	7	1055.5	0	0.662
mass ~ age + I(age <sup>2</sup> ) + Brood_Size + dBA	8	1057.4	1.97	0.247
mass ~ I(age <sup>2</sup> ) + Brood_Size + age * dBA	9	1059.4	3.97	0.091
<i>Nestling wing chord</i>				
wing ~ age + I(age <sup>2</sup> ) + Brood_Size	7	1326.6	0	0.595
wing ~ age + I(age <sup>2</sup> ) + Brood_Size + dBA	8	1328.4	1.77	0.245
wing ~ I(age <sup>2</sup> ) + Brood_Size + age * dBA	9	1329.3	2.64	0.159

**Table 2.5.**  $\beta$  estimates and 95% confidence intervals for fixed effects in top models of nestling mass and nestling wing chord. Variables with confidence intervals that do not overlap zero considered to have strong support. Italicized variables had confidence intervals that overlapped zero.

<b>Response Variable</b>	<b>Fixed Effect</b>	<b><math>\beta</math> estimate</b>	<b>95% CI</b>
Nestling mass	<i>(Intercept)</i>	-4.01	-10.269,2.25
	age	3.725	3.225,4.225
	I(age <sup>2</sup> )	-0.145	-0.177,-0.113
	<i>Brood_Size</i>	-0.415	-1.48,0.65
Nestling wing chord	<i>(Intercept)</i>	3.887	-6.001,13.775
	age	1.607	0.75,2.464
	I(age <sup>2</sup> )	0.195	0.14,0.25
	<i>Brood_Size</i>	-0.435	-2.105,1.236



## DISCUSSION

Previous studies on tree swallows and other secondary cavity nesting birds show that some individuals prefer to settle in quiet territories, rather than territories exposed to elevated noise levels (Halfwerk et al. 2016, Kleist et al. 2017, Injaian et al. 2018a). However, available nesting sites are often a limited resource for secondary cavity nesting species, thus avoidance of noise may not always be possible when establishing a territory (Halfwerk et al. 2016). We see evidence of high competition at our field sites, where we observe nearly 100% nest box occupation each year. Therefore, it is reasonable to expect that intraspecific differences will explain variation in nest site selection based on noise exposure. Here we confirm that an individual behavioral tendency (aggressiveness) varies with noise amplitude of an individual's territory, with more aggressive individuals preferentially settling in quieter boxes. There are two possible explanations for this pattern. It may be that quieter boxes are considered higher quality and aggressive individuals are better able to compete for those boxes (Duckworth 2006). Alternatively, aggressive tendency may relate to an individual's sensitivity to noise, such that aggressive individuals have a greater aversion to noise, as was found in great tits (*Parus major*) (Grunst et al. 2021). These two explanations are not mutually exclusive and may be operating in synchrony, though the latter explanation seems more consistent with our results. We saw that there were less aggressive individuals present in boxes exposed to lower amplitudes, but no highly aggressive individuals were observed in noisy boxes (Figure 2.1). Future studies looking at the order in which nest boxes get settled, as well as competitive interactions at nest boxes, would help elucidate why this pattern is observed.

We also evaluated how noise might affect mate assortment patterns. We observed a positive relationship between male and female aggressiveness, and average aggressiveness of the pair was negatively correlated with dBA (Figures 2.2 & 2.3). While the degree of assortment by

aggressiveness was not affected by noise amplitude (birds in high noise were not more or less likely to mate with a partner similar to themselves than birds in low noise), it is important to note that assortment is not observed under ambient noise conditions. In a prior study on this population, when birds were allowed to settle and choose mates before experimental noise treatments began there was no relationship between the aggressive tendencies of a pair (Chapter 1). This random assortment by aggressiveness has been seen in other populations of tree swallows without noise playbacks (Rosvall 2008). Given the results of these other prior studies, the relationship observed in this study between aggressiveness and dBA suggests that anthropogenic noise can alter who pairs up with whom during settlement.

We also evaluated whether noise affected breeding and reproductive success. We found no effect of noise on clutch initiation date, clutch size, nor nestling size. The lack of an effect on nestling size was somewhat surprising given prior studies where we did see a decrease in nestling size with increasing noise amplitude (Chapter 1, Injaian et al. 2018b, 2018c, 2018a). This disparity is perhaps due to the experimental design of this study. In this study, noise was played during territory settlement and resulted in positive assortative mating by aggressiveness and a relative lack of disassortative pairs. This is important to consider because significant effects of mate assortment by aggressiveness on reproductive success in tree swallows were driven by the degree of similarity of the pair, rather than the overall level of aggressiveness. Rosvall (2010) found that pairs that are dissimilar in aggressiveness have higher reproductive success, with greater brood size and heavier eggs. In a previous experiment in our population, in which noise playback began after mate assortment, we found that mates with similar aggressiveness (i.e. positive assortment) have smaller nestlings when experimentally exposed to high noise levels, but nestlings of mates with dissimilar aggressiveness are unaffected (Chapter 1). The lack of disassortative pairs when assortment occurs in noise may have impacts on

population health, because these pairs have higher reproductive success than assortative pairs (Rosvall 2010, Chapter 1).

While we did find noise drove mate assortment patterns by aggressiveness, we did not find an effect on assortment by measures of quality (body condition, breast feather brightness, mantle feather saturation). This might suggest that sensitivity to noise, rather than perceived habitat quality, is driving settlement patterns. If noisy boxes were of lesser quality, we would expect to see birds of higher quality avoiding them (Injaian et al. 2018a), but that is not what we observed in this study. Alternatively, our measures of quality might not reflect a bird's ability to either perceive noise as a stressor or to acquire territories.

In conclusion, this study demonstrates that the influence of noise on habitat use may be different during the settlement period than during later stages of breeding. This critical life history stage is when individuals make decisions about their breeding partner and where to build a nest, which can determine their breeding success for that year. The changes in nest box choice and mate assortment by aggressiveness in this study suggest that human activities that introduce elevated noise levels into the environments might inadvertently drive selection against specific behavioral phenotypes (Carrete and Tella 2010).

## **ACKNOWLEDGEMENTS**

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season. Permission was granted by the City of Davis for use of the South Fork Preserve and UC Davis for the use of the Putah Creek Riparian Reserve.

## SUPPLEMENTAL MATERIALS

**Supplemental Table 2.1.**  $\beta$  estimates and 95% confidence intervals for fixed effects in top model of clutch size.

<b>Fixed Effect</b>	<b><math>\beta</math> estimate</b>	<b>95% CI</b>
(Intercept)	692.064	-137.326,1521.454
clutch_int_julian	-0.038	-0.084,0.008
Edge	0.084	-0.301,0.47
Row	-0.036	-0.208,0.136
Timinglate	0.235	-0.42,0.89

**Supplemental Table 2.2.** Candidate models for clutch size. Note, fixed effects included in all models (Edge, Timing, Row, Clutch Initiation Date) not listed for brevity.

<b>Model</b>	<b>k</b>	<b>AICc</b>	<b><math>\Delta</math>AICc</b>	<b><math>w_i</math></b>
Clutch_Size ~ 1	6	65.1	0	0.803
Clutch_Size ~ dBA	7	68.2	3.09	0.171
Clutch_Size ~ dBA + dBA:clutch_int_julian	8	72	6.91	0.025

## **CHAPTER 3**

### **Individual variation in response to an unprecedented cold snap during the breeding season of a cavity-nesting bird**

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## ABSTRACT

Sudden inclement weather events have become increasingly common and have the potential for catastrophic effects on breeding birds. Here we present the results of an opportunistic observational study of a population of tree swallows (*Tachycineta bicolor*) in northern California that experienced a sudden cold snap during the spring 2019 breeding season, which resulted in high rates of nest failure and brood reduction. This cold snap took place during an experiment where we were exposing nest boxes to playbacks of traffic noise for the duration of the field season, beginning prior to adult territory establishment. We found that nestling age and male breast feather brightness explained likelihood of nest failure, and second-year females in their first breeding season were more likely to be absent from the breeding grounds after the event than males and older females. Females with brighter white plumage renested sooner after nest failure than less bright females. For nestlings that survived the storm, we found that relative position of the nest within the population, as well as clutch initiation date, influenced time to fledging. Generally, clutch initiation date was associated with nestling size, such that nestlings that hatched later in the season were smaller than nestlings that hatched earlier in the season, and nestlings that were very young at the time of the cold snap or were in the incubation period exhibited stunted growth. We also found that nestling mass declined with increased noise exposure for clutches initiated before the storm, but not late season clutches.

## INTRODUCTION

Climate change has been associated with an increase in extreme weather events (Easterling et al. 2000, Huber and Gullede 2011, IPCC 2013, Stott 2016), which can have major implications on wildlife when they are unable to adjust to the rapid onset of such events (Moreno and Møller 2011, Ummenhofer and Meehl 2017). Many birds have a narrow physiological threshold for such changes (Brenner 1965, West 1965) and face depleted food resources during cold seasons (Williams 1961, Graber and Graber 1979), hence their fall migratory behavior to warmer climates for the non-breeding season (Somveille et al. 2015). Additionally, there are many accounts of nest failure associated with sudden onset of cold temperatures during the breeding season (O'Connor and Morgan 1982, Neal et al. 1993, Ouyang et al. 2012, Winkler et al. 2013). Many factors may influence whether nestlings survive such events.

Age is important as it relates to size, as well as feather growth, particularly in altricial species, which typically hatch with little to no feathers and are unable to thermoregulate independently in the days immediately after hatching (Dawson and Evans 1957, 1960, Ricklefs and Hainsworth 1968, McNabb 2006). As a result, the parents will typically brood them during this period (Sanz and Tinbergen 1999). However, there may be a sensitive period for nestlings, when they are too large to be brooded, but have insufficient feather growth and mass to fully thermoregulate during times of extremely cold temperatures. This has been seen in a population of tree swallows (*Tachycineta bicolor*) in British Columbia, Canada, where nestlings 12 days old or younger, but older than 6 days of age, experienced the greatest rates of nest failure during a cold snap that took place during the breeding season (Griebel and Dawson 2019).

Brood size may also affect the thermal environment of the nest, through huddling behavior, with more nestlings resulting in greater warmth (Mertens 1969, Chaplin et al. 2002), and can also affect the age at which nestlings reach homeothermy (Clark 1982). Conversely,



there may be a trade-off between brood size and size of individual nestlings, such that larger broods result in great competition among siblings resulting in smaller individuals, which may have lower thermal capabilities compared to nestlings in smaller broods of the same age (Neuenschwander et al. 2003).

Aspects of nest construction may also insulate nestlings when cold weather strikes. Nest size, as well as presence of nesting materials, have been shown to explain levels of nest insulation in a variety of species (Deeming et al. 2020) and is associated with successful fledging of offspring (Lombardo 1994). A lab study testing the thermal properties of tree swallow nests found that the rate at which nests cool down is negatively related to the size of the nest, as well as the amount of feathers lining the nest (Windsor et al. 2013). One study, which experimentally manipulated nest box temperature, found that an increase in temperature by 5 C degrees resulted in significantly increased growth rate (mass and feather length), and overall greater nestling size and survival (Dawson et al. 2005).

When nests fail, renesting attempts are not uncommon (Thompson et al. 2001), however, not all individuals will attempt a second clutch, and of those that do, not all will be successful. For birds that are able to manage to successfully fledge offspring during stressful breeding seasons, what intrinsic factors facilitate this? We know that physiology is an important mediator when responding to acute stressors, including changes in temperature. Storms can impact corticosterone levels in birds, with lower temperatures associated with higher baseline and higher stress induced corticosterone levels (Romero et al. 2000, Crino et al. 2020). The impacts to corticosterone appear to be mediated in part by quality, with individuals that have greater fat deposits exhibiting less pronounced stress-induced corticosterone responses (Romero et al. 2000, Breuner and Hahn 2003). Sex can also play a role, as seen in song sparrows, where males, but not females, experience a rise in corticosterone in response to storms (Wingfield 1985). Changes

in stress hormone levels are often associated with behavioral response. White crowned sparrows that exhibit higher corticosterone responses during inclement weather, take longer to resume activity at the breeding site (Breuner and Hahn 2003).

In this study we assessed the effects of an unprecedented cold snap on a population of tree swallows, at the height of the breeding season. This extreme weather event occurred while we were conducting a field experiment testing the effects of anthropogenic noise on nest site selection. This allowed us to examine whether the negative effects of noise on tree swallows (Injaian et al. 2018a, 2018c, 2018b, 2019, Chapter 1) are exacerbated when faced with an additional unexpected environmental stressor. We also assessed whether nest characteristics, nestling and clutch traits, as well as parental attributes, influenced rates of nest failure, reproductive recovery, and overall reproductive success.

A number of nest characteristics may buffer the impacts of an extreme weather event. We looked at the impact of the relative position of the nest box within the population. Tree swallows have been shown to preferentially settle in cavities more central in the population before choosing cavities at the edge of the habitat (Rendell and Robertson 1990), which may indicate an aspect of quality of the nest boxes. We also expected there to be an advantage to occupying a box that was positioned closer to Putah Creek, a source of aerial insect emergence for our population. Additionally, we evaluated the potential insulative benefit of feathers present in the nest. Tree swallows line their nests with feathers, which may affect the thermal characteristics within the nest boxes (Windsor et al. 2013), and provide an advantage during times of inclement weather (Winkler 1993).

For adults, we focused on how body condition and plumage characteristics explained rates of nest failure, cessation of breeding, as well as renesting attempts. Various plumage attributes in tree swallows have been shown to be associated with behavior, physiological state,

as well as overall reproductive success. One study on a population of tree swallows in Ithaca, New York found that female breast brightness is positively associated with stress induced corticosterone levels and nest success, whereas mantle saturation is associated with lower baseline corticosterone and nest success (measured as at least 1 egg hatching) (Taff et al. 2019b). Mantle saturation for both male and female tree swallows also explains visit rates during provisioning (Dakin et al. 2016). Given this, we expected that individuals with higher body condition, brighter breast feathers, and more saturated mantle feathers would have lower rates of nest failure and rebound sooner following the storm.

## **METHODS**

We experimentally exposed 60 nest boxes to playbacks of traffic noise during the 2019 breeding season, as described in detail in Chapter 2. In brief, playbacks ran daily from 0700 to 1300, beginning in February (46 boxes), prior to territory establishment and nest box selection, and continued through the end of June. In March we added an additional 14 boxes to the field site to increase our sample size to a total of 60 boxes. All boxes were ultimately settled by either tree swallows (n=51) or Western bluebirds (n=9).

Birds began building nests in late March and egg laying began in early April. Nest boxes were checked daily starting April 1<sup>st</sup> to document egg laying date, clutch size and hatch date. We also documented the number of feathers lining the nest cup. On May 19<sup>th</sup> there was a storm accompanied by an extreme cold snap, where the daily minimum temperature dropped to approximately 6.7°C and the daily maximum temperature dropped to 15°C (See Supplemental Figure 3.1 for daily minimum and maximum temperatures for the month of May). The storm resulted in a high number of nest failures, the majority of which were observed the day after the cold snap. Deceased nestlings were removed from nest boxes and buried as per California Fish &

Wildlife protocol. We continued checking nestboxes daily to identify renesting attempts. If we observed initiation of a new clutch, we attempted to catch the female during incubation to determine whether it was the same female from the prior clutch, or a new individual. If it was the same female, we weighed her and then released her. Any new individuals were fully processed (measured, tagged, etc.) as described below.

### **Processing of Adults and Nestlings**

Adults were caught in the nest box by waiting for the bird to fly into the box and pulling a string attached to a wooden flap to cover the box entrance. Birds were then removed by hand. Females were caught during incubation (2-4 days after clutch completion). We caught males, and females a second time, during the provisioning period. Nestlings were measured and weighed on days 4, 8 and 12 post-hatch and banded on day 10.

We collected mass, wing chord, tarsus length (only on day 12 for nestlings) and tail measurements for all birds. Adults were color marked on their undertail coverts with a non-toxic paint so that individuals could be identified from a distance. Unbanded birds were issued a standard USGS aluminum band (upon first capture for adults, and on day 10 post-hatch for nestlings). We collected blood samples from adults during the provisioning period and from nestlings on day 12 post-hatch. We also collected contour feathers (3-5 from each body location) from the breast and mantle of adults. Feathers were placed in a plastic Ziploc bag and stored at room temperature until processing for plumage color characteristics, as outlined in Chapter 2.

### **Statistical Analyses**

For all analyses described below, we used the function *dredge* in the R statistical package MuMIn to build a set of candidate models that varied by the presence of all possible

combinations of our fixed effects, unless otherwise indicated. We used Akaike information criterion corrected for small sample size (AICc) and model weight to compare candidate models (Hurvich and Tsai 1989, Burnham and Anderson 2001). Models with  $\Delta\text{AICc}$  value less than 2, and fixed effects with 95% confidence intervals that did not overlap zero, were considered to have high support. Coefficients and confidence intervals are reported for models with highest support.

We ran a generalized linear model on nests that had nestlings present during the time of the storm to determine what factors influenced whether a nest failed after the storm. Fledge success was treated as a binomial response variable, where a value of 0 indicated all nestlings perished, and a value of 1 indicated at least one nestling successfully fledged. We included the following fixed effects: dBA (magnitude of noise experienced), nestling age at time of storm, the quadric effect of nestling age at time of storm, brood size, female body condition (residual mass/tarsus length), relative numbers of feathers lining the nest cup, Timing (whether the box was put out in February or March), Row (relative distance from Putah Creek), and relative distance from the edge of the nest box grid. Timing was included in all models. We were not able to collect feather samples from all adults, so we completed a second analysis on a subset of the data for which we did have feather data. We included any significant fixed effects from the original analysis, and our candidate model set varied by the following fixed effects: male body condition, male and female breast brightness (B2), and male and female mantle saturation (m.r.achieved). In female tree swallows, mantle saturation is negatively correlated with baseline corticosterone levels, and breast brightness is positively correlated with stress-induced corticosterone, as well as the amount of social interactions an individual engages in (Taff et al. 2019b). Furthermore, mantle saturation is associated with increased rates of provisioning (Dakin et al. 2016).

We also ran a generalized linear model with a binomial response variable on adult fate after the storm (0 = adult went missing and was not seen for remainder of the breeding season, 1 = adult was confirmed to still be breeding after the storm). We included the fixed effects of dBA, Age (SY = second year female, ASY = after second year female, M = unknown for males), and adult body condition (bci). We also included the following interactions: dBA:Age, bci:Age, dBA:bci.

For pairs that renested after experiencing nest failure as a result of the storm, we ran a linear model to test for effects on clutch initiation date of the renesting attempt. As our response variable, we used the julian date of when the first egg in the new clutch was laid. Candidate models varied by the fixed effects of female age, female body condition, male body condition, dBA, male and female breast brightness, and male and female mantle saturation. We also included the interactions of female age and female body condition, and male and female body condition. We included the categorical variable of Pair to account for whether both parents were the original individuals from the first clutch or a partial pair, where one individual was the original settler and the other individual was a new mate. Additionally, we included whether it was the first or second clutch for the female. First clutches for females would only be observed in partial pairs with a new female and the original male, therefore we included the interaction of Pair and Clutch to account for this.

For nests that did not experience full nest failure, we ran a linear model on time to fledge (i.e. number of days from hatch date to fledging date). Hatch date was considered the first date any nestlings were observed in the nest box and fledge date was the first date when no nestlings were found in the box. Candidate models of time to fledge included the fixed effects of dBA, clutch initiation date, number of fledglings, male and female body condition, Row, Timing, and Edge. We used number of fledglings rather than brood size, because many nests experiences

brood reduction after the storm. Number of fledglings was considered the number of nestlings present in the nest when we measured them at day 12. If any nestlings were found dead in the nest after day 12, we subtracted them to get our final count of number of fledglings.

Lastly, we ran several model comparisons to assess effects on nestling mass. We first ran a linear mixed effects model on nestling mass for all nestlings that lived through and survived the cold snap. We included nest box and nestling ID as random effects. Fixed effects included dBA, age, the quadratic effect of age, clutch initiation date, the quadratic effect of clutch initiation date, as well as Edge, Row and Timing. We also included the interactions of dBA and age, and clutch initiation date and age. Timing was not significant and therefore was ultimately removed from the candidate models to improve model fit. All candidate models included age, quadratic effect of age, clutch initiation date, edge and row, since we had a priori reasons to expect they would have an effect. Candidate models varied by the presence of the other fixed effects (dBA, quadratic effect of clutch initiation date, and all interactions). We then ran this same analysis on nestlings that hatched after the storm. Edge, Timing and Row were not significant, and therefore were removed for the final candidate model comparison.

## **RESULTS**

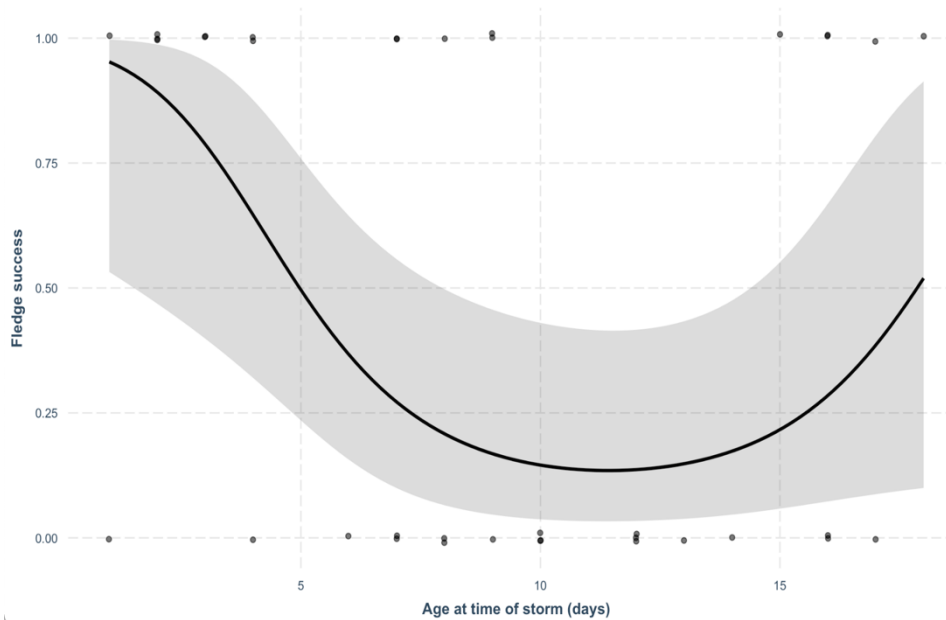
Prior to the cold snap, two nests had experienced complete nest failure, in which all offspring died or disappeared before fledging (one during incubation and one during provisioning). At the time of the cold snap there were 45 active tree swallow nests (1 egg laying, 7 incubating, 37 with nestlings). Complete failure was observed in 51.4% of nests with nestlings ( $n = 19$ ) and 43.9% of nests incubating ( $n=3$ ). The one nest in which the female was in the midst of egg laying at the time of the cold snap ultimately hatched and successfully fledged 2 nestlings. All of the pairs with nests that failed during incubation renested. Approximately 58% of boxes in

which clutches failed during the nestling stage (n=11) were re-nested by the original pair, and 21% (n=4) were re-nested by one of the original adults, paired with a new partner. Of the 18 nesting pairs with nestlings that did not experience full nest failure, 37.8% (n = 14) experienced brood reduction (i.e. at least one nestling died as a result of the cold snap), and 38.9% attempted a second clutch once the nestlings from their first breeding attempt had fledged.

The only variable to strongly predict nest failure versus success (failure = all nestlings perished, success = at least one nestling fledged) from the cold snap was the quadratic effect of nestling age (Figure 3.1, Tables 3.1 and 3.2). Very young nestlings and older nestlings were much more likely to survive than nestlings that were approximately 10 days old. Noise amplitude did not affect the likelihood of nest failure. Brood size was present in the top model, but confidence intervals overlapped zero and it was absent in the second ranked model (Table 3.1 and Table 3.2), suggesting a weak effect. Timing (i.e. whether the boxes were put out in February or March) was included in all models, and had confidence intervals that did not overlap zero in the top model, indicating boxes that were put out in March were slightly less likely to experience failure than boxes that were put out in February (Table 3.2). Noise amplitude, female body condition, and relative amount of feathers lining the nest were all absent from top models.



**Figure 3.1.** Effect of age of nestlings at time of cold snap on fledge success. Fledge success is a binary response variable, with a value of 1 indicating at least one nestling survived to fledging, and a value of 0 indicating nest failure, with zero nestlings surviving. Line and confidence intervals calculated from predicted values of top model of fledge success. Points represent raw data, slightly offset from 0 and 1 to show observations with the same values.



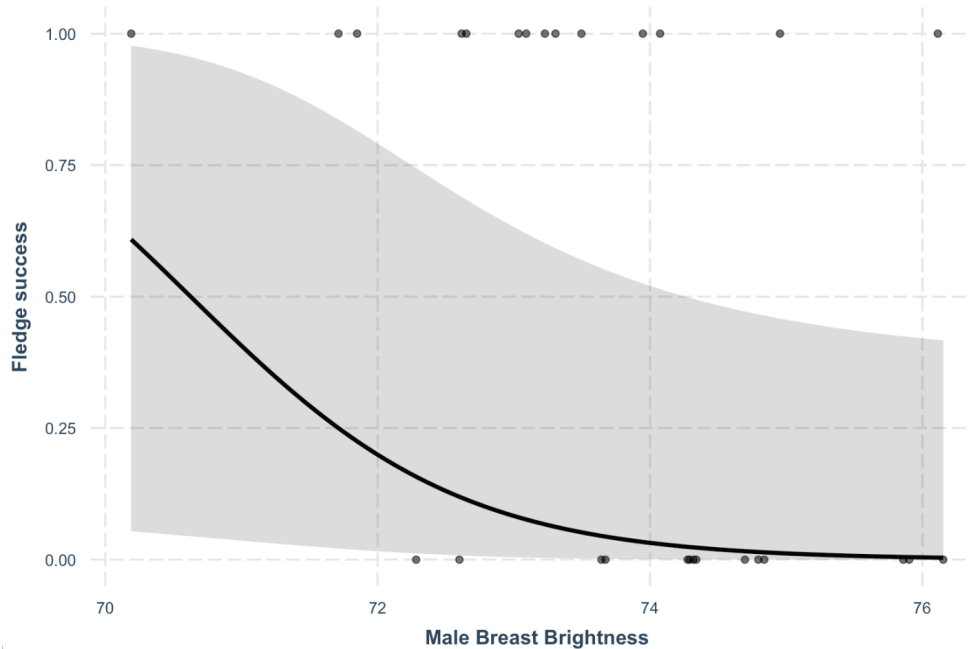
**Table 3.1.** Candidate models with greatest support ( $\Delta AICc < 2$ ) for nest failure and adult fate as a result of the storm. Analysis of nest failure post-storm (subset) is completed on nests for which we had data on plumage characteristics. Timing is included in all models of nest failure, but not listed for brevity. Full list of candidate models with  $w_i > 0.009$  can be found in Supplemental Tables 1-4.

Model	k	AICc	$\Delta AICc$	$w_i$
<i>Nest failure post-storm</i>				
Fledge_Success ~ Age_Storm + I(Age_Storm^2) + Brood_Size	5	49.4	0	0.168
Fledge_Success ~ Age_Storm + I(Age_Storm^2)	4	50	0.52	0.129
<i>Nest failure post-storm (subset)</i>				
Fledge_Success ~ Age_Storm + I(Age_Storm^2) + B2_M	5	32.7	0	0.306
Fledge_Success ~ Age_Storm + I(Age_Storm^2) + B2_F + B2_M	6	34.1	1.4	0.152
<i>Adult fate post-storm</i>				
adultfate ~ Age + bci * dBA	6	70.4	0	0.208
adultfate ~ Age + bci	4	70.4	0.05	0.203
adultfate ~ Age	3	72.1	1.72	0.088
adultfate ~ bci	2	72.1	1.75	0.087
<i>Clutch initiation date</i>				
Clutch_Initiation ~ B2_F + bci_M	4	97.3	0	0.093
Clutch_Initiation ~ B2_F	3	97.7	0.34	0.079
Clutch_Initiation ~ 1	2	98.6	1.22	0.051

**Table 3.2.**  $\beta$  estimate and 95% confidence intervals for fixed effects in top models of fledge success, fledge success on a subset of the data (nests for which we had data on adult plumage characteristics), and adult fate (whether they continued to breed or went missing after the storm). Italics indicated fixed effects with confidence intervals that overlapped zero, and are not considered to strongly explain response variable.

<b>Response Variable</b>	<b>Fixed Effect</b>	<b><math>\beta</math> estimate</b>	<b>95% CI</b>
Nest failure post-storm	<i>(Intercept)</i>	-1.467	-8.05,4.869
	Age_Storm	-1.022	-1.979,-0.309
	I(Age_Storm^2)	0.045	0.01,0.089
	<i>Brood_Size</i>	<i>0.997</i>	<i>-0.086,2.366</i>
	Timinglate	2.312	0.221,4.908
Nest failure post-storm (subset)	(Intercept)	95.45	23.402,209.075
	B2_M	-1.012	-2.294,-0.158
	Age_Storm	-4.192	-9.788,-0.822
	I(Age_Storm^2)	0.178	0.035,0.414
	Timinglate	3.065	0.081,7.807
Adult fate post-storm	(Intercept)	4.475	-0.564,9.944
	AgeSY	-2.66	-4.81,-0.733
	<i>AgeMale</i>	<i>-0.837</i>	<i>-2.501,0.703</i>
	bci	-57.761	-113.67,-9.92
	<i>dBA</i>	<i>-0.034</i>	<i>-0.139,0.072</i>
	bci:dBA	1.104	0.083,2.307
Clutch initiation date	(Intercept)	18120.683	18065.419,18175.947
	B2_F	-0.996	-1.763,-0.23
	<i>bci_M</i>	<i>-38.564</i>	<i>-81.491,4.362</i>

**Figure 3.2.** Nests raised by males with brighter white breast feathers had a higher likelihood of nest failure (i.e. fledge success = 0) from the cold snap than males with less bright breast feathers. Y-axis represents fledge success with 1 = at least one nestling fledged, and 0 = complete nestling mortality. Line and confidence intervals calculated from predicted values of top model of fledge success using a subset of the data for which we had adult plumage measures. Points represent raw data.



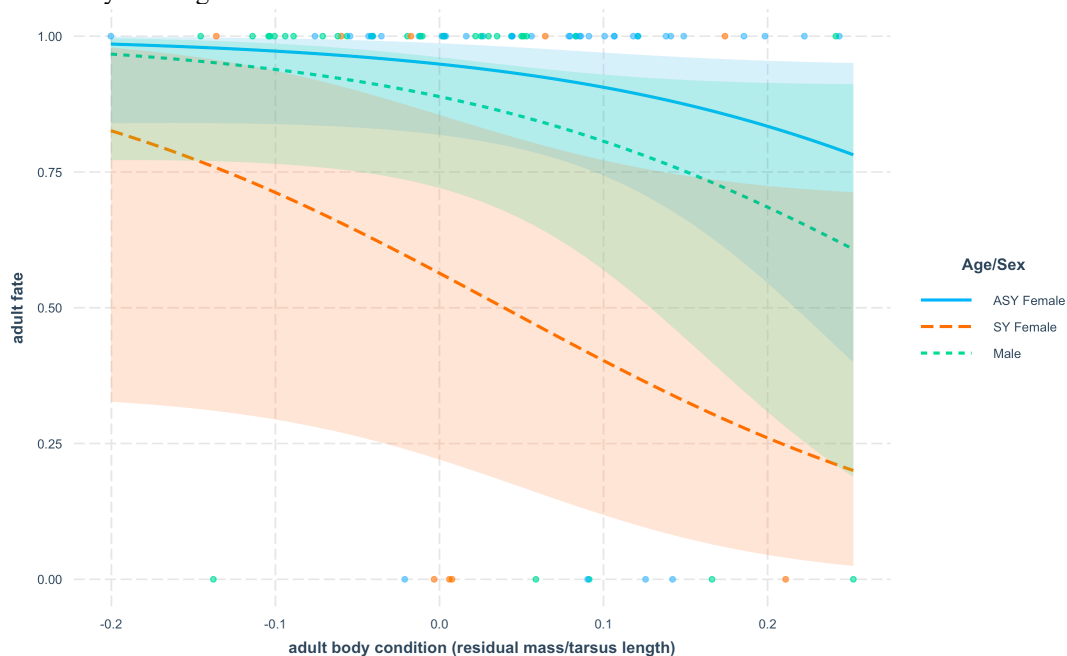
Our analysis that looked at a subset of nests for which we had plumage samples from both parents found an effect of male breast feather brightness on fledge success, with brighter males experiencing higher rates of nest failure (Figure 3.2, Tables 3.1 & 3.2). Female breast brightness was present in the second highest ranked model, but confidence intervals overlapped zero. Male body condition and male and female mantle feather saturation were not present in any of the top models.

Of the 19 pairs with nestlings at the time of the cold snap, 4 did not renest and 4 renested with a new partner, and in all cases the old partner was not seen again. Adult age and body condition explained whether an adult went missing after the cold snap (Figure 3.3, Tables 3.1 & 3.2). Second year (SY) females were more likely to go missing than after-second-year (ASY) females or males (U), as were individuals with higher body condition. We also found evidence of an interaction between noise amplitude and body condition, which was seen in the top model of

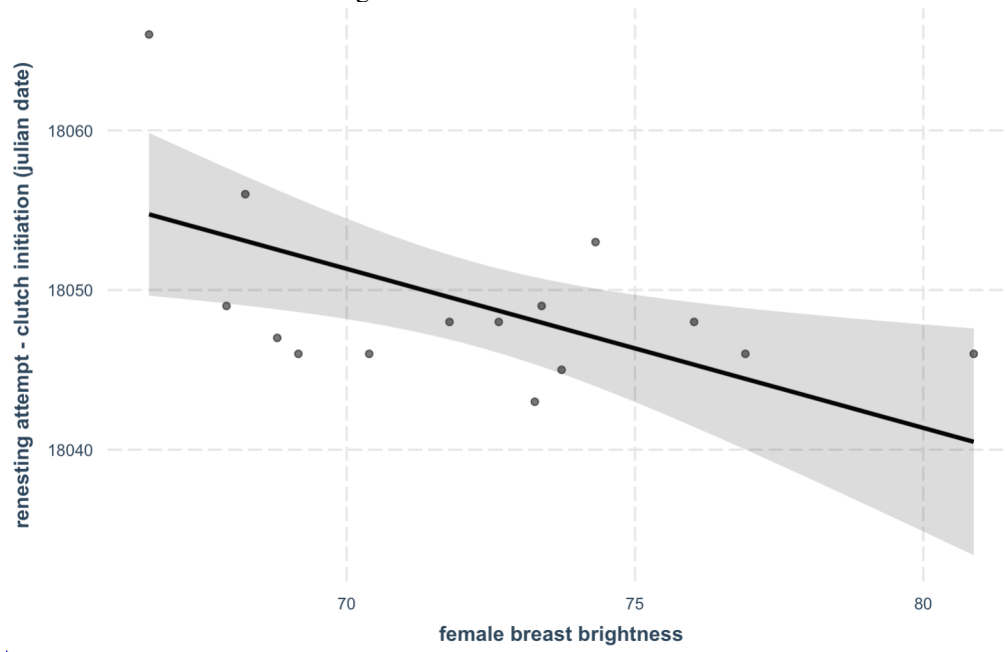
adult fate, with higher body condition being associated with disappearance for adults that settled in quiet boxes. However, the second ranked model had support nearly equal to the top model and did not include dBA, in an interaction or otherwise.

Analyses looking at renesting attempts after storm-induced nest failure found that females with brighter breast feathers initiated egg laying sooner than other females (Figure 3.4, Tables 3.1 & 3.2). We found no effect of dBA, male or female mantle saturation, female age or body condition, or whether the pair consisted of the original partners or had a new partner. Male body condition was present in the top model, but confidence intervals overlapped zero (Tables 3.1 & 3.2).

**Figure 3.3.** Second year females (orange dashed) are more likely to go missing after the storm than ASY females (blue solid) or males (green dotted), and individual body condition (residual mass/tarsus length) is also associated with adult fate post cold snap. Line and confidence intervals calculated from predicted values of top model of adult fate (1 = continued breeding after cold snap, 0 = not observed again after cold snap). Points represent raw data colored by adult age and/or sex.

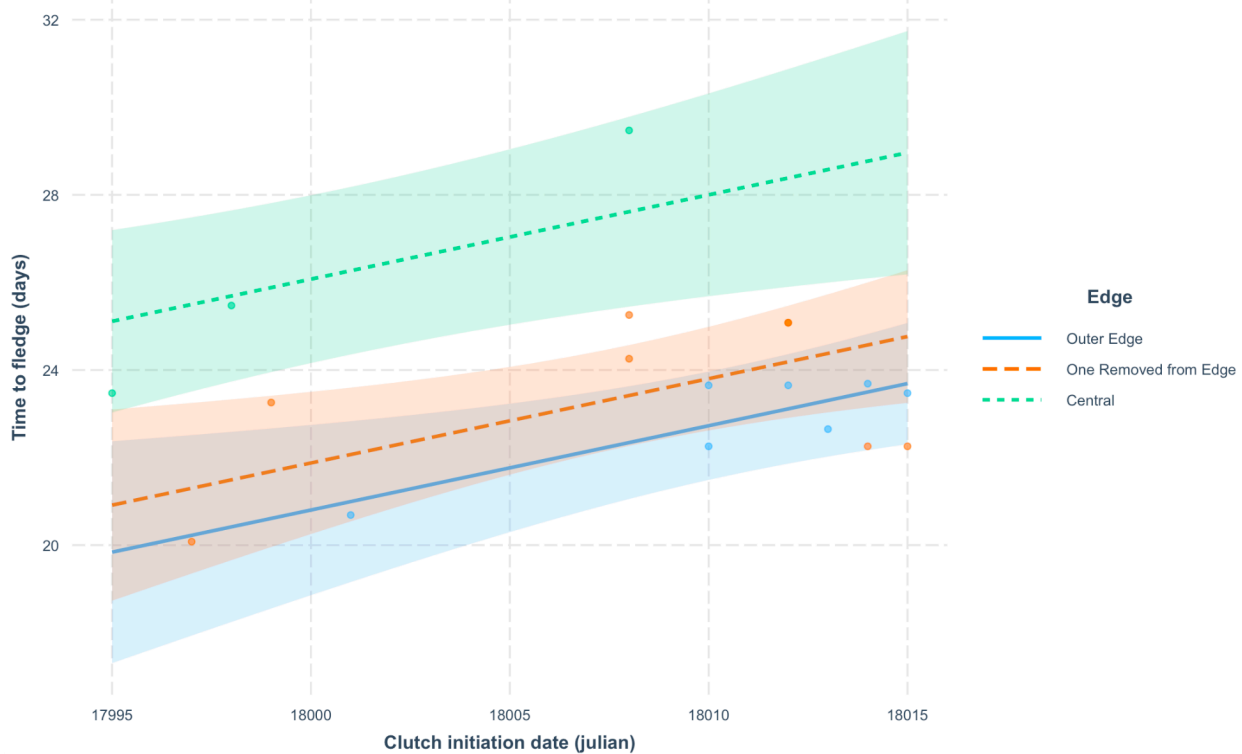


**Figure 3.4.** Partial residual plot, with 95% confidence intervals, of clutch initiation date of nesting attempts that took place after the cold snap by female breast brightness. Females with brighter breast feathers initiated new clutches sooner than females with less bright breast feathers.



For nests with nestlings that did not experience full failure as a result of the storm, we found that clutch initiation date significantly affected time to fledging (Figure 3.5, Tables 3.3 & 3.4). Clutches that were initiated late April/early May, and had recently hatched at the time of the cold snap, took longer to fledge than clutches that were initiated earlier in April, and were therefore older at the time of the cold snap. Nests took approximately 1 additional day to fledge for every 5 days later into the season a clutch was initiated. We also saw a strong effect of Edge (nests more central in the grid of nestboxes took longer to fledge than nests closer to the edge) and Row (nests closer to the creek took less time to fledge than nests farther from the creek) (Figure 3.5 & Supplemental Figure 3.2, Tables 3.3 and 3.4). We did not see an effect of noise amplitude (dBA), number of fledglings, or body condition of either parent on time to fledge.

**Figure 3.5.** Partial residual plot of predicted values, with 95% confidence intervals, from top model of days to fledge by clutch initiation date. Nests initiated later in the season (i.e. more recently before storm) take longer to fledge. Nests positioned more central in the population (green dotted line) take longer to fledge than nests on the outer edge (blue solid line) or nests one box removed from the outer edge (orange dashed line). Points colored by relative position to edge. For reference, Julian date for the cold snap was 18035.

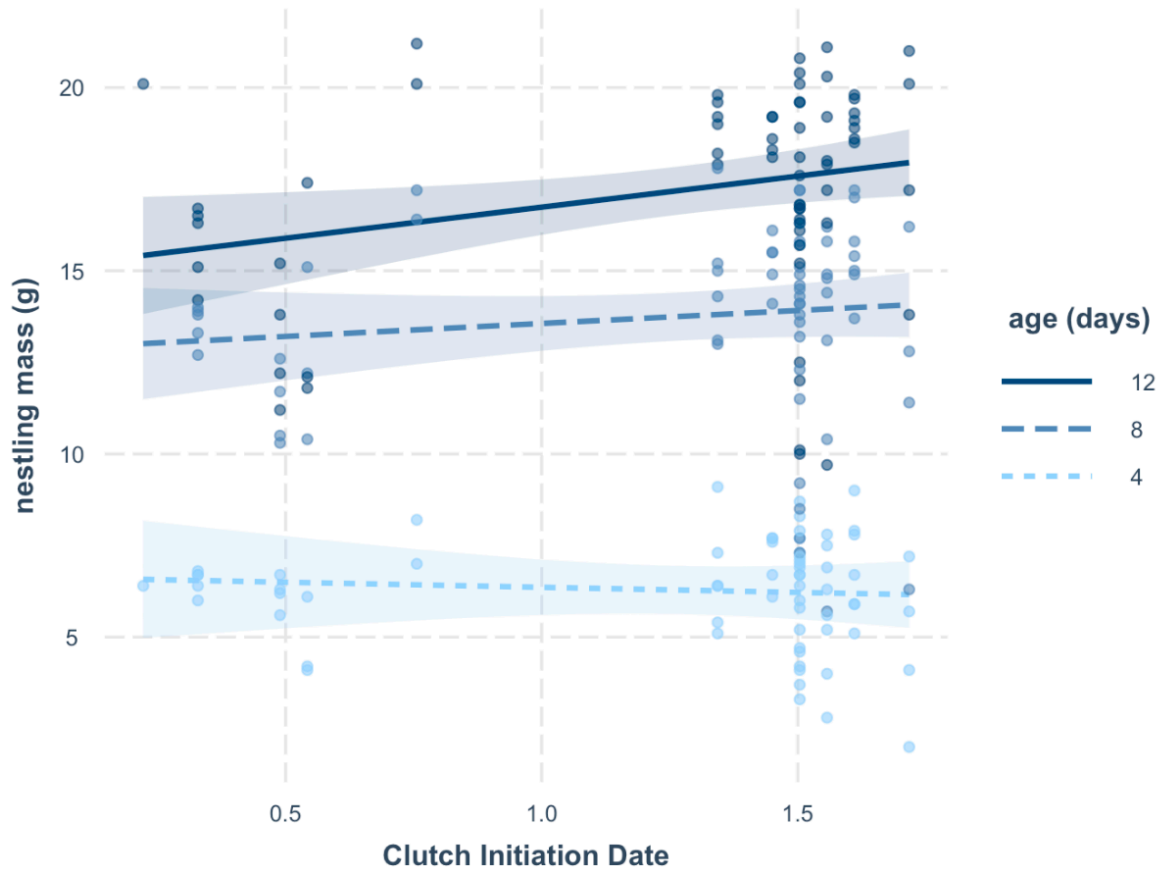


When we took a subset of the data to look at nestlings that survived the cold snap we found there was a negative effect of dBA on nestling mass (Table 3.3 & 3.4, Supplemental Figure 3.3). The top model of nestling mass also included the quadratic effect of clutch initiation date, such that nestlings whose clutches were initiated closer to the time of the cold snap had lower masses at all ages than nestlings whose clutches were initiated earlier in the season (Supplemental Figure 3.4). Edge and Row both had confidence intervals that did not overlap zero in the top model, indicating that nestling mass significantly varied across those variables (Tables 3.3 & 3.4). Nestling mass decreased with Row, meaning that nestlings that were raised closer to the creek were larger than nestlings that were raised further from the creek (Supplemental Figure 3.5). Additionally, nestlings raised in boxes furthest from the Edge of the grid of nest boxes were the smallest, and nestlings on the outermost Edge were the largest (Supplemental Figure 3.5).

An effect of dBA on nestling mass was not observed when looking at just the nestlings that hatched after the cold snap (Table 3.3). However, we did find a significant interaction between age and clutch initiation date (Tables 3.3 & 3.4). Four-day old and 8-day old nestlings did not significantly differ in size across clutch initiation dates, but for 12-day old nestlings, nests that were initiated later in the season had significantly larger nestling masses than those that were initiated sooner after the storm (Figure 3.6). This was likely driven by negative effects of the storm on nestling development in nests where females were incubating. When we look only at nestlings with lay dates after the storm, rather than hatch date after the storm, the interaction effect of age and clutch initiation date on mass dropped out of the top model (Table 3.3).

We also saw an effect of adult pair type on nestling mass. Pairs that consisted of both the original male and female had nestlings of lower quality than pairs that consisted of one original individual mated with a new partner. However, this effect appeared to be driven by one particularly large nestling who had no siblings. When we removed that individual from the analysis there was no longer a significant difference in nestling size for original vs. partial pairs (Table 3.3). We did not see a difference in nestling mass between first and second clutches, however our sample size for the number of first clutches laid after the storm was low. There was no effect of Edge, Timing, or Row on nestling mass for nestlings that hatched after the storm.

**Figure 3.6.** For nestlings that hatched after the cold snap, clutch initiation date (scaled and centered) explains nestling mass at day 12 of age (solid line), such that nestlings experiencing incubation at the time of the cold snap had smaller mass at day 12 than nestlings whose clutches were not initiated until after the cold snap. Line and confidence intervals calculated from predicted values of top model of nestling mass. Points represent raw data, colored by age.



## DISCUSSION

We found a strong effect of age at the time of the cold snap on nest success, with the youngest and oldest nestlings faring better than mid-age nestlings. This is as we expected, as very young tree swallow nestlings still receive the benefit of brooding by the female, but mid-development nestlings are too large to be fully brooded, but cannot independently thermoregulate until after 9 days of age (Dunn 1978, Marsh 1980). This corroborates what was found in other populations of tree swallows, that experienced high nestling mortality from a cold snap (Winkler et al. 2013, Griebel and Dawson 2019).



We also saw an effect of plumage brightness of breast feathers on nest fate, such that males with bright white breast feathers were more likely to have a nest that failed, rather than fledged offspring. This is contrary to what we expected, as previous studies of tree swallows found that males with brighter white breast plumage sire more within-pair offspring, and therefore are potentially higher quality (Whittingham and Dunn 2016). However, there is evidence that in female tree swallows, breast brightness is associated with higher levels of stress induced corticosterone (Taff et al. 2019b). If this relationship is also present in males, this may lend support for what has been found in other studies of great tits, where males, but not females, with higher stress induced corticosterone are more likely to abandon their nests, compared to males with lower stress-induced corticosterone, who are more likely to renest (Ouyang et al. 2012). Experimental studies have found similar results regarding abandonment and stress-induced corticosterone in pied flycatchers (Silverin 1986). It may be that such physiological responses function to divert energy away from reproduction when it is too costly (Wingfield 1988, Astheimer et al. 1995). Additionally, previous study found that males who exhibit high provisioning of offspring and have a female partner subjected to experimentally elevated corticosterone levels experience higher rates of brood loss than males whose partner receives a placebo treatment (Ouyang et al. 2015). This suggests there are some interesting dynamics between male and female tree swallows under stressful circumstances that warrant further investigation.

Given how sudden nest failure was observed, we believe direct effects, by the sudden drop in temperature, on nestlings is the strongest explanation for nestling mortality (McCarty 1995, McCarty and Winkler 1999). However, impacts to food availability might also have been a factor. This is particularly relevant for aerial insectivores, as poor weather is often associated with declines in insect abundance (Avery and Krebs 1984, Veistola et al. 1997). Even brief lulls

in insect abundance can have major repercussions on altricial species, as nestlings often experience extremely rapid development and therefore high caloric requirements (Ricklefs 1969). This can have not just short-term impacts to growth, but also long-term repercussions later in life. The nutritional stress hypothesis posits that adult quality is driven, in part, by conditions of the early developmental period, such that individuals who experience food deprivation at an early age suffer impacts to brain development, with effects into adulthood on various behaviors (Nowicki et al. 1998). For example, in an experiment done on swamp sparrows (*Melospiza georgiana*), experimental nestlings that were fed 30% less than control nestlings had notably slower growth rates, smaller brain volume as adults, and poorer quality of learned songs (Nowicki et al. 2002), an important indicator of male quality in many passerines (Nowicki and Searcy 2004). In another study, zebra finches (*Taeniopygia guttata*) that were raised under high versus low food conditions exhibited differences in spatial learning and memory (Kriengwatana et al. 2015). Future work on parental provisioning as it relates to nutritional stress during times of inclement weather may help elucidate these indirect effects on nest failure.

A previous study found that temperature had a positive direct effect on nestling growth in tree swallows, but also resulted in indirect effects to growth by increasing the number of insects available (McCarty and Winkler 1999). Additionally, they observed that insect availability mattered more for older nestlings than for younger nestlings, perhaps due to the difference in caloric needs. However, it is important to note that in our study we observed an increase in the time to fledge in nestlings that were younger at the time of the storm. This may indicate older nestlings were far enough along in their development at the time of the storm to be able to fledge relatively “on time”, despite any impacts the cold snap might have had on food availability. Another possibility is that, due to their smaller size and lower thermoregulatory capabilities,

younger nestlings were less able to engage in begging behavior in the days following the storm than older nestlings, which may have reduced provisioning by parents and therefore stunted growth. Indeed, an experiment subjecting tree swallow nestlings to food deprivation and cooling of the nest saw a decrease in begging behavior, which was particularly pronounced for smaller nestlings (Leonard and Horn 2001).

We saw no effects of brood size in our analyses, which supports what has been found in other studies. Dunn 1978 found that brood size did not affect tree swallow nestlings' ability to thermoregulate and speculated this was because of their huddling behavior, which is different from other species in that they do not stack on top of one another. Other studies have also reported brood size does not affect growth and/or nestling size in this species (Zach and Mayoh 1982, McCarty and Winkler 1999), and brood size does not seem to provide a benefit in terms of reduced nest failure during times of inclement weather for tree swallows (Ouyang et al. 2015, Griebel and Dawson 2019), or other species (Schöll and Hille 2020).

The relative number of feathers in the nest also did not explain the likelihood of nest failure. While the presence of feathers lining the nest cup has been shown to result in increased insulation in tree swallow nests (Windsor et al. 2013) and is associated with larger nestlings (Stephenson et al. 2009), the temperature drop we observed may have just been too great to overcome. Additionally, insulation from feathers may be more helpful for temperature regulation of eggs during the incubation period, rather than providing a benefit to nestlings. Anecdotally, we also notice that feathers in the nest lose their integrity as nestling age due to trampling and nestling excrement, which would further reduce any thermoregulatory benefit they can provide.

While most adults attempted to reneest after storm-induced nest failure, there were a number of individuals we did not observe attempting to breed again. Second year females were more likely to go missing after the cold snap than ASY females or males. SY females have been

shown to have lower reproductive success than ASY females (De Steven 1978, Leffelaar and Robertson 1985, Robertson and Rendell 2001), and may respond differently to stressors (Grunst et al. 2021, Zimmer et al. 2021). We also saw a potential interaction effect of noise amplitude and adult body condition. The top model of adult fate suggests that higher body condition was associated with a greater likelihood of disappearance, but only for birds that settled in boxes exposed to lower amplitudes. We consider these results inconclusive, because the second highest ranked model of adult fate did not include dBA or the interaction with body condition but had only slightly lower support with a model weight of 0.203 ( $\Delta AICc = 0.05$ ), whereas the top model had a model weight of 0.208 (Table 3.1). However, it is still unclear why individuals of higher body condition would be more likely to abandon breeding than individuals of lower body condition, though we are not the first to observe such results (Hörak et al. 1999).

It is challenging to draw any definitive conclusions regarding the fate of adults that we did not observe breeding again, due to small sample size and because we cannot be certain of the reason for their disappearance. We know some adults died after the storm, as two females (one SY and one ASY) were found in the field the day after the cold snap. But other individuals may have abandoned breeding for the season. One study on great tits found that individuals that abandoned nests after inclement weather, including young breeders, were no less likely to be present in future years (Bordjan and Tome 2014). Alternatively, it is possible individuals abandoned and sought out a different cavity in which to re-nest (Stanback and Rockwell 2003). However, this latter option seems unlikely given we observed 100% nest box occupancy and missing partners were quickly replaced with a new mate. Additionally, we suspect that birds have high cavity type fidelity and might be unlikely to switch from a nest box to a natural cavity (Valera and Václav 2021), which would be their only option as our nest boxes are the only ones present in our study area.

When we looked at factors that affected renesting attempts, we found that females with brighter breast feathers initiated clutches sooner after the cold snap than females with less bright breast feathers. Other studies have found females with brighter breast feathers are less likely to abandon nests when handicapped, exhibit greater levels of handling-induced corticosterone, (Taff et al. 2019b) and have better immune responses (Beck et al. 2015). Our findings, combined with these prior studies, may suggest breast brightness is an honest indicator of quality in female tree swallows.

We did see a negative relationship between mass and noise amplitude for nestlings that survived the storm, which supports what other studies on this population have found (Injaian et al. 2018b, 2018a, 2019, Chapter 1). Interestingly we saw no effect of dBA on nestling mass for nests initiated after the storm. The fact that we do not see an effect of dBA on nestlings later in the season may be associated with the lower nestling mass observed in nests initiated later in the breeding season. It may be that poor environmental conditions later in the season overshadow any negative effect of noise.

For nestlings that hatched after the storm, we observed an effect of clutch initiation date on mass at day 12, with earlier clutch initiation associated with smaller mass; this is the opposite of the typical pattern of declining nestling mass through the season (Bryant 1978, McCarty and Winkler 1999). The results observed in this analysis were likely because nestlings with the earlier clutch dates in this analysis included nestlings that were in incubation during the cold snap, which may have resulted in stunted growth. The interaction effect disappeared when we isolated the analysis to only include clutches that were initiated after the storm. However, if direct impacts of the storm on incubation fully explained this result, we would expect to see a difference at day 4 and 8 as well. Another possibility for this result may have to do with food availability, which may have been limited in the period after the storm but increased as more

time passed. Given the differences in the caloric demands of 4-day old nestlings compared to 12-day old nestlings, it may be that parents were able to get a sufficient amount of food for 4-day old nestlings, even soon after the storm, but as the nestlings got older the parents could not keep up with the demand. Impacts to adult condition from the storm could also explain this effect, if adults suffered a reduction in body mass and were less able to provision young in the period immediately following the cold snap.

Tree swallows have been exhibiting fluctuations in population density throughout North America, and it is thought that climate change may be playing a role (Shutler et al. 2012). This study highlights the need to assess not only impacts from average temperature shifts across large temporal and spatial scales, but also the impacts of short, yet extreme, fluctuations in local weather, which have become more common as the climate warms. In particular, evaluation of how males and females differ in their response to such stressors, mediated by behavior and physiology, may elucidate how population dynamics are altered under these conditions of environmental change.

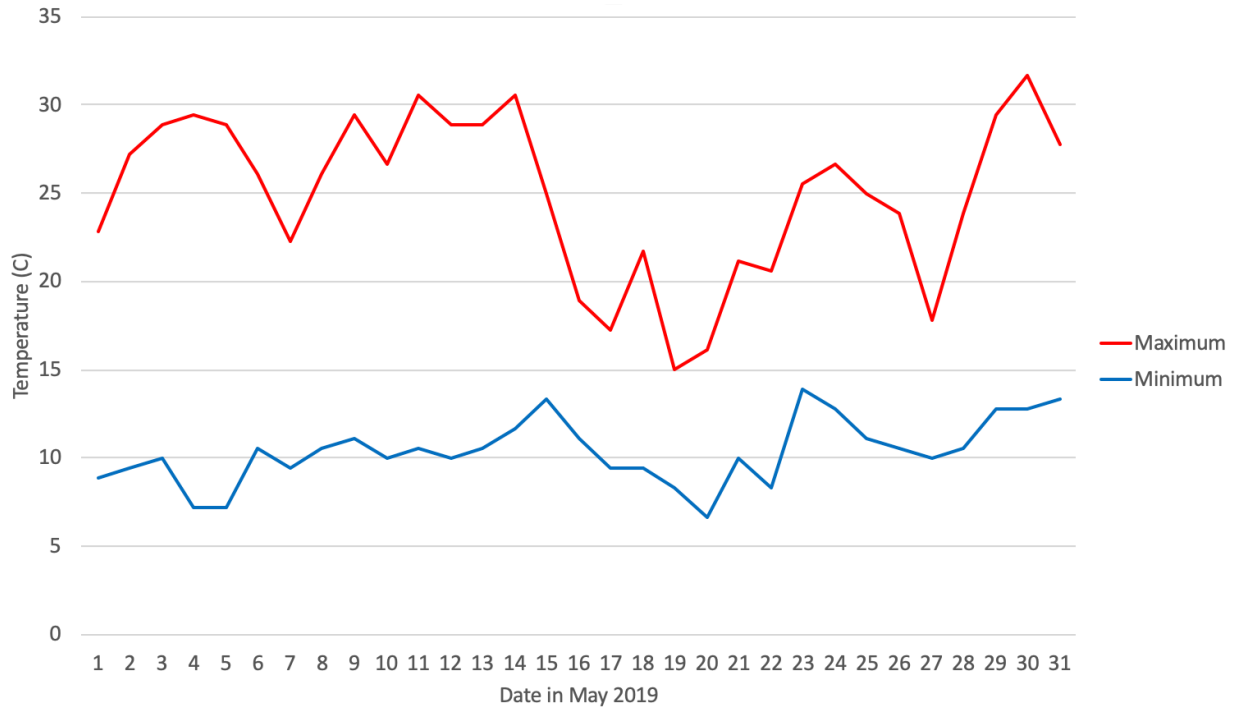
## **ACKNOWLEDGEMENTS**

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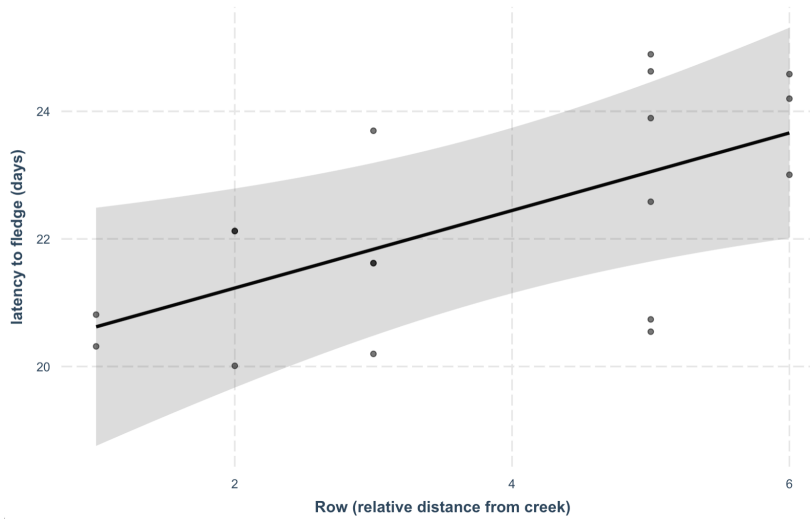
to help collect as much data as possible. Thank you to UC Davis for the use of the Putah Creek Riparian Reserve to conduct this study.

## SUPPLEMENTAL MATERIALS

**Supplemental Figure 3.1.** Daily minimum and maximum temperatures (C) during the month of May 2019 in Davis, CA (38 32 07 N, 121 46 30 W, Elevation: 18.29 m). The peak of the cold snap took place from May 19<sup>th</sup> to May 20<sup>th</sup>. Temperature data was downloaded from <http://atm.ucdavis.edu/weather/uc-davis-weather-climate-station/>.

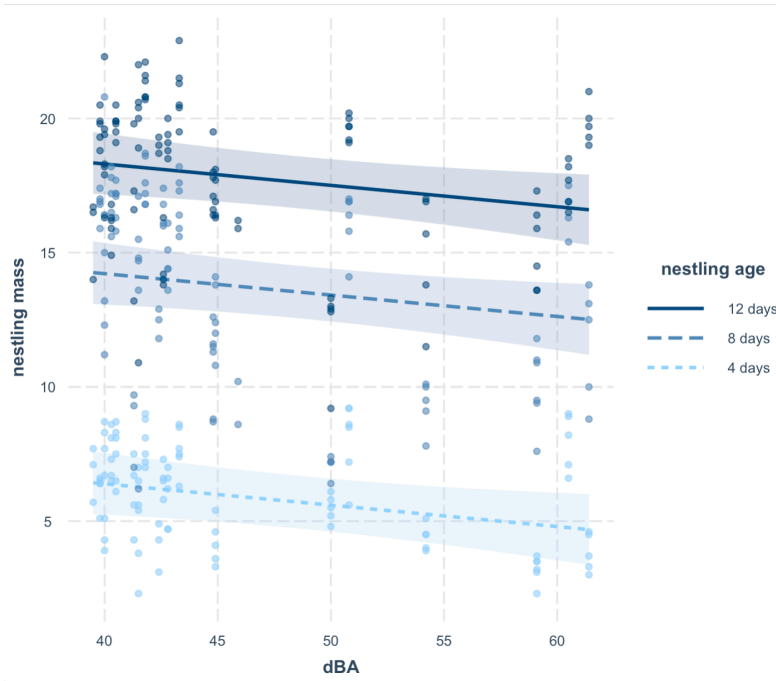


**Supplemental Figure 3.2.** Nests positioned further from Putah Creek took longer to fledge than nests closer to the creek.

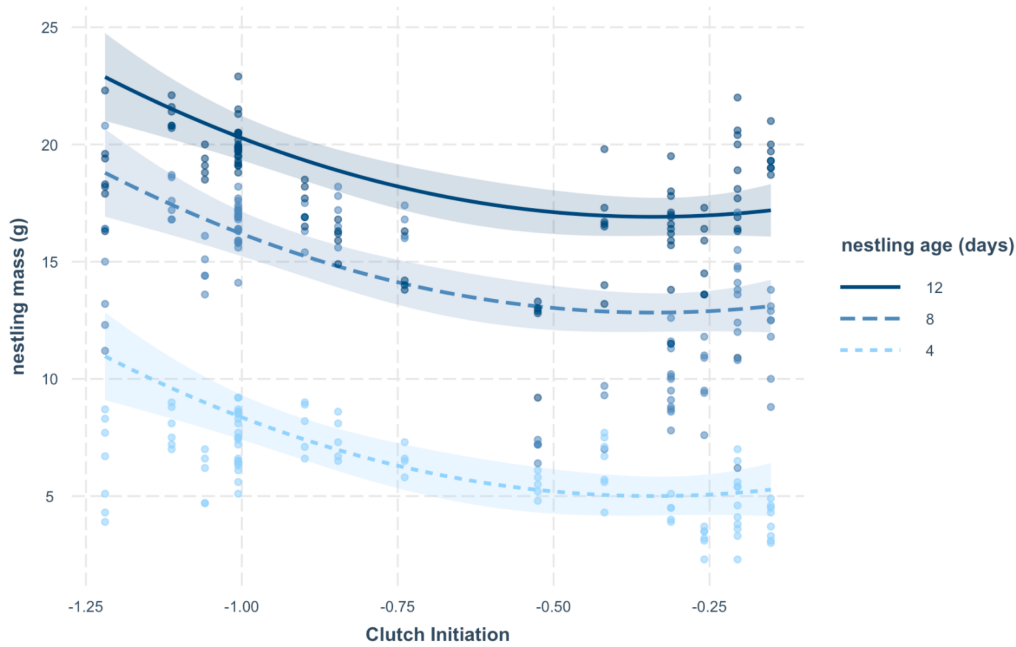




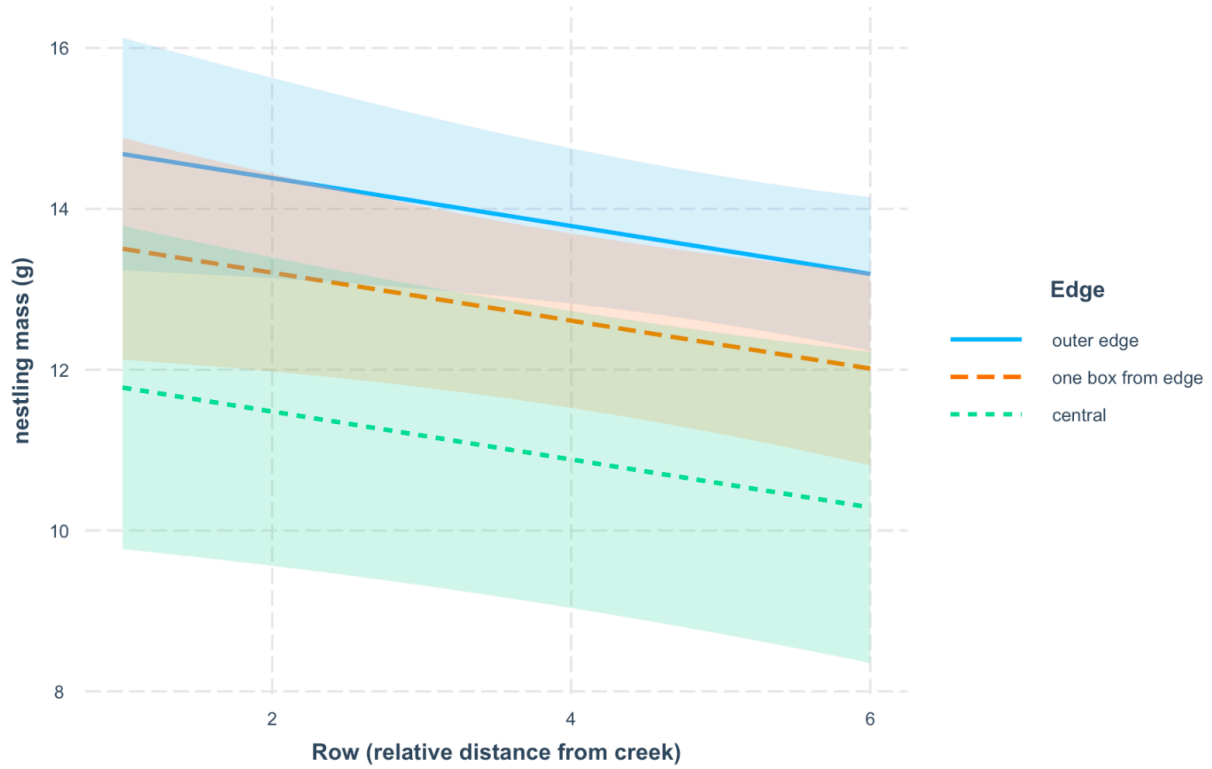
**Supplemental Figure 3.3.** For nestlings that lived through and survived the cold snap, mass is lower for nestlings raised in boxes exposed to higher noise levels for all ages.



**Supplemental Figure 3.4.** For nestlings that lived through the cold snap, nestling mass declines with clutch initiation date, such that nestlings that hatched earlier in the season and were therefore older at the time of the cold snap, had higher mass than nestlings that hatched later in the season and were younger at the time of the cold snap.



**Supplemental Figure 3.5.** Nestlings raised in boxes further from creek and more central in the population have smaller masses than nestlings raised closer to the creek and more on the edge of the population.



**Supplemental Table 3.1.** Candidate models for fledge success of nests that were provisioning at the time of the cold snap. Success considered when 1 or more nestlings fledged and failure considered when zero nestlings fledged. Models with less than 0.01 model weight not listed.

Model	k	AICc	$\Delta$ AICc	w <sub>i</sub>
Fledge_Success ~ Age_Storm + I(Age_Storm^2) + Brood_Size + Timing	5	49.4	0	0.168
Fledge_Success ~ Age_Storm + I(Age_Storm^2) + Timing	4	50	0.52	0.129
Fledge_Success ~ Age_Storm + I(Age_Storm^2) + bci_F + Timing	5	51.9	2.51	0.048
Fledge_Success ~ Age_Storm + I(Age_Storm^2) + bci_F + Brood_Size + Timing	6	52.1	2.68	0.044
Fledge_Success ~ Age_Storm + I(Age_Storm^2) + Brood_Size + dBA + Timing	6	52.3	2.82	0.041
Fledge_Success ~ Age_Storm + I(Age_Storm^2) + Brood_Size + Row + Timing	6	52.3	2.86	0.04
Fledge_Success ~ Age_Storm + I(Age_Storm^2) + Row + Timing	5	52.5	3.02	0.037
Fledge_Success ~ Age_Storm + I(Age_Storm^2) + dBA + Timing	5	52.6	3.13	0.035
Fledge_Success ~ Age_Storm + Brood_Size + Timing	4	53.4	3.99	0.023
Fledge_Success ~ Timing	2	53.8	4.35	0.019
Fledge_Success ~ Age_Storm + Timing	3	53.8	4.39	0.019
Fledge_Success ~ Age_Storm + I(Age_Storm^2) + Brood_Size + Feathers_Bin + Timing	7	54.2	4.73	0.016
Fledge_Success ~ Brood_Size + Timing	3	54.3	4.87	0.015
Fledge_Success ~ Age_Storm + I(Age_Storm^2) + Feathers_Bin + Timing	6	54.7	5.26	0.012
Fledge_Success ~ Age_Storm + I(Age_Storm^2) + bci_F + dBA + Timing	6	54.7	5.27	0.012
Fledge_Success ~ Age_Storm + I(Age_Storm^2) + bci_F + Row + Timing	6	54.8	5.36	0.011
Fledge_Success ~ Age_Storm + I(Age_Storm^2) + bci_F + Brood_Size + Row + Timing	7	55.1	5.67	0.01
Fledge_Success ~ Age_Storm + I(Age_Storm^2) + bci_F + Brood_Size + dBA + Timing	7	55.1	5.69	0.01
Fledge_Success ~ I(Age_Storm^2) + Timing + Age_Storm * dBA	6	55.2	5.72	0.01
Fledge_Success ~ I(Age_Storm^2) + Brood_Size + Timing + Age_Storm * dBA	7	55.2	5.74	0.01
Fledge_Success ~ Age_Storm + I(Age_Storm^2) + Brood_Size + Edge + Timing	7	55.2	5.74	0.01

**Supplemental Table 3.2.** Candidate models of fledge success on subsetting data of nests which were provisioning at the time of the storm for which we had plumage measurements of both adults. Success considered when 1 or more nestlings fledged and failure considered when zero nestlings fledged. Models with less than 0.01 model weight not listed. Timing was present in all models.

<b>Model</b>	<b>k</b>	<b>AICc</b>	<b>ΔAICc</b>	<b>w<sub>i</sub></b>
Fledge_Success ~ Age_Storm + I(Age_Storm^2) + B2_M	5	32.7	0	0.306
Fledge_Success ~ Age_Storm + I(Age_Storm^2) + B2_F + B2_M	6	34.1	1.4	0.152
Fledge_Success ~ Age_Storm + I(Age_Storm^2)	4	35.4	2.66	0.081
Fledge_Success ~ Age_Storm + I(Age_Storm^2) + B2_M + m.r.achieved_M	6	35.6	2.88	0.073
Fledge_Success ~ Age_Storm + I(Age_Storm^2) + B2_M + m.r.achieved_F	6	35.9	3.18	0.062
Fledge_Success ~ Age_Storm + I(Age_Storm^2) + B2_M + bci_M	6	36	3.27	0.06
Fledge_Success ~ Age_Storm + I(Age_Storm^2) + B2_F + B2_M + m.r.achieved_F	7	37.1	4.43	0.033
Fledge_Success ~ Age_Storm + I(Age_Storm^2) + B2_F + B2_M + bci_M	7	37.5	4.81	0.028
Fledge_Success ~ Age_Storm + I(Age_Storm^2) + bci_M	5	37.6	4.88	0.027
Fledge_Success ~ Age_Storm + I(Age_Storm^2) + B2_F + B2_M + m.r.achieved_M	7	37.6	4.92	0.026
Fledge_Success ~ Age_Storm + I(Age_Storm^2) + m.r.achieved_M	5	37.7	4.98	0.025
Fledge_Success ~ Age_Storm + I(Age_Storm^2) + B2_F	5	38.1	5.37	0.021
Fledge_Success ~ Age_Storm + I(Age_Storm^2) + m.r.achieved_F	5	38.3	5.59	0.019
Fledge_Success ~ Age_Storm + I(Age_Storm^2) + B2_M + m.r.achieved_F + m.r.achieved_M	7	39.1	6.38	0.013
Fledge_Success ~ Age_Storm + I(Age_Storm^2) + B2_M + bci_M + m.r.achieved_M	7	39.2	6.47	0.012
Fledge_Success ~ Age_Storm + I(Age_Storm^2) + B2_M + bci_M + m.r.achieved_F	7	39.4	6.72	0.011

**Supplemental Table 3.3.** Candidate models of adult fate after the cold snap (either missing or observed to continue breeding). Models with less than 0.01 model weight not listed.

<b>Model</b>	<b>k</b>	<b>AICc</b>	<b><math>\Delta</math>AICc</b>	<b>w<sub>i</sub></b>
adultfate ~ Age + bci * dBA	6	70.4	0	0.208
adultfate ~ Age + bci	4	70.4	0.05	0.203
adultfate ~ Age	3	72.1	1.72	0.088
adultfate ~ bci	2	72.1	1.75	0.087
adultfate ~ Age + bci + dBA	5	72.5	2.16	0.07
adultfate ~ 1	1	72.7	2.32	0.065
adultfate ~ bci * dBA	4	73.1	2.68	0.054
adultfate ~ Age * dBA + bci * dBA	8	73.1	2.69	0.054
adultfate ~ Age + dBA	4	74.2	3.78	0.031
adultfate ~ bci + dBA	3	74.2	3.84	0.03
adultfate ~ Age * bci	6	74.3	3.9	0.03
adultfate ~ Age * bci + bci * dBA	8	74.3	3.92	0.029
adultfate ~ dBA	2	74.7	4.32	0.024
adultfate ~ dBA + Age * bci	7	76.6	6.17	0.009
adultfate ~ bci + Age * dBA	7	76.8	6.37	0.009

**Supplemental Table 3.4.** Candidate models for clutch initiation date post-cold snap. Models with less than 0.01 model weight not listed.

<b>Model</b>	<b>k</b>	<b>AICc</b>	<b><math>\Delta</math>AICc</b>	<b>w<sub>i</sub></b>
Clutch_Initiation ~ B2_F + bci_M	4	97.3	0	0.093
Clutch_Initiation ~ B2_F	3	97.7	0.34	0.079
Clutch_Initiation ~ 1	2	98.6	1.22	0.051
Clutch_Initiation ~ Age_F + B2_F	4	100.1	2.74	0.024
Clutch_Initiation ~ B2_F + m.r.achieved_F	4	100.1	2.79	0.023
Clutch_Initiation ~ Age_F	3	100.4	3.02	0.021
Clutch_Initiation ~ B2_M	3	100.5	3.15	0.019
Clutch_Initiation ~ B2_F + B2_M	4	100.5	3.17	0.019
Clutch_Initiation ~ Age_F + B2_F + m.r.achieved_F	5	100.6	3.23	0.019
Clutch_Initiation ~ B2_F + B2_M + bci_M	5	101.1	3.73	0.014
Clutch_Initiation ~ B2_F + bci_M + Clutch	5	101.1	3.74	0.014
Clutch_Initiation ~ B2_F + bci_M + Pair	5	101.1	3.74	0.014
Clutch_Initiation ~ B2_F + bci_M + Clutch + Pair	5	101.1	3.74	0.014
Clutch_Initiation ~ B2_F + bci_M + Clutch * Pair	5	101.1	3.74	0.014
Clutch_Initiation ~ bci_M	3	101.2	3.86	0.014
Clutch_Initiation ~ B2_F + m.r.achieved_M	4	101.3	3.95	0.013
Clutch_Initiation ~ B2_F + bci_M + m.r.achieved_F	5	101.4	4.08	0.012
Clutch_Initiation ~ B2_F + bci_F	4	101.4	4.09	0.012
Clutch_Initiation ~ B2_F + dBA	4	101.5	4.14	0.012
Clutch_Initiation ~ B2_F + Clutch	4	101.5	4.16	0.012
Clutch_Initiation ~ B2_F + Pair	4	101.5	4.16	0.012
Clutch_Initiation ~ B2_F + Clutch + Pair	4	101.5	4.16	0.012
Clutch_Initiation ~ B2_F + Clutch * Pair	4	101.5	4.16	0.012
Clutch_Initiation ~ Age_F + B2_F + bci_M	5	101.5	4.18	0.012
Clutch_Initiation ~ bci_F	3	101.6	4.29	0.011
Clutch_Initiation ~ B2_F + bci_M + dBA	5	101.6	4.3	0.011
Clutch_Initiation ~ Clutch	3	101.6	4.31	0.011
Clutch_Initiation ~ Pair	3	101.6	4.31	0.011
Clutch_Initiation ~ Clutch + Pair	3	101.6	4.31	0.011
Clutch_Initiation ~ Clutch * Pair	3	101.6	4.31	0.011
Clutch_Initiation ~ m.r.achieved_F	3	101.7	4.33	0.011
Clutch_Initiation ~ dBA	3	101.7	4.37	0.011
Clutch_Initiation ~ m.r.achieved_M	3	101.7	4.37	0.01
Clutch_Initiation ~ B2_F + bci_M + m.r.achieved_M	5	101.9	4.6	0.009
Clutch_Initiation ~ B2_F + bci_F + bci_M	5	102	4.62	0.009

**Supplemental Table 3.5.** Candidate models for time to fledge for nestlings that lived through and survived the cold snap. Models with less than 0.01 model weight not listed.

<b>Model</b>	<b>k</b>	<b>AICc</b>	<b>ΔAICc</b>	<b>w<sub>i</sub></b>
time_fledge ~ Clutch_Initiation + Edge + Row + Timing	7	84.5	0	0.709
time_fledge ~ Edge + Row + Timing	6	88.4	3.83	0.104
time_fledge ~ bci_M + Clutch_Initiation + Edge + Row + Timing	8	90	5.47	0.046
time_fledge ~ bci_F + Clutch_Initiation + Edge + Row + Timing	8	90.6	6.12	0.033
time_fledge ~ Clutch_Initiation + dBA + Edge + Row + Timing	8	91.1	6.56	0.027
time_fledge ~ Edge + Fledgelings + Row + Timing	7	91.1	6.57	0.027
time_fledge ~ Clutch_Initiation + Edge + Fledgelings + Row + Timing	8	91.2	6.73	0.025
time_fledge ~ dBA + Edge + Row + Timing	7	93.4	8.92	0.008
time_fledge ~ bci_F + Edge + Row + Timing	7	93.8	9.26	0.007
time_fledge ~ bci_M + Edge + Row + Timing	7	93.8	9.3	0.007

**Supplemental Table 3.6.** Candidate models of nestling mass for nests that lived through and survived the cold snap. with less than 0.01 model weight not listed.

<b>Model</b>	<b>k</b>	<b>AICc</b>	<b>ΔAICc</b>	<b>w<sub>i</sub></b>
mass ~ age + I(age <sup>2</sup> ) + Clutch_Initiation.s + I(Clutch_Initiation.s <sup>2</sup> ) + dBA + Edge + Row	12	1307.3	0	0.339
mass ~ I(age <sup>2</sup> ) + I(Clutch_Initiation.s <sup>2</sup> ) + dBA + Edge + Row + age * Clutch_Initiation.s	13	1308.6	1.35	0.172
mass ~ I(age <sup>2</sup> ) + Clutch_Initiation.s + I(Clutch_Initiation.s <sup>2</sup> ) + Edge + Row + age * dBA	13	1309.4	2.13	0.117
mass ~ age + I(age <sup>2</sup> ) + Clutch_Initiation.s + I(Clutch_Initiation.s <sup>2</sup> ) + Edge + Row	11	1309.8	2.48	0.098
mass ~ I(age <sup>2</sup> ) + I(Clutch_Initiation.s <sup>2</sup> ) + Edge + Row + age * Clutch_Initiation.s + age * dBA	14	1310.4	3.14	0.071
mass ~ age + I(age <sup>2</sup> ) + Clutch_Initiation.s + dBA + Edge + Row	11	1310.9	3.62	0.055
mass ~ I(age <sup>2</sup> ) + I(Clutch_Initiation.s <sup>2</sup> ) + Edge + Row + age * Clutch_Initiation.s	12	1311	3.76	0.052
mass ~ I(age <sup>2</sup> ) + dBA + Edge + Row + age * Clutch_Initiation.s	12	1312.3	4.98	0.028
mass ~ age + I(age <sup>2</sup> ) + Clutch_Initiation.s + Edge + Row	10	1312.6	5.3	0.024
mass ~ I(age <sup>2</sup> ) + Clutch_Initiation.s + Edge + Row + age * dBA	12	1313	5.74	0.019
mass ~ I(age <sup>2</sup> ) + Edge + Row + age * Clutch_Initiation.s	11	1313.9	6.59	0.013
mass ~ I(age <sup>2</sup> ) + Edge + Row + age * Clutch_Initiation.s + age * dBA	13	1314	6.76	0.012

**Supplemental Table 3.7.** Candidate models of nestling mass for nests that hatched after the cold snap. Models with less than 0.01 model weight not listed.

<b>Model</b>	<b>k</b>	<b>AICc</b>	<b>ΔAICc</b>	<b>w<sub>i</sub></b>
mass ~ I(age <sup>2</sup> ) + age * Clutch_Initiation.s	8	815.3	0	0.443
mass ~ I(age <sup>2</sup> ) + I(Clutch_Initiation.s <sup>2</sup> ) + age * Clutch_Initiation.s	9	816.9	1.67	0.192
mass ~ I(age <sup>2</sup> ) + dBA.s + age * Clutch_Initiation.s	9	817.2	1.92	0.169
mass ~ I(age <sup>2</sup> ) + age * Clutch_Initiation.s + age * dBA.s	10	818.4	3.15	0.092
mass ~ I(age <sup>2</sup> ) + I(Clutch_Initiation.s <sup>2</sup> ) + dBA.s + age * Clutch_Initiation.s	10	819.1	3.86	0.064
mass ~ I(age <sup>2</sup> ) + I(Clutch_Initiation.s <sup>2</sup> ) + age * Clutch_Initiation.s + age * dBA.s	11	820.4	5.11	0.034

**Supplemental Table 3.8.** Candidate models of nestling mass for nests that were initiated after the cold snap. Models with less than 0.01 model weight not listed.

<b>Model</b>	<b>k</b>	<b>AICc</b>	<b>ΔAICc</b>	<b>w<sub>i</sub></b>
mass ~ age + I(age <sup>2</sup> ) + Clutch_Initiation.s	7	636.1	0	0.301
mass ~ I(age <sup>2</sup> ) + age * Clutch_Initiation.s	8	637	0.82	0.2
mass ~ age + I(age <sup>2</sup> ) + Clutch_Initiation.s + I(Clutch_Initiation.s <sup>2</sup> )	8	638.2	2.04	0.109
mass ~ age + I(age <sup>2</sup> ) + Clutch_Initiation.s + dBA.s	8	638.3	2.18	0.101
mass ~ I(age <sup>2</sup> ) + I(Clutch_Initiation.s <sup>2</sup> ) + age * Clutch_Initiation.s	9	639	2.89	0.071
mass ~ I(age <sup>2</sup> ) + dBA.s + age * Clutch_Initiation.s	9	639.2	3.02	0.066
mass ~ I(age <sup>2</sup> ) + Clutch_Initiation.s + age * dBA.s	9	640.4	4.22	0.036
mass ~ age + I(age <sup>2</sup> ) + Clutch_Initiation.s + I(Clutch_Initiation.s <sup>2</sup> ) + dBA.s	9	640.4	4.28	0.035
mass ~ I(age <sup>2</sup> ) + age * Clutch_Initiation.s + age * dBA.s	10	640.5	4.35	0.034
mass ~ I(age <sup>2</sup> ) + I(Clutch_Initiation.s <sup>2</sup> ) + dBA.s + age * Clutch_Initiation.s	10	641.3	5.16	0.023
mass ~ I(age <sup>2</sup> ) + Clutch_Initiation.s + I(Clutch_Initiation.s <sup>2</sup> ) + age * dBA.s	10	642.5	6.36	0.012
mass ~ I(age <sup>2</sup> ) + I(Clutch_Initiation.s <sup>2</sup> ) + age * Clutch_Initiation.s + age * dBA.s	11	642.7	6.52	0.012



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