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Predictors of nestling survival during harsh weather events in an aerial insectivore, the tree swallow (*Tachycineta bicolor*)

Ilsa A. Griebel^{*1}, and Russell D. Dawson¹

¹Ecosystem Science and Management Program, University of Northern British Columbia, 3333 University Way, Prince George, BC V2N 4Z9, Canada

***Corresponding author and present address:**

Ilsa A. Griebel

Ecosystem Science and Management Program, University of Northern British Columbia

3333 University Way

Prince George, BC V2N 4Z9, Canada

Phone: 306-370-3721

Email: griebel@unbc.ca

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Abstract:

Extreme weather events influence the population dynamics of wild animals. For organisms whose food source is affected by environmental conditions, such as aerial insectivorous birds, periods of inclement weather can have devastating effects. Here, we examine predictors of survival of individual nestlings and whole broods in tree swallows (*Tachycineta bicolor* (Vieillot, 1808)) during an extreme, two-day harsh weather event in central British Columbia, which co-occurred with experimental reduction of nest ectoparasite loads using an anti-parasite drug (ivermectin) or heat-treating nests. A curvilinear relationship existed between survival and brood age, such that middle-aged broods were least likely to survive. Survival of broods and nestlings was higher when raised by males with bluer plumage, whereas nestling survival was lower when female parents had brighter and more UV-reflective plumage. Within broods, smaller nestlings had a lower chance of surviving than their larger siblings. Nestlings in broods where half of the offspring received ivermectin injections had significantly higher chances of surviving than nestlings from non-experimental broods, suggesting that parasite loads can influence survival during inclement weather. Our results identify several factors influencing resiliency of nestlings to harsh weather and are particularly relevant in the context of declining aerial insectivorous bird populations and climate change.

Key words: aerial insectivore, anti-parasite treatment, brood age, brood size hierarchy, harsh weather, plumage characteristics, *Tachycineta bicolor*, tree swallow.

Draft

Introduction

Extreme weather events can play a major role in the population dynamics of wild animals and are particularly concerning in the context of climate change (e.g., Easterling et al. 2000), as the frequency of such events is predicted to increase (IPCC 2014). Weather conditions can affect the reproductive success of individuals, as demonstrated across a diversity of taxa (insects: Weisser et al. 1997; reptiles: Rock and Cree 2003; mammals: Grassel et al. 2016; amphibians: Greenberg et al. 2017; fish: Moll et al. 2018). Specifically in birds, environmental variables, such as temperature and precipitation, can influence nestling phenotype (McCarty and Winkler 1999; Ambrosini et al. 2006) and reproductive success of adults (Dawson and Bortolotti 2000; Arbeiter et al. 2016). For example, during inclement weather (cool, windy, and rainy conditions), nestling American kestrels (*Falco sparverius* (L., 1758)) were less likely to fledge (Dawson and Bortolotti 2000). Young birds may differ, however, in their tolerance of poor weather conditions, due to both intrinsic (e.g., age; Boyle et al. 2013) and extrinsic (e.g., ectoparasites; Merino and Potti 1996) factors, which in turn may influence their survival. Although these factors are known to affect nestling survival, they are less well studied in the context of extreme or harsh weather events.

Intrinsic factors that can affect brood and nestling survival include their age, brood size and within-brood size hierarchies. Survival of nestlings, or number of young fledged, generally increases with brood size, though often at the expense of individual chick size (Reid 1988; Arnold 1993; Gilliland et al. 2016). Specifically during cold snaps, larger broods may have a better chance of surviving by reducing heat loss through huddling behaviour (Gilbert et al. 2010). Depending on an organism's pattern of morphological and physiological development, nestlings may be more vulnerable to poor weather conditions at certain ages. For example, 6–9 day old

tree swallows (*Tachycineta bicolor* (Vieillot, 1808)), which have developed some thermoregulatory ability (Dunn 1979), but growth of feathers is insufficient to provide adequate insulation, had the highest mortality risk during periods of cold weather (Boyle et al. 2013). When size hierarchies exist within a brood due to asynchronous hatching, brood reduction may occur more efficiently, as the smallest nestling within a brood is expected to die quickly due to its competitive disadvantage and lack of resources (the ‘brood reduction hypothesis’; Lack 1947). The rapid death of the smallest nestling in asynchronous broods may allow parents to cope with poor environmental conditions better than parents of more synchronous broods, where brood reduction will occur more slowly (Slagsvold 1982, 1986; Gibbons 1987). In red-winged blackbirds (*Agelaius phoeniceus* (L., 1766)), when temperatures were cool, more marginal (i.e., last-hatched) nestlings died, whereas no such effect was observed on core (i.e., first-hatched) nestlings (Forbes et al. 2001).

Extrinsic factors, such as condition and quality of parents, can also affect brood and nestling survival. Parental phenotype can influence reproductive success, either because the trait provides some direct advantage to the adult (e.g., morphologically) or because it provides an indirect advantage via sexual selection (e.g., plumage colouration). For example, larger adult size has been associated with greater reproductive success in many bird species (Forstmeier 2002; Blums and Clark 2004; but see Mänd et al. 2005). Plumage characteristics, such as brightness and badge size, have also been associated with reproductive success and females may use ornaments displayed by males to select higher quality mates that provide better parental care (the ‘good parent hypothesis’; Hoelzer 1989). In support, plumage ornamentation of male birds has been positively correlated with male feeding rate (e.g., Siefferman and Hill 2003; Silva et al. 2008) and the number of young fledged (e.g., Silva et al. 2008; Moreno et al. 2013). Females can

also display variation in plumage ornamentation. While these visual ornaments may arise due to genetic correlations between the sexes (Lande 1980; Dale et al. 2015), female plumage ornamentation may also signal social dominance if female birds compete for limited resources, such as food, mates or nesting cavities (Irwin 1994). Lastly, the ‘good parent hypothesis’ could also explain female ornamentation, with male birds selecting females with more elaborate plumage ornamentation if it is a signal of the quality of parental care a female can provide (Owens and Thompson 1994; Johnstone et al. 1996; Massaro et al. 2004; reviewed in Tobias et al. 2012). Indeed, female plumage has been positively correlated with female feeding rate, clutch size, number of fledglings produced, and nestling mass and immune response (Linville et al. 1998; Silva et al. 2008; Remeš and Matysioková 2013; Morrison et al. 2014). The relationship between plumage ornamentation and reproductive success may depend on current environmental conditions, as different phenotypes may arise as adaptations for different environmental contexts. For example, nestling pied flycatchers (*Ficedula hypoleuca* (Pallas, 1764)) raised by black males were lighter than nestlings raised by brown males when the temperatures were relatively low, but when the temperatures were relatively high, the reverse pattern was observed, with brown males raising lighter nestlings than black males (Järvisjö et al. 2015). During a year with poor weather and unfavourable breeding conditions, female plumage colouration of great tits (*Parus major* (L., 1758)) was negatively related to number of fledglings, whereas the year prior when conditions were favourable, no relationship between plumage and reproductive success was observed (Mänd et al. 2005).

The nest environment, which includes parasite load and microclimate, is another extrinsic factor that can play a role in nestling and brood survival. Ectoparasites can negatively affect nestling survival (Shields and Crook 1987; Pinkowski 1977) and negative effects of parasites on

nestlings can be amplified in years with poor environmental conditions, such as lower temperatures and higher rainfall (Dufva and Allander 1996; Allander 1998; Merino and Potti 1996). The composition of nest material (Mainwaring and Hartley 2008; Heenan et al. 2015) and, for cavity nesting birds, the physical characteristics of the cavity itself (e.g., wall thickness; Wiebe 2001; Fairhurst et al. 2012) can influence nest microclimate with important consequences for nestling phenotype (e.g., Ardia et al. 2010; Fairhurst et al. 2012), survival (e.g., Siikamäki 1996; Dawson et al. 2005), and fledging success (e.g., Ardia 2013; Deeming and Pike 2015).

Poor weather conditions can be especially detrimental for species where the availability of their food source depends on environmental conditions. Aerial insectivorous birds are particularly vulnerable to short-term changes in temperatures, as the availability of flying insects is reduced during cool, windy conditions (Bryant 1975, 1978; Arbeiter et al. 2016). A study on tree swallows in Ithaca, NY, USA, identified 18.5°C as the critical temperature below which flying insect availability begins to decline (Winkler et al. 2013). Nestling survival was best predicted by three consecutive days with maximum daily temperatures below 18.5°C (i.e., “cold snaps”) and brood age, whereas brood survival was best predicted by cold-snap durations of one or two days, brood age, and year (Winkler et al. 2013). This demonstrates that mortality in nestling aerial insectivores was determined not only by temperature and duration of cold periods, but also by age of young, an intrinsic factor.

Here, we investigate the factors that were most important in influencing nestling and brood survival in tree swallows during a harsh weather event. During 2016, two days of harsh weather resulted in the death of 49% and 86% of the broods at two field sites in central British Columbia, Canada. On June 15th, the temperature range was 4.1–9.1°C, with an average of 6.6°C, and on June 16th, it ranged from 4.3–10.9°C, with an average of 7.6°C (Environment and

Climate Change Canada 2017). Total precipitation was 25.7 and 20.3 mm on these two days, respectively (Environment and Climate Change Canada 2017). This harsh weather event provided a unique opportunity to investigate how the characteristics of a nestling's parents, brood and nest environment influenced survival of both individual nestlings and broods during inclement weather, which can all be important in determining nestling success (e.g., Pinkowski 1977; Forbes et al. 2001; Blums and Clark 2004; Losdat et al. 2013). The relative importance, however, of these influential factors on nestlings during a harsh weather event have to our knowledge not been simultaneously examined. Furthermore, this harsh weather event co-occurred with an experiment reducing loads of ectoparasites at both the level of the individual nestling and the brood, using a broad spectrum, anti-parasite drug, ivermectin, and heat treatment of nests, respectively. Understanding how aerial insectivorous birds, whose populations are declining across North America (Nebel et al. 2010), respond to such events may be particularly important in the face of climate change, as the frequency of extreme weather events is predicted to increase (IPCC 2014).

As indicators of adult condition, quality, age, and initial reproductive investment (e.g., Bitton and Dawson 2008; Bitton et al. 2008; Canestrari et al. 2011; Berzins and Dawson 2016), we predicted that parental mass, size (length of ninth primary flight feather), and plumage colour, as well as yolk and egg size, would be positively associated with survival of young. We further predicted that larger brood size would increase the chance of the brood surviving through huddling behaviour (Gilbert et al. 2010), but may decrease survival of last-hatched offspring (the 'brood reduction hypothesis'; Lack 1947), as tree swallows show moderate hatching asynchrony (Zach 1982). We expected middle-aged broods, where nestlings have begun expending energy to thermoregulate but have poor feather insulation to retain the energetically costly heat they

generate (Boyle et al. 2013), to have lower survival than nestlings in older and younger broods. Previous studies have demonstrated that the negative effects of parasites, such as larval blow flies (*Protocalliphora* and *Trypocalliphora* spp.; Whitworth 2003), on nestlings can be amplified in years with poor environmental conditions, such as lower temperatures and higher rainfall (Dufva and Allander 1996; Merino and Potti 1996; Allander 1998). Therefore, we predicted that nestlings either injected with ivermectin, an anti-parasite drug, or from broods where the nest was heated to kill ectoparasites would be less parasitized and have higher survival than control and non-experimental nestlings that must cope with the combined costs of harsh weather and parasites.

Materials and methods

Study area and species

We studied the tree swallow, an aerial insectivorous bird, near Prince George, BC, Canada (53°N, 122°W) at two study sites within 10 km of each other (colloquially referred to as Stewards and Western) between May and August of 2016. Tree swallows are secondary-cavity nesters that also readily breed in nest boxes. The Stewards site was composed of predominantly hay fields with 139 nest boxes mounted on fence posts (~1.0 m above the ground). Approximately 75% of these nest boxes were situated in hay fields, while the remaining nest boxes were positioned along a fence line that ran between a rural, gravel road and cattle pasture. The Western site was characterized by a series of managed wetlands, with 60 nest boxes positioned around the perimeters of the wetlands on fence posts (~1.5 m above the ground).

Larval blow flies are a common haematophagous ectoparasite of nestlings in our tree swallow population. The life cycle begins with adult females laying eggs in the nest material of birds (Sabrosky et al. 1989). Upon hatching, larvae live in the nest material and feed intermittently on the blood of nestlings, except for one species (*T. braueri*) that imbeds under the nestling's skin for extended periods of time. After the third instar, larvae pupate and develop into adult flies (Hall et al. 2017).

General field methods

Nest boxes were visited daily beginning in the second week of May to document nest building and egg laying. As eggs were laid, they were individually marked with a non-toxic felt pen. The day after an egg was laid, it was weighed using an electronic balance (nearest 0.01 g) and a digital photograph was taken of the egg within an "ovolux" device (Ardia et al. 2006), which illuminated the egg. Using ImageJ software (Rasband 1997), we took four measurements of the yolk diameter from each photo and used the average of these four measurements to calculate yolk volume.

Once the laying of a clutch was completed, the nest was not checked again until the estimated hatch date (12 days following clutch completion; Winkler et al. 2011), at which point the nest was checked daily to determine actual hatching date. Once all viable eggs had hatched, adult birds were captured in nest boxes when feeding offspring. Adults were banded (or the band number recorded, if previously banded) and measured. Body mass was determined using a spring scale (nearest 0.25 g), length of ninth primary flight feather, tail and outer rectrix were measured using a ruler (nearest 0.5 mm), and the combined length of the head and bill ('head-bill')

measured using digital calipers (nearest 0.01 mm). Rump feathers from adults were collected and stored in opaque envelopes at room temperature until used for colour analysis (details below).

At day 2 post-hatch, nestlings were weighed with an electronic balance (nearest 0.01 g). In tree swallows, a negative relationship has been demonstrated between hatching order and nestling mass within a few days of hatching (Bitton et al. 2006), which makes mass at day 2 a good proxy for the degree of hatching asynchrony within a brood. Nestlings were measured every two days from day 4 until day 16. Nestlings were weighed using a spring scale (nearest 0.125 g). Length of head-bill was measured using digital calipers (nearest 0.01 mm) and length of ninth primary feather using a ruler (nearest 0.5 mm). Ninth primary measurements did not begin until day 8 when the primaries typically have emerged.

Experimental procedure

At the Stewards field site, broods were matched by hatching date (± 1 day) and brood size (± 1 nestling) to form pairs of treatment and control broods. On day 6, nestlings in treatment broods were ordered by mass and every other nestling was injected with ivermectin (IVM), a broad-spectrum, anti-parasite drug, at a dose of 0.2 mg/kg body mass. This drug was expected to reduce the level of parasitism individual nestlings encountered from larval blow flies (Levot and Sales 2002, 2008). Ivomec[®] 1% Injection for Cattle and Swine was diluted with sterile sesame oil to a concentration of 0.06 mg ivermectin/1 mL oil and appropriate volumes, calculated for the mass of each nestling, were injected subcutaneously, using a 0.3 mL syringe with a 29 ga. needle. Nestlings in treatment broods that did not receive IVM injections were given pure oil injection to control for possible negative effects of subcutaneous injection and possible positive

effects of additional nutrients provided by the oil. In control broods, all nestlings received pure oil injections.

At the Western field site, parasite reduction at the individual level (i.e., IVM treatment) was combined with parasite reduction at the nest level using a heat treatment in a 2x2 design, resulting in four treatment combinations. To reduce nest-dwelling ectoparasites at the nest level, at half of the nests offspring were temporarily removed and nests were heated in a microwave appliance (powered by a generator) every two days, from day 4 to 16. This is an effective method for reducing the number of nest-dwelling ectoparasites, such as larval blow flies, mites, and fleas (O'Brien and Dawson 2008; I.A. Griebel, unpublished data), with an average reported effectiveness of 98% (Hund et al. 2015). Nests were placed in a sealable plastic bag to reduce loss of moisture during heating. To ensure equal handling, control nests were removed from nest boxes every two days and returned without heating. Within the two levels of the heat treatment (heated and control nests), the IVM experiment was applied, with broods paired, as described above, and assigned as either control (all nestlings in a brood injected with oil) or treatment broods (half of the nestlings in a brood injected with IVM and half injected with oil). All field methods complied with the principles and guidelines of the Canadian Council on Animal Care and were reviewed and approved by the University of Northern British Columbia's Animal Care and Use Committee (protocol #2016-10) on behalf of the Canadian Council on Animal Care.

Plumage spectrometry

The spectral characteristics of rump feathers from adult birds ($n = 80$ males, 83 females) were measured using an Ocean Optics USB2000 spectrometer (Dunedin, FL) with a deuterium tungsten halogen light source (Avantes, Broomfield, CO). Four feathers from each individual

were mounted onto a piece of thick, black paper, in an overlapping position to mimic their natural positioning on the body. A bifurcate probe, which was fixed in a cylindrical sheath to ensure the probe was perpendicular to the feather surface and eliminated ambient light, was used to take three measurements for each set of feathers. Reflectance was determined as the proportion of light reflected relative to a WS-1 white standard (Ocean Optics, Dunedin, FL) over the range of wavelengths perceived by songbirds (300–700 nm; Hart 2001). Using the `pavo` package (Maia et al. 2013) in R version 3.3.0 (R Core Team 2016), we extracted hue (the wavelength of maximal reflectance; $R_{\max}$), mean brightness (mean relative reflectance over the range visible to birds; $\text{total } R_{300-700 \text{ nm}} / n_w$), blue chroma (the relative contribution of the blue range to overall brightness; $\text{total } R_{400-512 \text{ nm}} / \text{total } R_{300-700 \text{ nm}}$), and ultraviolet (UV) chroma (the relative contribution of the UV range to overall brightness; $\text{total } R_{300-400 \text{ nm}} / \text{total } R_{300-700 \text{ nm}}$) (Montgomerie 2006). Following the extraction of these variables, the three measurements taken for each bird were averaged for each colour variable.

Statistical analysis

Survival of broods (Stewards = 43 broods, Western = 37 broods) was analyzed using generalized linear mixed effects models (logit link and binomial family) with a binary response variable (0 = all nestlings in a brood died, 1 = at least one nestling in a brood survived) and site included as a random effect (random intercept). As explanatory variables, we initially included IVM brood treatment, nest heat treatment, brood age and age², brood size, relative hatching asynchrony (the largest minus the smallest day two mass within a brood, divided by the mean day two brood mass), plumage colouration of each parent (brightness, hue, UV, and blue chroma), morphology of each parent (body mass and length of ninth primary feather), mean egg

mass, and mean relative yolk volume. Age and age² were both included to test for nonlinear relationships. Prior to analysis, all explanatory variables were tested for collinearity, but no variables had tolerance values less than 0.2. The interaction between IVM treatment and relative hatching asynchrony was also tested.

Survival of individual nestlings (Stewards = 41 broods, 222 nestlings, Western = 33 broods, 189 nestlings) was analyzed using generalized linear mixed effects models (logit link and binomial family), which allowed for a binary response variable (0 = died, 1 = survived) and random effects for nest identity and site to account for variation due to individual nests and clustered data effects. As explanatory variables, we included IVM treatment, nest heat treatment, brood age and age², brood size, relative hatching asynchrony, nestling relative mass within the brood at day two (each nestling's mass minus mean brood mass, divided by the standard deviation), plumage colouration of both parents (brightness, hue, UV and blue chroma), morphology of both parents (mass and length of ninth primary feather), total egg mass, and mean relative yolk volume. Nestling morphology variables could not be included due to collinearity issues (tolerance < 0.2) with age and age², but all other variables had tolerance values greater than 0.2. The following interactions were also tested: treatment*relative hatching asynchrony and treatment*relative nestling size. If nestlings were not weighed until day four, then mass at day four, rather than at day two, was used to calculate relative size within the brood and relative hatching asynchrony ($n = 33$ of 460 nestlings).

For survival of both broods and nestlings, we began with a full model with all variables and interactions of interest included and then used a backward-stepwise procedure to eliminate any interactions and variables that did not approach significance ($P > 0.10$; Dupont 2009; Montgomery et al. 2012). Using a threshold value of $P = 0.10$ reduces the risk of excluding

important effects and the use of a higher threshold has been recommended to allow the inclusion of variables that approach significance (Golberg and Cho 2004; Moreira et al. 2005). One at a time, we first removed interactions, followed by single variables, in order of decreasing *P*-value. All analyses were performed using Stata (StataCorp 2015).

Results

Brood survival

The relationship between brood survival and age at the time of the harsh weather event was curvilinear, such that broods of younger and older ages had a higher chance of at least one offspring surviving the event compared to middle-aged broods (Table 1; Fig. 1a). The chance of broods surviving also was negatively related to male hue, where broods being raised by bluer males had higher survival (Fig. 2a). Neither the IVM nor heat treatment had an effect on brood survival. No female plumage characteristics or any other male plumage characteristics predicted survival. Parent morphology and initial female reproductive investment (i.e., mean egg mass and relative yolk volume), as well as brood size and relative hatching asynchrony, were also not significant in predicting brood survival.

Nestling survival

A curvilinear relationship existed between individual nestling survival and brood age, such that nestlings from relatively young or relatively old broods had a higher chance of survival than nestlings from middle-aged broods (Table 2; Fig. 1b). The nestling's relative size within the brood positively predicted survival (Fig. 3). Nestling survival also was negatively related to hue

of the male's plumage, where nestlings being raised by bluer males had higher survival (Fig. 2b), while nestlings raised by females that had brighter and more UV-reflective plumage had lower survival (Fig. 4). Nestlings from broods where half of the nestlings received IVM-injections had a higher chance of survival, regardless of whether they received a control- or IVM-injection, compared to nestlings from non-experimental broods (Fig. 5). The survival of nestlings from control broods (all nestlings received control-injections), however, did not differ significantly from the survival of nestlings from either non-experimental broods or IVM broods. Nestlings from heated nests (reduced ectoparasite loads) had lower survival than nestlings from control nests (natural ectoparasite loads; Fig. 6). Morphology of parents, initial female reproductive investment (i.e., total egg mass and mean relative yolk volume), brood size, and relative hatching asynchrony were not significant in predicting nestling survival.

Discussion

Two factors predicted both brood and nestling survival of tree swallows: brood age and plumage hue of males (Table 1, 2). Survival displayed a curvilinear relationship with brood age and negative relationship with plumage hue of males. Five additional factors predicted nestling, but not brood, survival: IVM treatment, heat treatment, relative nestling size, and brightness and UV chroma of female plumage (Table 2). Nestlings from broods where half the nestlings received IVM injections were more likely to survive than nestling not involved in the experiment. In contrast, nestlings from parasite-free nests (i.e., heated nests) were less likely to survive than nestlings from parasite-infested nests (i.e., control nests). Nestling survival was positively related to relative nestling size and brightness and UV chroma of female plumage.

The relationship between survival and brood age was curvilinear, such that middle-aged broods and nestlings were less likely to survive than younger or older broods and nestlings (Fig. 1). In tree swallows, the age of physiological endothermy is 9.5 days, but effective homeothermy can range from 4–8 days once brood size is accounted for (Dunn 1979). Therefore, middle-aged nestlings are beginning to thermoregulate, an energetically expensive activity, but have poorly developed feathers and a limited capacity to retain the heat they generate. This makes middle-aged nestlings particularly vulnerable to cold periods. For nestling tree swallows, Boyle et al. (2013) identified the age most at-risk of mortality during cold snaps as 6–9 day old. This agrees with our results, although we also observed low survival in nestlings up to 12 days old (Fig. 1).

Brood and nestling survival decreased with male plumage hue (Fig. 2). This supports the ‘good parent hypothesis’, which predicts that females use ornaments displayed by males to select higher quality mates that provide better parental care (Hoelzer 1989). Males with bluer plumage (lower hue values) may have provided better care for the nestlings, increasing the brood’s chance of surviving. As male tree swallows do not brood the nestlings, this better care would have to be provided as improved provisioning or acquisition of higher quality territory. Plumage ornamentation of male birds has been positively associated with feeding rate (e.g., Pagani-Núñez and Senar 2014), the number of young fledged (Silva et al. 2008; Moreno et al. 2013), brood mass (Saetre et al. 1995), and mass of young at fledging (Siefferman and Hill 2003). Specifically in our population, older male tree swallows were found to be bluer and brighter than younger males (Bitton and Dawson 2008). This result appeared to be caused by individuals increasing in brightness over time and the higher likelihood of bluer males returning to the breeding site. Thus, bluer males may be of higher quality and have more breeding experience, which could have improved the chance of their young surviving compared to younger, less experienced males with

greener plumage. Alternatively, younger males with greener plumage may have favoured a self-maintenance strategy to improve their chance of future reproductive success, whereas older males with bluer plumage may have invested more in their current reproductive attempt. Furthermore, adults may adjust their level of parental care in response to the quality of plumage ornamentation displayed by their mate. In a meta-analysis, Horváthová et al. (2012) concluded that when paired with a more attractive mate, females in general invested more into reproduction. Therefore, the females paired with males displaying more blue plumage also may have provided better care to the nestlings, thereby increasing the brood/nestling's chance of surviving. In tree swallows, however, Dakin et al. (2016) showed that adults (females and males) paired with a partner with greener plumage, had higher feeding rates, which contradicts the previous possibility. It is important to note, however, that Dakin et al. (2016) quantified provisioning when offspring were only 3 days old and demands on parents would have been small. Moreover, they quantified rate of feeding, but not the quantity or quality of food that was delivered. Thus, bluer males may feed at a lower rate, but provide young with more food and/or higher quality food (Twining et al. 2016).

Female plumage brightness and UV chroma both negatively predicted nestling survival (Fig. 4), contradicting the 'good parent hypothesis' that predicts that male birds select a mate using female plumage ornamentation as a signal of the quality of parental care the female can provide (Owens and Thompson 1994; Johnstone et al. 1996). Female tree swallows with brighter, bluer plumage, however, have been shown to produce nestlings with lower body condition (Bentz and Siefferman 2013), supporting our results. In contrast, in our population of tree swallows, females with bluer plumage produced more fledglings than females with greener plumage (Bitton et al. 2008), which appears to contradict our findings. It is important to

recognize, however, that Bitton et al. (2008) examined general reproductive success, whereas we examined reproductive success during a specific, unfavourable situation. Alternatively, if males reduced their care in response to female brightness and/or UV chroma (and females were unable to compensate), then nestling survival may have been negatively affected. Previous studies of other species have documented males decreasing (Limbourg et al. 2013) or increasing (Mahr et al. 2012) their level of parental care when paired with females displaying higher quality ornamentation. For example, when the UV reflectance of crown feathers in female blue tits (*Cyanistes caeruleus* (L., 1758)) was experimentally reduced, male feeding rate was lower than males paired with sham-treated, control females (Mahr et al. 2012). A previous experiment in our population of tree swallows found that manipulating female plumage brightness, either making them brighter or duller, did not influence male feeding rate (Berzins and Dawson 2016). Unfortunately, since we did not directly measure parental effort, we cannot identify how adults with certain plumage characteristics produced nestlings with higher survival during a harsh weather event.

A nestling's chance of survival increased with its relative size within the brood, with the smallest nestling having the lowest chance of survival and the largest nestling having the highest chance of survival (Fig. 3). With the fewest body reserves to generate heat and endure starvation, and the least developed feathers to retain body heat, the smallest nestling within a brood is often expected to be the first to die when conditions are poor (the 'brood reduction hypothesis'; Lack 1947; Howe 1978).

Treatment of half of the nestlings in a brood with a broad-spectrum, anti-parasite drug, ivermectin, resulted in higher survival of nestlings than those from non-experimental broods (Fig. 5). Following two field seasons of the IVM experiment, analyses found that nestlings from

ivermectin-treated broods faced marginally lower parasite loads (number of larval blow flies per nestling) and had longer and faster growing flight feathers, higher haemoglobin concentrations, and greater fledging success than nestlings from control broods (I.A. Griebel, unpublished data). Fewer parasites in IVM broods may have meant nestlings had more resources available to endure starvation and, for older nestlings, to invest in thermoregulation. Haemoglobin concentration in birds is related to their oxygen-carrying capacity (Minias 2015) and thus, for nestlings that had begun thermoregulating, the higher haemoglobin concentrations of nestlings from IVM broods may have improved their thermoregulatory capabilities compared to nestlings from control and non-experimental broods (Petit and Vézina 2014). Therefore, we would have expected the survival of nestlings from IVM broods to not only be greater than non-experimental nestlings, but also greater than nestlings from control broods, but this was not the case. Possibly the carrier oil used to deliver the IVM, which all nestlings involved in the experiment received injections of, provided the nestlings with additional nutrients and energy, making them more resilient to the harsh weather. This does not seem likely, however, because nestlings received less than 30 μ L of oil. Alternatively, there may have been a lack of statistical power and differences may have been detected if sample sizes were larger.

Nestling survival was lower in heated nests than unheated nests (Fig. 6). This contradicts our prediction that lower parasite loads would permit nestlings to allocate more energy to coping with the effects of harsh weather. Rather, our results suggest that nestlings exposed to higher parasite loads were more resilient to harsh weather. This result, however, may be an artifact of site differences. The heat treatment was only applied at one site, Western, which experienced higher rates of mortality than Stewards (Western: 86% brood mortality, Stewards: 49% brood mortality). Breeding chronology was approximately one week ahead at Western compared to

Stewards (mean brood age at time of harsh weather event $\pm$ SE; Stewards = 5.7 ± 0.45 , Western = 10.6 ± 0.53). Thus, the relationship between heat treatment and survival may have been a consequence of more middle-aged nestlings occurring in heated nests due to study design and temporal differences between the two field sites. The results of the IVM treatment, which was applied evenly across both sites and suggest that nestlings exposed to lower parasite loads may have higher survival, support this possible explanation.

In conclusion, we have identified several possible key factors influencing survival of broods and individual nestlings in a species of aerial insectivorous bird during a single harsh weather event. Two of the key factors (age and plumage hue of the male) predicted survival at both the brood and nestling level, while the other factors only predicted nestling survival (relative size of the nestling, female brightness and UV chroma, and two different anti-parasite treatments). Aerial insectivores are declining across North America (Nebel et al. 2010) and our analysis of survival during harsh weather may be important within the broader context of climate change. As climate change progresses, it is predicted that the frequency of extreme weather events will increase (IPCC 2014). Thus, the knowledge gained from this study, and research like it, may become crucial for understanding dynamics of aerial insectivorous bird populations in the future.

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Draft

Table 1. Results of a generalized linear mixed effects model examining the survival of broods of tree swallows (*Tachycineta bicolor* (Vieillot, 1808)) during a 2-day harsh weather event in central British Columbia, Canada, during June 2016.

Response Variable	<i>n</i>	Model Variables	Coefficient	SE	<i>z</i>	<i>P</i>	95% Conf. Interval	
Brood survival	80	age	-1.119	0.365	-3.06	0.002	-1.84	-0.40
		age ²	0.065	0.021	3.12	0.002	0.02	0.11
		male hue	-0.057	0.025	-2.28	0.023	-0.11	-0.01

Draft

Table 2. Results of a generalized linear mixed effects model examining the survival of individual nestling tree swallows (*Tachycineta bicolor* (Vieillot, 1808)) during a 2-day harsh weather event in June 2016 in central British Columbia, Canada.

Response Variable	<i>n</i>	Model Variables	Coefficient	SE	<i>z</i>	<i>P</i>	95% Conf. Interval	
Nestling survival	411	IVM treatment:						
		0 vs. 1	1.721	1.18	1.46	0.146	-0.60	4.04
		0 vs. 2	3.443	1.21	2.85	0.004	1.08	5.81
		0 vs. 3	3.680	1.23	2.99	0.003	1.27	6.09
		1 vs. 2	1.722	1.17	1.47	0.141	-0.57	4.01
		1 vs. 3	1.958	1.18	1.65	0.098	-0.36	4.28
		2 vs. 3	0.237	0.64	0.37	0.712	-1.02	1.49
		heat treatment:						
		ctl vs. heat	-3.300	1.49	-2.22	0.026	-6.21	-0.39
		age	-1.893	0.49	-3.87	<0.001	-2.85	-0.93
		age ²	0.109	0.03	3.87	<0.001	0.05	0.16
		relative nestling size	-0.677	0.27	2.49	0.013	0.14	1.21
		male hue	-0.155	0.04	-3.52	<0.001	-0.24	-0.07
		female brightness	-0.408	0.18	-2.29	0.022	-0.76	-0.06
		female UV chroma	-26.743	10.53	-2.54	0.011	-47.38	-6.11

Note: Nestlings were involved in an experiment that used an anti-parasite drug, ivermectin (IVM), to reduce parasite load within nests. Nestlings from non-experimental broods (0) were not involved in the anti-parasite experiment. Nestlings from control broods (1) received sham-injections of sesame pure oil, while half of the nestlings in IVM broods received control injections of sesame oil (2) and the other half received IVM injections (3); see Methods for details.

Figure 1. The probability that (A) broods and (B) individual nestling tree swallows (*Tachycineta bicolor* (Vieillot, 1808)) survived a 2-day harsh weather event in June 2016 was higher for younger and older aged broods, but lower for middle-aged broods. Brood survival was defined as all nestlings dying within a brood (0) or at least one nestling surviving in a brood (1). Nestling survival was defined as 0 when a nestling died and 1 when a nestling survived. The prediction lines were estimated using generalized linear mixed effects models (logit link and binomial family). Data points have been offset slightly from 0 and 1 to show their distribution.

Figure 2. The probability that (A) broods and (B) individual nestling tree swallows (*Tachycineta bicolor* (Vieillot, 1808)) survived a 2-day harsh weather event in June 2016 decreased with male plumage hue, i.e., males with bluer plumage (lower hue values) had higher brood survival than males with greener plumage (higher hue values). See Methods for details of measuring plumage hue. Brood survival was defined as all nestlings dying within a brood (0) or at least one nestling surviving in a brood (1). Nestling survival was defined as 0 when a nestling died and 1 when a nestling survived. The prediction lines were estimated using generalized linear mixed effects models (logit link and binomial family).

Figure 3. The probability of individual nestling tree swallows (*Tachycineta bicolor* (Vieillot, 1808)) surviving a 2-day harsh weather event in June 2016 was higher for the largest nestlings within a brood and lower for the smallest nestlings within a brood. Survival was defined as 0 when a nestling died and 1 when a nestling survived. The prediction line was estimated using a generalized linear mixed effects model with a logit link and binomial family.

Figure 4. The probability of nestling tree swallows (*Tachycineta bicolor* (Vieillot, 1808)) surviving a 2-day harsh weather event in June 2016 decreased with (A) brightness and (B) UV chroma of parent females. See methods for details of quantifying plumage brightness and UV chroma. Survival was defined as 0 when a nestling died and 1 when a nestling survived. The prediction lines were estimated using generalized linear mixed effects models with a logit link and binomial family.

Figure 5. Mean survival ($\pm$ SE) of nestling tree swallows (*Tachycineta bicolor* (Vieillot, 1808)) during a harsh weather event in June 2016. Nestlings from non-experimental broods were not experimentally manipulated ($n = 117$ nestlings), while nestlings from control broods received sham-injections of pure sesame oil ($n = 120$ nestlings). Within ivermectin (IVM) broods, half of the nestlings received injections with a broad-spectrum, anti-parasite drug (IVM-IVM; $n = 85$ nestlings) and the other half received control injections of sesame oil (IVM-control; $n = 89$ nestlings); see Methods for details. Treatments that share the same letter were not significantly different ($P > 0.05$).

Figure 6. Mean nestling survival ($\pm$ SE) of tree swallows (*Tachycineta bicolor* (Vieillot, 1808)) during a harsh weather event in June 2016. Nestlings from nests that were heated in a microwave oven repeatedly to kill all nest-dwelling ectoparasites (heat nest treatment; $n = 17$ broods, 102 nestlings) had significantly lower survival than nestlings from unheated nests (control nest treatment; $n = 57$ broods, 309 nestlings).

Figure 1. The probability that (A) broods and (B) individual nestling tree swallows (*Tachycineta bicolor* (Vieillot, 1808)) survived a 2-day harsh weather event in June 2016 was higher for younger and older aged broods, but lower for middle-aged broods. Brood survival was defined as all nestlings dying within a brood (0) or at least one nestling surviving in a brood (1). Nestling survival was defined as 0 when a nestling died and 1 when a nestling survived. The prediction lines were estimated using generalized linear mixed effects models (logit link and binomial family). Data points have been offset slightly from 0 and 1 to show their distribution.

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Figure 2. The probability that (A) broods and (B) individual nestling tree swallows (*Tachycineta bicolor* (Vieillot, 1808)) survived a 2-day harsh weather event in June 2016 decreased with male plumage hue, i.e., males with bluer plumage (lower hue values) had higher brood survival than males with greener plumage (higher hue values). See Methods for details of measuring plumage hue. Brood survival was defined as all nestlings dying within a brood (0) or at least one nestling surviving in a brood (1). Nestling survival was defined as 0 when a nestling died and 1 when a nestling survived. The prediction lines were estimated using generalized linear mixed effects models (logit link and binomial family).

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