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# Factors influencing pre-fledging mass recession of nestling Tree Swallows

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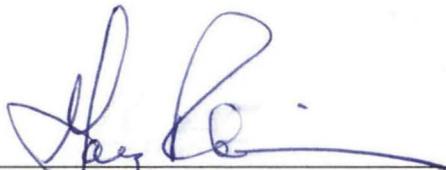
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Factors influencing pre-fledging mass recession of nestling Tree Swallows

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Factors influencing pre-fledging mass recession of nestling Tree Swallows

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Submitted to the Faculty of the Graduate School of  
Eastern Kentucky University  
in partial fulfillment of the requirements  
for the degree of  
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## DEDICATION

This thesis is dedicated to Michelle Martin for first introducing me to biology,  
Dr. Dawn Wilkins for being a mentor in science and in life,  
and all my friends and family, without whom I would not have made it this far.

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## ABSTRACT

Fledglings of some aerial insectivores experience pre-fledgling mass recession, possibly to achieve an optimum wing loading by the time of fledging. However, studies of aerial insectivores to date have been limited to two species of swifts (Apodidae), and additional studies of species of aerial insectivores are needed to determine if factors contributing to pre-fledgling mass recession vary among species. Thus, my objective was to examine factors contributing to pre-fledgling mass recession by nestling Tree Swallows (*Tachycineta bicolor*). My study was conducted during the 2015 breeding season at the Blue Grass Army Depot in Madison County, Kentucky. Nestling Tree Swallows (n = 127) in 29 broods were divided into half-weighted (n = 32), full-weighted (n = 36), and control (n = 59) treatment groups. Lead weights weighing 2.5% (0.6 g) or 5% (1.2 g) of the nestling's mass were glued to the back feathers of half-weighted and full-weighted nestlings, respectively, between 9 and 11 days post-hatching. Video recordings were used to monitor parental provisioning behavior and nestling begging behavior. I found no differences among treatment groups in mass at fledging, amount of mass lost, or wing loading at fledging. In addition, adult provisioning rates and the proportion of time spent begging by nestlings did not vary during the period from day 11 to day 19 post-hatching. These results suggest that mass loss by nestling Tree Swallows prior to fledging is not due to changes in either parental or nestling behavior, but, rather, is likely a physiological process resulting from the loss of water from maturing feathers and other tissues. In contrast, the results of studies of two species of

swifts (Apodidae) suggest that changes in nestling behavior influenced the extent of pre-fledging mass recession such that weighted nestlings lost more mass than control nestlings, apparently to optimize wing loading at fledging. This difference between swifts and Tree Swallows in the apparent cause of pre-fledging mass recession may be due to differences in the duration of nestling periods (several days longer for swifts) and wing loading (higher in swifts than Tree Swallows). With greater wing loading, optimum mass as fledging may be more critical for swifts than for Tree Swallows.

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## CHAPTER 1

### INTRODUCTION

The mass of nestlings in some species of birds increases with increasing age, peaks several days prior to fledging, and then decreases until the day of fledging (Ricklefs 1968, Morbey et al. 1999, Gray and Hamer 2001, Sprague and Breuner 2010). Such mass recession has been documented in several taxa, including seabirds (such as Procellariidae and Sulidae), swifts (Apodidae), and swallows (Hirundinidae; Ricklefs 1968, Gray and Hamer 2001). One possible function of such pre-fledging mass recession may be to induce fledging, i.e., nestlings lose mass because parents reduce provisioning rates to induce fledging when it is no longer beneficial for young to remain in the nest (Morbey et al. 1999). Another possible function of pre-fledging mass recession is that it helps optimize wing loading for newly fledged young (i.e. wing-loading hypothesis; Ricklefs 1968, Martins 1997, Shultz and Sydeman 1997, Morbey et al. 1999). Among aerial insectivores, such as swifts and swallows, newly fledged young must be able to catch insects in flight (Michaud and Leonard 2000, Wright et al. 2006) and may also need to evade predators after fledging. This is especially important for species who receive little, if any, post-fledging care (Fischer 1958, Martins 1997, Winkler et al. 2011). For such species, mass recession prior to fledging may result in wing loading that will permit greater maneuverability and agility in flight and conserve energy (Witter and Cuthill 1993, Sprague and Breuner 2010, Goodpaster and Ritchison 2014). Thus, pre-fledging mass recession could enhance the foraging success and likelihood of survival of

young aerial insectivores. However, this hypothesis has been rejected in other cases (Morbey et al. 1999).

The factors contributing to pre-fledging mass recession appear to vary among species. For example, the results of studies of Barn Swallows (*Hirundo rustica*) and Common Swifts (*Apus apus*) suggest that mass recession is physiological, caused by water and lipid loss from maturing tissues, drying of feathers, or use of lipid stores (Ricklefs 1968, Martins 1997). However, the results of studies of several species of seabirds and Chimney Swifts (*Chaetura pelagica*) suggest that mass recession is nestling-driven and potentially results from increased levels of nestling activity (e.g., wing flapping; Sealy 1968, Goodpaster and Ritchison 2014), behavioral anorexia (Mauck and Ricklefs 2005), or less begging (Wright et al. 2006). Morbey et al. (1999) hypothesized that parent Cassin's Auklets (*Ptychoramphus aleuticus*) caused mass recession by reducing their provisioning rates. Gray and Hamer (2001) suggested that pre-fledging mass recession by nestling Manx Shearwaters (*Puffinus puffinus*) could result from changes in the behavior of both parents and nestlings, with a reduction in parental provisioning rates possibly caused by a decrease in solicitation by nestlings.

Wright et al. (2006: 1895-1896) proposed two hypotheses to address the possibilities that pre-fledging mass recession is caused either physiologically or behaviorally. The inflexible growth schedule hypothesis posits that “. . . pre-fledging mass recession [is] physiologically pre-programmed to match each nestling's body size . . .” The facultative mass adjustment growth hypothesis states that “. . . individual nestlings assess changes in their body mass and wing length and facultatively adjust

their personal rate of mass loss. . ." Possible facultative responses include reducing begging intensity (Gray and Hamer 2001, Wright et al. 2006) or increasing levels of activity such as wing flapping (Sealy 1968, Wright et al. 2006, Goodpaster and Ritchison 2014). In addition, a reduction in parental provisioning rates could contribute to mass loss by nestlings (Morbey et al. 1999, Gray and Hamer 2001).

Several investigators have examined the growth and development of nestling Tree Swallows (*Tachycineta bicolor*; Quinney et al. 1986, Clotfelter et al. 2000, Michaud and Leonard 2000, McCarty 2001, Ardia 2006). These studies have revealed that nestling mass peaks at about 22 g between days 11 to 13 post-hatching (Zach and Mayoh 1982, McCarty 2001), then declines until fledging sometime between days 20 to 24 post-hatching (Zach and Mayoh 1982, Quinney et al. 1986, Michaud and Leonard 2000, McCarty 2001). In addition, investigators have studied the begging behavior of nestling Tree Swallows (Leech and Leonard 1996; Leonard and Horn 1998, 2001, 2006) and adult provisioning behavior (Leonard and Horn 1996, 2001; Leonard et al. 2009). However, no one to date has examined how possible changes in these behaviors might contribute to pre-fledging mass recession and, therefore, wing loading at fledging.

The objective of my study was to examine the behavior of nestling and adult Tree Swallows during the period of nestling mass recession to determine if changes in their behavior contributed to nestling mass recession. More specifically, by examining the behavior of nestlings, I sought to determine if either the inflexible growth schedule hypothesis or facultative mass adjustment growth hypothesis could explain mass recession by nestling Tree Swallows. To do so, weights were attached to some nestlings

to manipulate their apparent mass (Wright et al. 2006, Goodpaster and Ritchison 2014). The inflexible growth schedule hypothesis would be supported if I found no changes in nestling behavior and weighted nestlings and non-weighted (control) nestlings lost similar amounts of mass. The facultative mass adjustment growth hypothesis would be supported if weighted nestlings lost more mass as a result of reduced food intake, increased activity levels, or both, and had similar wing-loading and fledging mass as control nestlings (Wright et al. 2006, Goodpaster and Ritchison 2014). If changes in parental provisioning behavior appeared to be the primary cause of nestling mass recession, neither hypothesis would be supported.

## CHAPTER 2

### MATERIALS AND METHODS

#### *Study Area*

My study was conducted from March through July 2015 at the Blue Grass Army Depot (BGAD) in Madison County, Kentucky. Tree Swallows begin arriving in Kentucky as early as mid-March, and most adults arrive by 1 April (Palmer-Ball 1996). The BGAD is approximately 6,070 ha and contains woodlots, open fields, and ponds and reservoirs that provide suitable nesting and foraging habitat for Tree Swallows (Palmer-Ball 1996, Winkler et al. 2011). Nest boxes (N = 73) were already present in the study area (Ritchison, pers. comm.).

#### *Sample Size*

Use of nesting Tree Swallows was approved by the Institutional Animal Care Use Committee (IACUC) prior to the beginning of the experiment (IACUC protocol number 04-2015). Fifty-six Tree Swallow clutches consisting of 306 eggs were initiated from March-July 2015 at the BGAD. Of those, 51 broods consisting of 262 nestlings inhabited nest boxes. Nestlings in were lost during the experiment due to predation, bird mite infestation, inclement weather, and abandonment (n = 117), and 18 nestlings whose the fate is unknown were removed from the experiment due to brood reduction. This left 29 broods consisting of 127 nestlings that survived to fledging and were included in analyses.

### *Nest Box Monitoring and Individual Identification*

Nest boxes were checked at least twice weekly beginning on 20 March to determine which boxes were being used by Tree Swallows. Nest boxes containing swallow nests were then checked every other day to determine dates of egg laying, clutch sizes, and when females began incubation. The incubation period of Tree Swallows is typically 13 or 14 days (Winkler et al. 2011), so nests were checked daily after about 10 days of incubation to determine when eggs hatch.

The day a nestling Tree Swallow was discovered in the nest was considered its hatch day (hatch day = day 1 post-hatching). Individual nestlings (n = 127) were identified by different colored thread tied around their tarsi or colored felt-tip marker on the tarsi until about 10 days old when each received uniquely colored leg bands. The identification color and associated number a nestling received was based on hatching order, i.e. the eldest nestling was red, followed by orange, yellow, green, blue, purple, then either black or white consecutively. In the event that two or more nestlings hatched on the same day, the larger of the two was considered to be the older, or if there was no size difference, then color was assigned arbitrarily. A random number sequence generator was used to determine which colors/numbers would receive treatment to account for the different growth trends experienced by earlier hatched and later hatched nestlings (Zach 1982).

Nestling Tree Swallows were handled daily from hatching to fledging. McCarty (2001) indicated that nestling Tree Swallows may fledge early if handled after day 15 post-hatching so, after nestlings were returned to nests on days 16, 17, or 18 days post-

hatching, I placed a wadded paper towel in the nest-box entrance for 1 – 2 min to help ensure that the nestlings were no longer agitated and less likely to leave nest boxes prematurely. After quietly removing the paper towel and walking about 10 m away, nest boxes were watched for 5 min to make sure that all nestlings remained inside.

### *Manipulations*

I used the experimental mass manipulation procedure described by Wright et al. (2006) to test the hypotheses. Beginning between days 9 to 12 post-hatching, nestlings were weighed daily using a digital scale ( $\pm 0.1$  gm; hatch day = day 1; McCarty 2001) when members of the brood received treatment. Nestlings with experimentally manipulated mass (hereafter weighted nestlings) had either half-weights (2.5% of peak nestling mass = 0.6 g; n = 32) or full-weights (5% of peak nestling mass = 1.2 g; n = 36) attached to their back feathers using cyanoacrylate glue. The nestlings varied in the rate at which the back feathers grew, causing variation in the age at which treatment was applied and the first mass measurement. Lead weights were attached between days 9 and 12 post-hatching (mean =  $10.7 \pm 0.1$  [SE] days post-hatching), prior to attainment of peak mass of nestling Tree Swallow (Zach and Mayoh 1982, Quinney et al. 1986, McCarty 2001). In broods of three to five nestlings, one nestling was randomly selected per brood for each treatment, and in broods of six to seven, two nestlings were assigned to each treatment group. Any remaining nestlings in each brood were assigned to the control group (n = 59). A random sequence generator was used to determine which nestlings received treatments. In broods of 3 -5, the first number in the sequence would

receive the full-weight, the second number received half-weight, and the remaining nestlings were controls. In broods of 6 or 7, the first two numbers received full-weights, the next two numbers received half-weights, and the remaining nestlings were controls. On days when weights are added or removed from weighted nestlings, control nestlings were handled and touched on the back as if they were receiving treatment. If a brood was reduced due to death to one or two nestlings more than two days prior to fledging, the remaining nestlings were removed from the experiment. Weights were removed when the primaries and secondaries had little or no remaining sheath, and prior to days 20 or 21 post-hatching when Tree Swallows typically fledge (Michaud and Leonard 2000, McCarty 2001).

### *Wing loading*

The right wing of each nestling was traced on paper on the day weights were removed to calculate an average wing surface area (cm<sup>2</sup>) for each individual. A cardboard cutout was used to create a boundary arch on the leading edge of the wing so that wings were extended a consistent amount for all tracings. Pins were used to secure the feathers on a cardboard surface to prevent the feathers from moving from their natural position during tracing. The outline of the wing was traced, and the outline was scanned into the program Image J (National Institutes of Health, Bethesda, Maryland). Each wing outline was traced in random order on the program three times (scale: 119 pixels = 1 cm) and the wing surface area from these were averaged. The average wing surface area was then doubled to calculate a total average wing surface

area for that individual. Nestling mass on the day wings were traced was divided by wing surface area to calculate wing loading ( $\text{g}/\text{cm}^2$ ).

### *Video recordings*

After eggs hatched and before nestlings were 8 days old, a section of the back of each nest box was removed, a wire screen was attached to keep nestlings in the nest box, and a plastic container (23 cm wide x 32 cm long x 15 cm high) was attached to permit video-recording. A 'fake' camcorder (made of cardboard and the same size as the actual camcorder) was placed in the plastic container at least two days prior to video-recording and was left in the box whenever video recording was not taking place to allow nestlings and adults to habituate to its presence.

Nests were video-recorded almost daily for at least two hours from the time treatments were applied until the last nestling in the brood fledged to determine parental provisioning rates and percent time spent begging. Nests were not video-recorded on days when it rained and, on some days, the number of nests recorded was limited by the number of available camcorders. The first hour of each recording was not used in my analyses because visits to nests to place camcorders in the plastic containers and begin recording may alter parental provisioning behavior (Murphy et al. 2015). All video recordings ( $n = 211$ ) took place between approximately 08:00 and 11:00 to minimize the possible effect of daily variation in adult provisioning rates.

### *Statistical analyses*

To determine the possible effect of the lead weights on nestling mass, I compared the daily mass of nestlings with and without weights from day 11 post-hatching until the day weights were removed (mean =  $18.3 \pm 0.1$  [SE] days post-hatching; range = day 17 – day 21 post-hatching). I also compared the mass and wing loading of control and weighted nestlings on the day weights were removed. The surface area of wings of nestlings in the three treatments was also compared to ensure that any differences in wing loading would only be due to differences in mass. These analyses were conducted using a general linear model (GLM) with nest ID as a random effect to account for the non-independence of nestlings in the same nest. All analyses were conducted using the Statistical Analysis System (SAS Enterprise Guide 6.1, SAS Institute Inc., Cary, NC).

I also examined possible variation in parental provisioning rates and the proportion of time spent begging by nestlings throughout the experimental period using the video recordings. Begging time was defined as proportion of time nestlings uttered begging calls (Goodpaster and Ritchison 2014). Nestlings were considered begging as long as one or more nestlings could be heard uttering begging calls in video-recordings and not begging during any period of two or more seconds when no calls could be heard (McCarty 1996, Brzęk and Konarzewski 2014). Parental provisioning rates were measured as the number of times adults (males and females combined) fed nestlings per hour per nestling. Begging data were normally distributed. However, provisioning data were not normally distributed so were square-root transformed prior to analysis to

normalize the data. Analysis of both provisioning data and begging data were conducted using repeated measures ANOVA with nestling age as a main effect and nest ID as a random effect to account for non-independence of provisioning by adults at the same nest. All analyses were conducted using the Statistical Analysis System (SAS Enterprise Guide 6.1, SAS Institute Inc., Cary, NC). Values are presented as means  $\pm$  SE.

## CHAPTER 3

### RESULTS

#### *Effect of manipulation of nestling mass*

The mean age of nestlings when wings were traced and fledging mass was measured did not differ among treatments ( $F_{2,49} = 0.7$ ,  $P = 0.51$ ; control =  $18.5 \pm 0.1$  days, half-weighted =  $18.2 \pm 0.2$ , and full-weighted =  $18.3 \pm 0.1$  days). Nestlings reached an average peak mass of  $21.6 \pm 0.2$  g (range = 16.9 - 26.1 g) at a mean age of  $15.4 \pm 0.2$  days post-hatching, with mass then declining until they were weighed a final time before fledging (between days 17 and 21 post-hatching). The amount of mass lost by nestling Tree Swallows prior to fledging did not differ among treatments ( $F_{2,50} = 0.8$ ,  $p = 0.48$ ), with a mean of  $2.3 \pm 0.2$  g (range = 0 – 4.9 g) lost for control nestlings,  $2.7 \pm 0.2$  g (range = 0.8 – 5.3 g) for half-weighted nestlings, and  $2.5 \pm 0.3$  g (range = 0 – 5.8 g) for full-weighted nestlings. Similarly, the mean mass of nestlings when wings were traced did not differ among treatments, either with weights still attached ( $F_{2,44} = 0.3$ ,  $p = 0.72$ ) or removed ( $F_{2,44} = 2.0$ ,  $P = 0.16$ ).

Including the weight of the lead weights, nestling mass differed among treatments from days 11 to 18 post-hatching (all  $P \leq 0.011$ ; Table 1<sup>1</sup>, Figure 1<sup>2</sup>). Specifically, half-weighted nestlings had greater mass than control nestlings on days 13, 15, and 16 post-hatching ( $P \leq 0.0072$ ). Full-weighted nestlings had greater mass than control nestlings on days 11-18 post-hatching ( $P \leq 0.011$ ). Full-weighted nestlings had

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<sup>1</sup> Refer to Appendix: Tables for all tables

<sup>2</sup> Refer to Appendix: Figures for all figures

greater mass than half-weighted nestlings on day 11 ( $P = 0.0005$ ). However, the added mass of the weights accounts for these difference. Excluding the added weight of the lead weights, I found no differences among treatment groups in nestling mass from day 11 to day 21 post-hatching (all  $P \geq 0.063$ ; Table 2, Figure 2).

#### *Effect of manipulations on wing loading*

Nestling Tree Swallows that fledged from days 17 to 21 post-hatching were included in the wing loading analyses, and the interaction between treatment and age was not significant ( $F_{3,44} = 2.2$ ,  $P = 0.10$ ). Mean surface area of the wings of nestlings did not differ among treatments ( $F_{2,49} = 0.4$ ,  $P = 0.67$ ), with means of  $60.8 \pm 0.7 \text{ cm}^2$  for control nestlings,  $61.5 \pm 0.9 \text{ cm}^2$  for half-weighted nestlings, and  $61.3 \pm 0.8 \text{ cm}^2$  for full-weighted nestlings. Including the weights, mean wing loading did not differ among treatments ( $F_{2,48} = 0.4$ ,  $P = 0.67$ ), with means of  $0.328 \pm 0.005 \text{ g/cm}^2$  for control nestlings,  $0.332 \pm 0.006 \text{ g/cm}^2$  for half-weighted nestlings, and  $0.334 \pm 0.006 \text{ g/cm}^2$  for full-weighted nestlings. Similarly, with weights removed, I found no difference among treatments ( $F_{2,48} = 0.8$ ,  $P = 0.45$ ) in mean wing loading among control ( $0.328 \pm 0.005 \text{ g/cm}^2$ ), half-weighted ( $0.323 \pm 0.005 \text{ g/cm}^2$ ), and full-weighted ( $0.315 \pm 0.006 \text{ g/cm}^2$ ) nestlings.

*Begging behavior and provisioning rates*

For the period from day 11 to day 19 post-hatching, I found no differences in either proportion of time spent begging by nestlings ( $F_{8,118} = 1.5$ ,  $P = 0.18$ ; Figure 3) or the parental provisioning rates ( $F_{8,188} = 0.9$ ,  $P = 0.55$ ; Figure 4).

## CHAPTER 4

### DISCUSSION

#### *Peak mass, mass recession, and wing loading*

The variation in mass of nestling Tree Swallows during the nestling period in my study was similar to that reported in previous studies, with peak mass achieved several days before fledging followed by mass recession until fledging (Paynter 1954, Zach and Mayoh 1982, Quinney et al. 1986, McCarty 2001). Loss of mass in the days prior to fledging appears to be common among species in the family Hirundinidae, with pre-fledging loss of mass reported in Violet-green Swallows (*Tachycineta thalassina*; Edson 1943), Tumbes Swallows (*Tachycineta stolzmanni*; Stager et al. 2012), Hispaniolan Golden Swallows (*Tachycineta euchrysea sclateri*; Proctor 2016), Barn Swallows (*Hirundo rustica*; Ricklefs 1968), Pacific Swallows (*Hirundo tahitica*; Bryant and Hails 1983), Bank Swallows (*Riparia riparia*; Petersen 1955), Cliff Swallows (*Petrochelidon pyrrhonota*; Stoner 1945), Southern Rough-winged Swallows (*Stelgidopteryx ruficollis*; Lunk 1962), House Martins (*Delichon urbica*; Bryant and Gardiner 1979), and Asian House Martins (*Delichon dasypus*; Zhou et al. 2012).

Small differences in the mass of nestling Tree Swallows in my study (i.e., attaching 0.6 and 1.2 g weights) did not affect the amount of mass lost prior to fledging, providing support for the inflexible growth schedule hypothesis. The loss of mass by nestling Tree Swallows prior to fledging in my study was not due to changes in the behavior of either parents or nestlings, with no changes in either adult provisioning rates or the proportion of time spent begging by nestlings during the period from day 11

to day 19 post-hatching. Other investigators have also found that provisioning rates of adult Tree Swallows and the begging behavior of nestlings did not change during the period just prior to and during nestling mass recession (Leonard and Horn 1996, McCarty 1996, Michaud and Leonard 2000). With no changes in adult or nestling behavior, one possible explanation for mass recession prior to fledging by nestling Tree Swallows is a reduction in the water content of maturing tissue. In nestling Barn Swallows (*Hirundo rustica*), Ricklefs (1968) found that a reduction in the water content of maturing tissues, particularly feathers, skin, and the liver, was the primary cause of mass recession prior to fledging, with little change in lean dry mass or lipid content after day 14 post-hatching. Mass recession prior to fledging was also found to result primarily from loss of water content in maturing tissues in Pacific Swallows (Bryant and Hails 1983) and House Martins (Bryant and Gardiner 1979).

In contrast to my results, the results of similar studies of nestling Common Swifts (*Apus apus*; Wright et al. 2006) and Chimney Swifts (*Chaetura pelagica*; Goodpaster and Ritchison 2014) supported the facultative mass adjustment hypothesis, with weighted nestlings losing more mass prior to fledging than control nestlings. Wright et al. (2006) suggested that nestling Common Swifts lost mass before fledging by begging less and, therefore, being fed less by adults. In addition, young Chimney Swifts are known to leave their nests and cling to the walls of chimneys or other nesting structures as long as two weeks prior to fledging (i.e., flying from nest sites; Fischer 1958). During that period, young swifts climb and flap their wings, perhaps allowing them to gauge their wing loading (Fischer 1958, Steeves et al. 2014, Goodpaster and Ritchison 2014). Energy

expended during these activities may also contribute to pre-fledging mass recession in swifts (Wright et al. 2006, Goodpaster and Ritchison 2014). Nestling Tree Swallows, in contrast, may be more limited in their opportunity to flap their wings and gauge wing loading in small cavity nests.

Optimum wing loading at fledging is likely important for swifts because they are not fed by parents after leaving nest sites (Steeves et al. 2014) and so, as aerial insectivores, must be sufficiently fast and maneuverable in flight to be able to capture their insect prey (Witter and Cuthill 1993, Warrick 1998). The extent to which young Tree Swallows may be fed by parents after fledging is unclear. Some investigators have reported that parents feed fledgling Tree Swallows for as much as several days after leaving nests (Kuerzi 1941, Winkler et al. 2011). Others, however, have reported that young Tree Swallows fly well after leaving nests and feed themselves (Winkler et al. 2011). The flying ability and extent to which fledgling Tree Swallows feed themselves likely depends on their age and wing length at fledging (Michaud and Leonard 2000, Winkler et al. 2011). However, regardless of fledging age, Tree Swallows have a relatively short post-fledging period during which fledglings are at best fed progressively less food by parents (Michaud and Leonard 2000). As such, fledgling Tree Swallows must be able to forage efficiently at, or shortly after, the time of fledging (Michaud and Leonard 2000) and, therefore, optimum wing loading at or shortly after fledging is important. McCarty (2001) found that Tree Swallows that fledged with longer wings were more likely to be recaptured the following year, suggesting that longer wings, and

perhaps correspondingly lower wing loading, improves the likelihood of fledglings surviving their first year of life.

For both swifts and Tree Swallows, and likely other hirundines as well, optimum or near optimum wing loading at fledging may be important (Martins 1997, Wright et al. 2006, Goodpaster and Ritchison 2014). However, my results suggest that, in contrast to Common and Chimney swifts (Wright et al. 2006, Goodpaster and Ritchison 2014), mass loss by nestling Tree Swallows prior to fledging results from natural physiological processes rather than via a facultative mechanism. At least two factors may contribute to this difference between swifts and Tree Swallows. First, the nestling periods of Common and Chimney swifts average about 31 days and 28 to 30 days, respectively (Wright et al. 2006, Steeves et al. 2014), and peak mass is achieved a week or even two before fledging (Wright et al. 2006, Steeves et al. 2014). In contrast, the nestling period for Tree Swallows ranges from 18 to 22 days (mean = 20 days; Michaud and Leonard 2000), with peak mass typically attained sometime between days 12 and 16 post-hatching (Zach and Mayoh 1982, Quinney et al. 1986, McCarty 2001, Winkler et al. 2011, this study). In my study, mean age at fledging was  $20.9 \pm 0.2$  (range = 18 – 22 days post-hatching) days post-hatching and the mean age at peak mass was  $15.4 \pm 0.2$  days post-hatching (n = 127 nestlings, range = 11 – 20 days post-hatching), a mean difference of 5.5 days. On average, therefore, nestling Tree Swallows would have less time than swifts to gauge their wing loading. In addition, wing length continues to increase until and even after fledging for young Tree Swallows (McCarty 2001, Winkler et al. 2011). With mass declining and wings growth during the days prior to fledging, wing loading of

nestling Tree Swallows even a few days before fledging will likely not match that at fledging, possibly making any facultative adjustment of mass more difficult.

A second difference between Common and Chimney swifts and Tree Swallows is their typical wing loading values. Wing loading values for nestling Tree Swallows in my study averaged about  $0.32 \text{ g cm}^{-2}$  (or  $3.2 \text{ mg mm}^{-2}$ ) whereas wing loading values for young Chimney Swifts just prior to fledging averaged about  $0.4 \text{ g cm}^{-2}$  (or  $4.0 \text{ mg mm}^{-2}$ ; Goodpaster and Ritchison 2014). For young Common Swifts, wing loading values at fledging average about  $0.4 - 0.45 \text{ g cm}^{-2}$  (or  $4.0 - 4.5 \text{ mg mm}^{-2}$ ; Martins 1997). With greater wing loading plus the absence of parental care after fledging, optimum mass and wing loading at fledging may be more critical for swifts than for Tree Swallows. In support of this hypothesis, adult female Tree Swallows were found to lose an average of 4 gm (about 20% of their body mass) during the period between early incubation and the late nestling period (Boyle et al. 2012). This loss of mass increases flight efficiency and reduces the energetic cost of feeding nestlings (Boyle et al. 2012). However, these results also suggest that adult Tree Swallows can forage efficiently even with a 20% change in body mass (and, therefore, wing loading). Similarly, for fledgling Tree Swallows, limited variation in mass and wing loading may not strongly impact their flying ability. If so, mass and optimum wing loading at fledging may be less critical for young Tree Swallows than for young Chimney or Common swifts, possibly favoring a strategy of inflexible growth rather than facultative mass adjustment.

## *Conclusions*

Nestling Tree Swallows with experimentally added weights did not differ from control nestlings in either the amount of mass lost prior to fledging or wing loading at fledging, providing support for the inflexible growth schedule hypothesis (Wright et al. 2006, Goodpaster and Ritchison 2014). Nestlings do not appear to control the amount of mass loss by decreasing the amount of time spent begging. Rather, mass loss prior to fledging is likely due to loss of water as tissues mature (Ricklefs 1968). Differences between Common and Chimney swifts and Tree Swallows, and perhaps other hirundines, in how mass recession occurs prior to fledging may be due to differences in the duration of nestling periods and wing loading. With greater wing loading, optimum mass as fledging may be more critical for swifts than for Tree Swallows and other hirundines.

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APPENDIX:

TABLES

Table 1. Mean daily mass ( $\pm$  SE) of nestling Tree Swallows in the three treatment groups (including added mass of lead weights) from day 9 to day 21 post-hatching at the Blue Grass Army Depot in Madison County, Kentucky, in 2015. Numbers in parentheses are the sample sizes.

Days post-hatching	Treatment			Statistics		
	Control	Half-weighted <sup>A</sup>	Full-weighted <sup>B</sup>	<i>F</i>	df	<i>P</i>
11	18.9 $\pm$ 0.3 (48)	19.4 $\pm$ 0.4 (28)	20.6 $\pm$ 0.3 (29)	9.2	2,42	0.0005
12	19.6 $\pm$ 0.3 (58)	20.4 $\pm$ 0.4 (32)	21.4 $\pm$ 0.3 (36)	8.9	2,50	0.0005
13	20.0 $\pm$ 0.3 (58)	21.0 $\pm$ 0.4 (32)	21.6 $\pm$ 0.4 (36)	7.2	2,50	0.0018
14	20.5 $\pm$ 0.3 (58)	21.2 $\pm$ 0.3 (32)	21.7 $\pm$ 0.4 (36)	5.8	2,50	0.0056
15	20.8 $\pm$ 0.3 (58)	21.6 $\pm$ 0.3 (32)	21.9 $\pm$ 0.4 (36)	5.9	2,50	0.005
16	20.7 $\pm$ 0.2 (58)	21.4 $\pm$ 0.3 (32)	21.7 $\pm$ 0.4 (36)	5.5	2,50	0.0072
17	20.5 $\pm$ 0.2 (58)	21.0 $\pm$ 0.3 (32)	21.3 $\pm$ 0.3 (36)	5	2,50	0.011
18	19.9 $\pm$ 0.3 (58)	20.5 $\pm$ 0.3 (32)	20.8 $\pm$ 0.3 (35)	5.3	2,49	0.0082
19	19.8 $\pm$ 0.2 (52)	19.9 $\pm$ 0.3 (26)	19.8 $\pm$ 0.3 (30)	0.8	2,41	0.46
20	19.1 $\pm$ 0.3 (34)	19.3 $\pm$ 0.4 (21)	19.0 $\pm$ 0.4 (23)	0.4	2,30	0.67
21	18.5 $\pm$ 0.4 (18)	18.7 $\pm$ 0.5 (9)	18.4 $\pm$ 0.7 (10)	0.6	2,12	0.59

<sup>A</sup> Half-weighted = lead weight equal to 2.5% of peak mass (0.6 g) attached to back feathers

<sup>B</sup> Full-weighted = lead weight equal to 5% of peak mass (1.2 g) attached to back feathers

Table 2. Mean daily mass ( $\pm$  SE) of nestling Tree Swallows (not including the mass of experimentally added weights) in the three treatment groups from day 9 to day 21 post-hatching at the Blue Grass Army Depot in Madison County, Kentucky, in 2015. Numbers in parentheses are the sample sizes.

Days post-hatching	Treatment			Statistics		
	Control	Half-weighted	Full-weighted	F	df	P
11	18.9 $\pm$ 0.3 (48)	18.8 $\pm$ 0.4 (28)	19.4 $\pm$ 0.3 (29)	3	2,41	0.063
12	19.6 $\pm$ 0.3 (58)	19.8 $\pm$ 0.4 (32)	20.2 $\pm$ 0.3 (36)	1.9	2,50	0.16
13	20.0 $\pm$ 0.3 (58)	20.4 $\pm$ 0.4 (32)	20.4 $\pm$ 0.4 (36)	0.5	2,50	0.64
14	20.5 $\pm$ 0.3 (58)	20.6 $\pm$ 0.3 (32)	20.5 $\pm$ 0.4 (36)	0.8	2,50	0.47
15	20.8 $\pm$ 0.3 (58)	21.0 $\pm$ 0.3 (32)	20.7 $\pm$ 0.4 (36)	0.1	2,50	0.94
16	20.7 $\pm$ 0.2 (58)	20.8 $\pm$ 0.3 (32)	20.5 $\pm$ 0.4 (36)	0.1	2,50	0.98
17	20.5 $\pm$ 0.2 (58)	20.4 $\pm$ 0.3 (32)	20.5 $\pm$ 0.3 (36)	0.2	2,50	0.84
18	19.9 $\pm$ 0.2 (58)	19.9 $\pm$ 0.3 (32)	19.6 $\pm$ 0.3 (36)	0.1	2,49	0.92
19	19.8 $\pm$ 0.2 (52)	19.7 $\pm$ 0.3 (26)	19.2 $\pm$ 0.3 (30)	1.2	2,41	0.32
20	19.1 $\pm$ 0.3 (34)	19.3 $\pm$ 0.4 (21)	18.8 $\pm$ 0.4 (23)	0.1	2,30	0.99
21	18.5 $\pm$ 0.4 (18)	18.6 $\pm$ 0.5 (9)	18.1 $\pm$ 0.7 (10)	0.2	2,12	0.81

<sup>A</sup> Half-weighted = lead weight equal to 2.5% of peak mass (0.6 g) attached to back feathers

<sup>B</sup> Full-weighted = lead weight equal to 5% of peak mass (1.2 g) attached to back feathers

APPENDIX:  
FIGURES

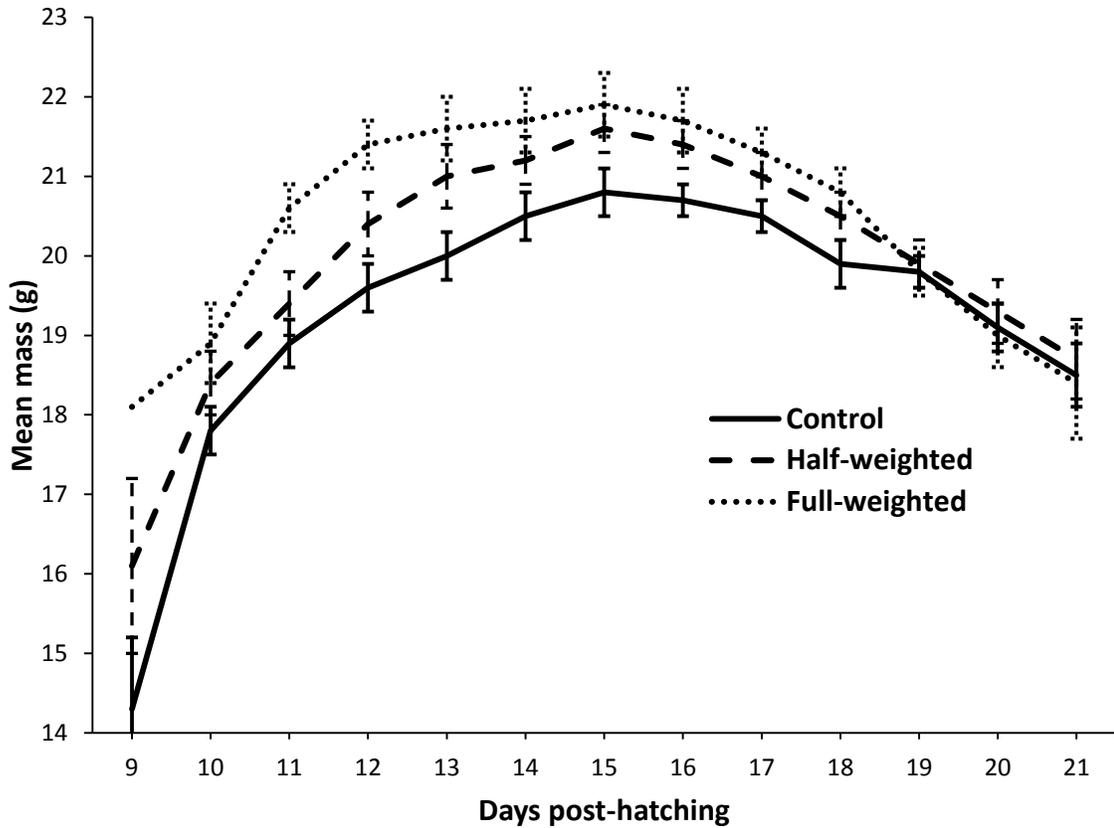


Figure 1. Mean daily mass ( $\pm$  SE) of nestling Tree Swallows in the three treatment groups including added mass of lead weights from day 9 to day 21 post-hatching (hatch day = day 1) at the Blue Grass Army Depot in Madison County, Kentucky, in 2015. Half-weighted nestlings had lead weight equal to 2.5% of peak mass (0.6 g) attached to back feathers, and full-weighted nestlings had lead weights equal to 5% of peak mass (1.2 g) attached to back feathers.

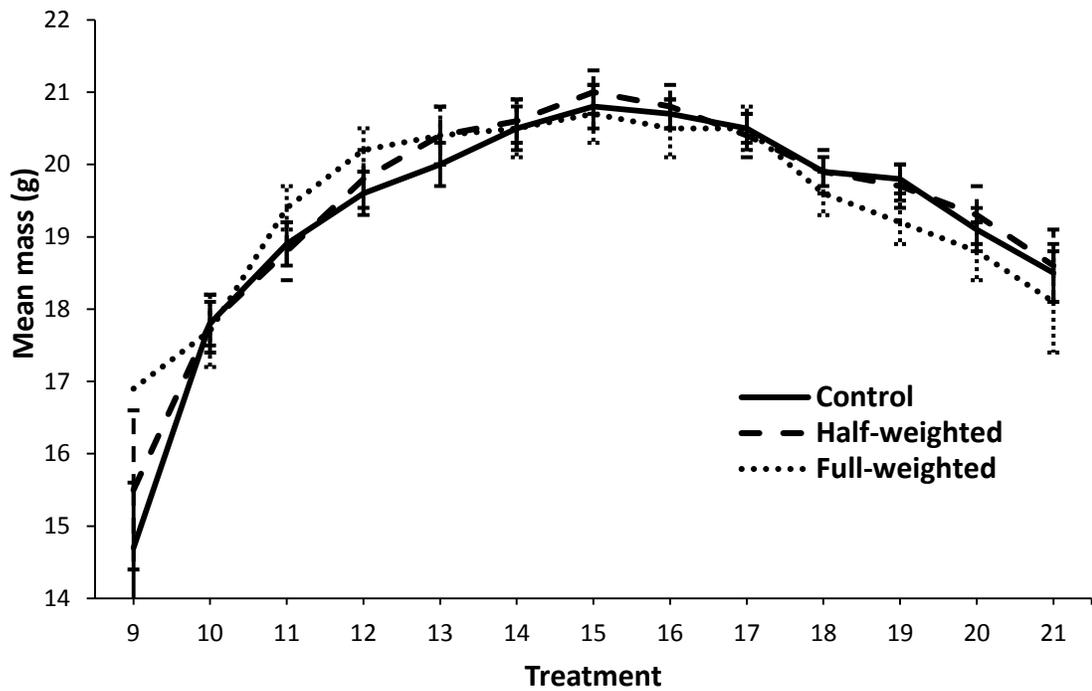


Figure 2. Mean daily mass ( $\pm$  SE) of nestling Tree Swallows in the three treatment groups without the added mass of experimentally added weights from day 9 to day 21 post-hatching (hatch day = day 1) at the Blue Grass Army Depot in Madison County, Kentucky, in 2015. Half-weighted nestlings had lead weight equal to 2.5% of peak mass (0.6 g) attached to back feathers, and full-weighted nestlings had lead weights equal to 5% of peak mass (1.2 g) attached to back feathers.

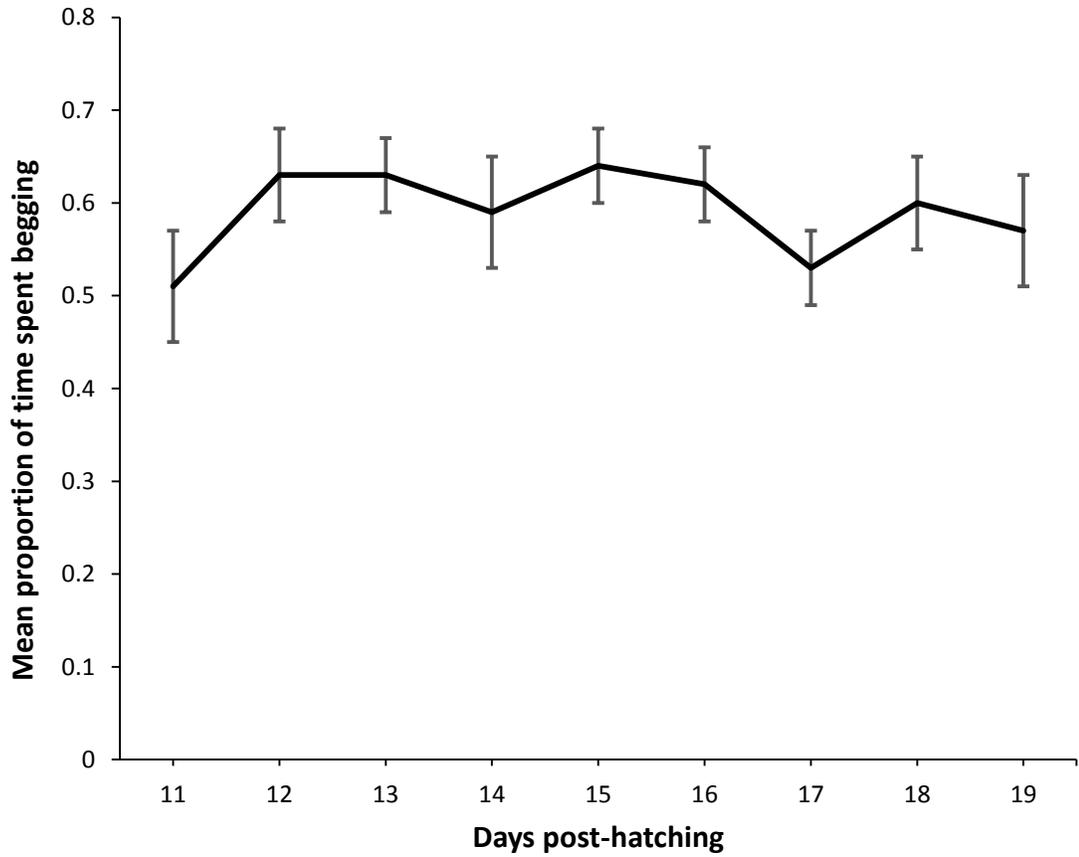


Figure 3. Mean daily proportion of time spent begging per hour ( $\pm$  SE) by nestling Tree Swallows from day 11 to day 19 post-hatching (hatch day = day 1) at the Blue Grass Army Depot in Madison County, Kentucky, in 2015.

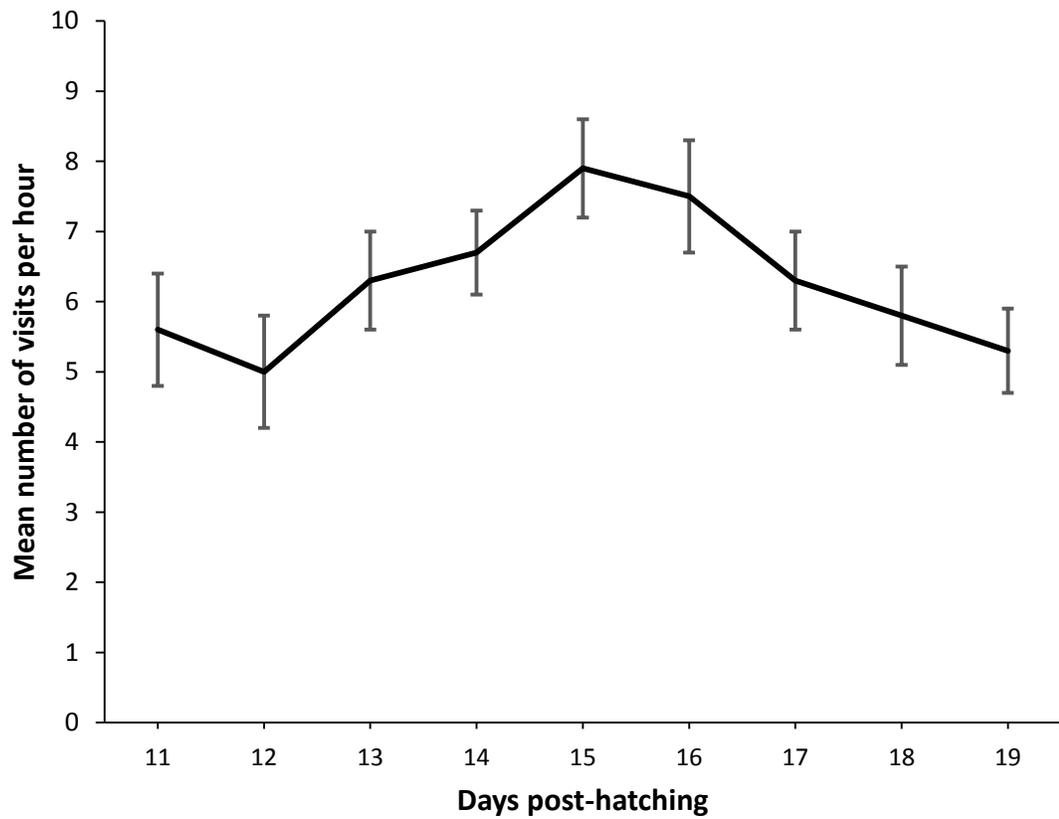


Figure 4. Mean provisioning rates ( $\pm$  SE) of adult Tree Swallows (males and females combined) from day 11 to day 19 post-hatching (hatch day = day 1) at the Blue Grass Army Depot in Madison County, Kentucky, in 2015.

## VITA

Katrina DeAnn Reeda Moeller was born in Coronado, California, on August 10, 1992. She later lived in San Antonio, Texas, Virginia Beach, Virginia, and Atoka, Tennessee. She graduated salutatorian of her Munford High School class in 2010. She later graduated from the University of Tennessee at Martin with a Bachelor of Science in Biology: Organismal Concentration, summa cum laude, a University Scholar, and Phi Kappa Phi National Honor Society. She conducted a previous study entitled *Effect of census method and season on the number and types of vocalizations uttered by Barred Owls in the area surrounding Reelfoot Lake, Tennessee* co-authored by Dr. Dawn Wilkins. Lastly, she graduated from Eastern Kentucky University with a Master of Science in Biology Degree in December 2016.