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# Facultative adjustment of pre-fledging mass recession by nestling Chimney Swifts (Chaetura pelagica)

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# Facultative adjustment of pre-fledging mass recession by nestling Chimney Swifts (*Chaetura pelagica*)

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Bachelor of Science
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2011

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# DEDICATION

This thesis is dedicated to my wonderful mother, for always believing in me, and for proofreading every paper I have ever written. Hopefully this will be the last for a while!

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# ABSTRACT

In species that are susceptible to mass-dependent flight costs, particularly seabirds and aerial insectivores, mass recession is a crucial aspect of the nestling period, ensuring fledglings will have an appropriate wing loading. My objectives were to determine if mass recession by Chimney Swift (*Chaetura pelagica*) nestlings is intrinsically controlled or facultatively adjusted by nestlings, and if mass recession is driven by changes in parental behavior (i.e., reduced provisioning rates) or nestling behavior (i.e., reduced solicitation of feedings). Nestling swifts ($N = 69$) were divided into three groups: controls, half-weighted, or weighted. Half-weighted and weighted nestlings had 0.6-0.7-g or 1.2-1.3-g lead weights, respectively, glued to the tips of the body feathers in the middle of the back during the period from 16 to 24 days post-hatching. Weighted nestlings lost more mass than both controls ($t_{48} = 2.4$, $P = 0.009$) and half-weighted nestlings ($t_{40} = 1.8$, $P = 0.04$). Control nestlings had a higher average wing loading than both half-weighted ($t_{44} = 1.9$, $P = 0.03$) and weighted nestlings ($t_{48} = 1.9$, $P = 0.03$). Video recordings of nests showed that provisioning rates of adult swifts did not vary throughout the nestling period. The percentage of time nestlings spent begging increased slightly with age, approaching significance ($F_{6,\,128} = 2.0$, $P = 0.07$). Changes in body mass among nestlings allowed those in each treatment to converge toward a similar wing loading value, which is likely optimal for flight efficiency. The mechanism(s) involved in this process remain unclear because parental provisioning rates were similar throughout the latter part of nestling period (days 12-26 post-hatching) whereas percent begging time by nestlings tended to increase with nestling age. Because I was not able to distinguish

individual nestlings, weighted nestlings may have solicited less food from adults than control nestlings, allowing them to lose more mass. Additionally, weighted nestlings may have been more active, exercising more and thus losing more mass than controls. Finally, because of their greater mass (i.e., more tissue), weighted nestlings may have also lost more water due to tissue maturation.

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# CHAPTER 1

# INTRODUCTION

After leaving nests, young birds undergo a dramatic transition from a sedentary lifestyle to one of sustained flight; from being fed by parents, to beginning to forage for themselves (Sprague and Bruener 2010). Although fledglings of some species remain with parents for a period of time and gradually become independent, others are on their own from the start (Lack 1956). Particularly for young birds in the latter category, body condition at the time of fledging is integral to their survival.

During the initial phase of development, nestlings gain weight daily (Shultz and Sydeman 1997). At their peak mass, nestlings may outweigh their parents (Phillips and Hamer 1999, Mauck and Ricklefs 2005). Several hypotheses have been proposed to explain such mass gain. Stores of body fat may prevent starvation during prolonged periods of fasting due to bad weather or poor foraging conditions (Lack 1968, Ricklefs and Schew 1994). In addition, extra fat may serve as insurance against variation in parental foraging success (Ricklefs 1990, Ricklefs and Schew 1994), and may be used to meet the greater metabolic costs experienced later in development (Phillips and Hamer 1999). Fat stores might also increase the likelihood of survival after leaving the nest, while fledglings are still improving their foraging skills (Perrins et al. 1973).

In contrast to species where young increase in mass throughout the nestling period (e.g., Putnam 1949, Sealy 1973), nestlings in some species lose mass during the period just prior to fledging. This pattern is most often seen in seabirds (e.g., Ricklefs 1968a, Phillips and Hamer 1999, Mauck and Ricklefs 2005), but weight recession is also characteristic of aerial insectivores, including Common Swifts (*Apus apus*; Wright et al. 2006). Their aerial lifestyle and foraging habits make swifts susceptible to mass-dependent flight costs. Flying with excess mass requires more energy and decreases maneuverability (Witter and Cuthill 1993). Thus, for swifts, the chances of survival after fledging might be influenced by their mass when they fledge.

The mechanism of mass recession varies among species (Sprague and Bruener 2010). In some, mass recession may be parent-driven, with parents decreasing provisioning rates as the chicks near fledging. This has been documented in several albatross species (Huin et al. 2000, Berrow and Croxall 2001, Hedd et al. 2002). In other species, mass loss may occur because chicks refuse food (Sprague and Breuner 2010). For example, Mauck and Ricklefs (2005) found that young Leach's Storm-petrels (*Oceanodroma leucorhoa*) abruptly switch to behavioral anorexia late in the nestling period. This switch seems to be triggered intrinsically by completion of structural development as the chicks near fledging age (Mauck and Ricklefs 2005, Sprague and Breuner 2010).

Each mechanism of mass recession likely has distinct consequences. If mass recession is parent-driven, then no amount of begging by nestlings will make the parents provide more food. If nestlings refuse food, a reduction in the intensity of nestling begging might be expected (Martins 1997). However, these two mechanisms may not be mutually exclusive, with parents unlikely to maintain provisioning rates if nestlings do not accept food. To determine which mechanism might be driving mass loss by nestlings, it would be necessary to determine whether parents or nestlings first change their behavior.

In addition to losing mass, nestlings in some species of birds become more active as they near fledging. For example, swift nestlings flap their wings rapidly in short bursts just like adult swifts in flight (Cink and Collins 2002, Wright et al. 2006). In addition to exercising and stretching the flight muscles, such behavior may also allow nestlings to assess their wing size or area (Wright et al. 2006). To be efficient fliers, swifts and other birds must attain the proper wing loading, the ratio of body mass to wing area. Wing flapping behavior may allow young birds to assess their wing loading (Wright et al. 2006). Swift nestlings may also perform “push-ups,” extending their wings and lifting their bodies off the nest for 2-9 seconds (Lack 1956). This behavior may also allow nestlings to assess their body mass relative to their wing length (Martins 1997). These behaviors combined would give nestlings an accurate idea of when the optimum wing loading is reached. This optimal level must fall below a critical wing loading ratio to fly efficiently, without jeopardizing the energetic reserves needed while fledglings learn to forage for themselves (Sprague and Breuner 2010).

Wright et al. (2006) discussed two possible hypotheses to describe weight recession in Common Swifts. The inflexible growth hypothesis suggests that weight recession is physiologically programmed to match each nestling’s body size. Once the initial growth phase is completed, nestlings will automatically switch to a phase of mass recession so that the final body mass is appropriate for the overall body size. Although each chick may have a slightly different rate of mass loss, the main goal is to reach an optimal wing loading ratio that will be similar for all young. In contrast, the facultative adjustment hypothesis posits that individual nestlings can assess changes in their own body mass and wing length and adjust their rate of weight recession accordingly. Rather than being controlled by physiological processes, nestlings are aware of their body condition – possibly through the exercises mentioned above – and can accelerate or decelerate their rate of weight recession as needed.  These hypotheses may also explain mass recession of young Chimney Swifts (*Chaetura pelagica*), an aerial insectivore that breeds in eastern North America. Mass recession has not explicitly been studied in Chimney Swifts, but Cink and Collins (2002) noted that young swifts reach a peak mass of about 24-25 g at about 20 days post-hatching, with mass declining to about 21-22 g when they first fly (28-30 days post-hatching).

My objectives were to determine the mechanism behind and the hypothesis that best explains mass recession by nestling Chimney Swifts prior to fledging. The hypothesis that best explains this process was determined using two different experimental treatments, weighting chicks within two weeks of fledging by applying temporary weights that were either approximately 2.5% or 5% of nestling body mass (based on Wright et al. 2006).  Based on the facultative adjustment hypothesis, if nestlings can adjust their rate of mass loss, then those that were experimentally manipulated would be able to detect the additional mass and adjust their wing loading accordingly. If, instead, nestlings are subject to an inflexible growth schedule, they would have no control over their own mass loss and would fledge with inappropriate wing loadings. To determine the mechanism involved – whether mass recession is parentally driven or driven by the nestlings themselves – interactions between adults and nestlings were videotaped. This allowed me to observe parental provisioning rates as well as nestling begging behavior.

# CHAPTER 2

# MATERIALS AND METHODS

### *Study Area*

My study was conducted from 17 May through 10 August 2012 at the Bluegrass Army Depot in Madison County, Kentucky. Chimney Swifts nest in 20-25 concrete shelters within the depot (Ritchison, pers. observ.). These shelters (about 2.5 x 5 x 2.5 m, with two openings through which people and swifts can enter and exit) are distributed throughout the depot and were constructed in the 1940's to provide army personnel with protection in case of emergencies. However, they are no longer used by Army personnel. Swifts typically arrive in breeding areas in mid-April, but do not begin building nests until May (Dexter 1969). Eggs are laid soon after nests are built, usually from late May through early June, and hatch within 19-20 days. Hatchlings typically reach their peak mass by day 20, at around 24-25 g, with mass declining to about 21-22 g by the time of their first flight (28-30 days; Cink and Collins 2002).

### *Locating Nests and Initial Measurements*

Beginning on 17 May, shelters where swifts had nested in previous years (N = 25) were checked every two days for signs of nest-building activity (i.e., sticks attached to a wall with fresh saliva). Progression of nest building and subsequent egg laying was then monitored every one or two days to determine hatching date. Once eggs hatched, nestling mass was determined every two days. Mass (± 0.1 g) was measured using an Ohaus CS series portable digital scale (CS200-001, 200g x 0.1g). Nestlings were initially identified by individual markings with permanent marker, until they were large enough to be banded with uniquely colored leg bands (about six days old).

### *Manipulations*

The experimental procedure involved two different weight manipulations: full weights and half weights. Experimentally weighted nestlings had either a 0.6-0.7 g (half-weight) or a 1.2-1.3 g (full weight) lead weight (~1.3 cm long and 0.1 cm wide) attached to body feathers (~4-5 feathers) in the middle of their back using cyanoacrylate glue, following the methods of Wright et al. (2006). Weights were attached on either day 16 or 17 post-hatching, and were removed on day 24, 25, or 26 post-hatching by cutting off the tips of the body (contour) feathers. As with weighted and half-weighted nestlings, control nestlings were taken from nests on day 16 or 17. However, control nestlings were put through a mock treatment, i.e., held for about 4 min (approximate time needed to attach weights) and repeatedly touched in the middle of the back as would occur in the gluing process.

The typical brood sizes of Chimney Swift nests (3 – 5; Cink and Collins 2002) allowed comparisons within and among treatments. Swift broods in my study consisted of 3 to 5 nestlings. In each brood in my study (N = 18), nestlings were randomly assigned to one of the treatments (control, weighted, or half-weighted). For specific nests, the number of nestlings assigned to each treatment varied with brood size, but was always either one or two. Overall, 24 nestlings were weighted, 22 nestlings were half-weighted, and 30 nestlings served as controls. Of these 76 nestlings, 69 survived to fledging (four died due to predation, and three due to starvation). Only nestlings that fledged were included in my analyses.

After the initial treatments, mass was measured every other day until day 24, 25, or 26 post-hatching, when weights were removed from the manipulated nestlings. The treatment period ended no later than day 26 post-hatching because, although young swifts often remained in shelters after day 26, they became increasing mobile (and increasingly able to fly) with increasing age and attempts to capture them after day 26 could have caused premature fledging (i.e., leaving the shelters where nests were located). On the day weights were removed, I traced the outline of each nestling's right wing onto graph paper (10 lines per 2.54 cm) to determine wing surface area and permit determination of wing loading.

### *Wing Loading Calculations*

Wing surface area ($mm^2$) was calculated by analyzing scanned images of wing tracings with the free software program ImageJ (Public Domain, NIH). Due to variation in surface area calculations (± 10 $mm^2$), each image was traced five times and subsequent surface area measurements were averaged. Only the right wing of each nestling was traced, with the left wing assumed to have the same surface area. Wing loading was calculated by dividing body mass at the end of the experiment (day 24-26 post-hatching) by the total surface area of both wings, ignoring adjacent body area (Bowlin 2007).

### *Video Recordings*

In addition to the manipulations, nests (N = 18) were also recorded to allow interactions between parents and nestlings to be observed. Camcorders mounted on tripods were placed 2 m from nests for 2 hours every day between 08:00 and 13:00. Two days prior to the first taping session, tripods were put in place so adults could habituate to their presence. Videotaping began at 12-15 days post-hatching and continued to the end of the experimental period (24-26 days post-hatching). This allowed the behavior of adults and nestlings to be monitored both when nestlings were gaining and losing mass. I subsequently viewed videos and determined provisioning rates of adults (number of provisioning trips per hour) and begging intensity of nestlings (percentage of time spent calling).

### *Statistical Analysis*

I compared the maximum mass, mass loss, and wing loading on day 24-26 (when young were last weighed) among nestlings in each treatment (control, weighted or half-weighted) using independent sample t-tests and within each nest using paired t-tests. This allowed comparison to the results of Wright et al. (2006).

Effects of brood size on mass were compared using ANOVA and post-hoc Tukey’s tests. Factorial ANOVA was then used to compare mass among treatments and brood sizes, as well as the interaction between these variables.

To determine if the behavior of adults or nestlings changes, provisioning rates of adults (provisioning rates per hour) and begging intensity of nestlings (percent time spent begging) were compared among age groups (12-13 days, 14-15 days, 16-17 days, 18-19 days, 20-21 days, 22-23 days, and 24-26 days post-hatching) using ANOVA. Age groups were used because not all broods were weighed on the same days post-hatching. A feeding was counted when parents visibly provided food to young. Begging time was considered the length of time vocalizations of at least one nestling could be heard. This value was then divided by the total time of each video to calculate the percent begging time.

Statistical analyses were conducted using IBM SPSS Statistics (Version 20). All means are provided ± SD and statistical significance was set at $P = 0.05$.

# CHAPTER 3

# RESULTS

*Effects of mass manipulations*

The mean maximum mass was 22.8 ± 1.3 g for control nestlings (N = 27), 22.3 ± 1.3 g for half-weighted nestlings (N = 19), and 23.1 ± 1.2 g for weighted nestlings (N = 23). The maximum mass of control nestlings did not differ from that of either half-weighted nestlings ($t_{44} = 1.3$, $P = 0.10$) or weighted nestlings ($t_{48} = -0.8$, $P = 0.21$). However, weighted nestlings had a higher peak mass than half-weighted nestlings ($t_{40} = -2.1$, $P = 0.023$) (Figure 1[1]).

For nestlings in different-sized broods, the mean maximum mass was 23.7 ± 1.0 g for broods of three (N = 18), 22.4 ± 1.5 g for broods of four (N = 19), 22.4 ± 1.4 g for broods of five (N = 15), and 22.6 ± 0.9 g for broods of six (N = 17). These differences were significant ($F_{3, 65} = 4.7$, $P = 0.005$). A post-hoc comparison (Tukey's test) revealed that nestlings in broods of three had a higher peak mass than those in broods of four ($P = 0.01$), five ($P = 0.02$), and six ($P = 0.04$) (Figure 2). Differences in maximum mass for nestlings in broods of four, five, and six, however, were not significant ($P \geq 0.96$). The interaction between brood size and experimental treatment was not significant ($F_{6, 57} = 0.3$, $P = 0.96$).

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[1] Refer to Appendix for all figures.

Nestling mass declined with nestling age (16-17 days, 18-19 days, 20-21 days, 22-23 days, and 24-26 days post-hatching, respectively) for all three treatment groups (Figure 3). The mean loss of mass (from day of maximum mass to the last day nestlings were weighed) was 2.1 ± 1.2 g for control nestlings, 2.2 ± 1.3 g for half-weighted nestlings, and 3.0 ± 1.4 g for weighted nestlings (Figure 4). Weighted nestlings lost more mass than both control nestlings ($t_{48} = 2.4$, $P = 0.009$) and half-weighted nestlings ($t_{40} = 1.8$, $P = 0.042$). The difference in mass loss between half-weighted and control nestlings was not significant ($t_{44} = 0.4$, $P = 0.40$).

The amount of mass lost also varied with brood size ($F_{3, 65} = 4.0$, $P = 0.012$). Tukey post-hoc comparisons indicated that nestlings in broods of three (-3.2 ± 1.3 g) lost significantly more mass than those in broods of five (-1.7 ± 1.3 g; $P = 0.006$), but no other differences were significant ($P \geq 0.20$).

*Wing Loading*

On the last day nestlings were weighed (days 24-26 post-hatching), control nestlings (0.00398 ± 0.00038 g/mm$^2$) had a higher average wing loading than both half-weighted (0.00378 ± 0.00027 g/mm$^2$; $t_{44} = 1.9$, $P = 0.03$) and weighted (0.00376 ± 0.00041 g/mm$^2$; $t_{48} = 1.9$, $P = 0.03$) nestlings (Figure 6). Wing loading of half-weighted and weighted nestlings did not differ ($t_{38.501} = 0.2$, $P = 0.43$). Similarly, wing loading did not differ among nestlings in different-sized broods ($F_{3, 65} = 0.1$, $P = 0.97$), with an overall mean wing loading of 0.0038 g/mm$^2$.

### *Begging and Feeding Rates*

Provisioning rates of adult swifts did not differ with nestling age ($F_{6, 128} = 0.8$, $P = 0.58$; Figure 7a). The percentage of time nestlings spent begging increased with increasing nestling age (Figure 7b), with the difference approaching significance ($F_{6, 128} = 2.0$, $P = 0.07$). Both provisioning rates ($F_{3, 131} = 6.6$, $P < 0.001$) and percent begging time ($F_{3, 131} = 8.7$, $P < 0.001$) increased with brood size (Figure 8). Post-hoc comparison (Tukey's test) of provisioning rate indicated that broods of three were provisioned at lower rates than broods of five ($P = 0.04$) and broods of six ($P < 0.001$), and broods of four were provisioned at lower rates than broods of six ($P = 0.01$). Post-hoc comparison of percent begging time revealed that nestlings in broods of three ($P < 0.0001$) and four ($P = 0.002$) spent less time begging than broods of six.

# CHAPTER 4

# DISCUSSION

### *Peak mass and mass recession*

After peak mass was attained, the subsequent loss of mass by nestling Chimney Swifts differed significantly among treatments in my study, with weighted nestlings losing more mass than half-weighted and control nestlings (Figure 4). These results suggest that weighted nestlings detected the experimentally added weight and adjusted their levels of mass recession accordingly, consistent with the facultative adjustment hypothesis. Although half-weighted nestlings also lost more mass than controls, the difference was not significant, possibly because the added weight was insufficient to elicit a significant response. Wright et al. (2006) also observed significantly greater mass loss in weighted nestling Common Swifts, as predicted by the facultative adjustment hypothesis.

Control nestlings in my study also had a higher wing loading than half-weighted and weighted nestlings, indicating that nestling swifts with weights and half-weights lost more mass relative to wing surface area than control nestlings. Similarly, Wright et al. (2006) also reported convergence toward a similar wing loading value for weighted and control nestlings.

Provisioning rates of adult swifts in my study remained relatively constant, whereas percent time spent begging increased slightly with age, approaching significance. Wright et al. (2006) suggested that mass recession by nestling Common Swifts was due to nestlings decreasing their begging effort and limiting their food intake in the days leading up to fledging. However, the percent time spent begging by nestling Chimney Swifts in my study did not decline during the period prior to fledging (i.e., during the period of mass recession) and adults provisioned nestlings at similar rates. Thus, my results do not support Wright et al.'s (2006) suggestion that mass recession was due to reduced begging effort and food intake by nestlings.

I also found that adult provisioning rates were similar before and after the period of nestling mass recession. However, I did not collect provisioning rate data prior to day 12 post-hatching (Figure 7a), and it is possible that adults provisioned nestlings at higher rates during the first 11 days post-hatching. For example, both Kendeigh (1952) and Fischer (1958) reported that the interval between feedings by adult Chimney Swifts increased with increasing nestling age. In contrast, Zammuto and Franks (1981) found that the time between provisioning visits by adult Chimney Swifts did not vary with nestling age. Given these conflicting results, the extent to which a possible decline in adult provisioning rates might contribute to mass recession by nestling swifts remains unclear.

However, an additional factor that may contribute to, or may be a primary cause of, mass recession by nestling Chimney Swifts is the increase in activity that occurs as young approach fledging age. In contrast to the young Common Swifts in Wright et al.'s

(2006) study that nested in nest boxes and, therefore, had limited room to flap their wings, Chimney Swifts typically nest in chimneys and buildings (such as the shelters in my study) and young leave nests to perch on nearby walls several days before fledging (about 18-22 days post-hatching; Cink and Collins 2002). On the walls, young Chimney Swifts spend much time exercising their wings and, where space permits, taking short flights (Fischer 1958, Cink and Collins 2002). Although not quantified, I often observed such behavior by young Chimney Swifts while viewing the videotapes made to document adult provisioning rates. This increased level of activity during a period when adult provisioning rates appear to either remain similar or, based on the observations of some previous investigators (Kendeigh 1952, Fischer 1958), even decline, could contribute to mass recession by nestling swifts.

Another factor likely contributing to mass recession by pre-fledging Chimney Swifts is the loss of water due to tissue maturation (Ricklefs 1968b, Phillips and Hamer 1999). Ricklefs (1968b) reported that mass recession by young Barn Swallows (Hirundo rustica) was entirely due to water loss, with the water content of fully mature tissues and feathers lower than that of embryonic tissues. Ricklefs (1968b) further noted that the additional water present in growing nestling Barn Swallows increased their body mass by several grams above that of adults when young were 10 to 12 days old, but, from then until fledging (about 20 days old), weight recession occurred as maturing tissues lost water.

Although other investigators have rejected the wing-loading hypothesis as a reason for mass recession (Morbey et al. 1999), reaching some level of flight efficiency is likely more important for swifts than other species because of the lack of post-fledging care and the need to be in constant flight (Martins 1997). The reductions in body mass observed in Common Swifts by Martins (1997) created the highest rate of change in lift:drag ratio, decreasing the cost of flight and increasing flight efficiency by 9.6%. Reduced body mass also led to reduced flight speed and increased maneuverability, qualities that improve foraging efficiency (Martins 1997). Thus, fledging with appropriate wing loading likely helps ensure that swift nestlings will be able to forage efficiently.

### *Effects of Brood Size*

Average maximum mass and change in mass were greater for smaller broods, whereas provisioning rates and begging rates were higher for larger broods. These results are consistent with those of Martins (1997) and Wright et al. (2006). In Common Swifts, parents only feed one nestling at a time after about a week post-hatching (Lack 1956), so, to deliver equivalent amounts of food per nestling, more nestlings in a brood would require higher provisioning rates. However, Martins (1997) found that this increase in provisioning rate was not proportional to the number of nestlings, so each chick in larger broods received less food. Thus, nestlings in larger broods have a lower peak mass and, as a result lose less mass prior to fledging. Wing loading did not differ among nestlings in different-sized broods in my study, suggesting that the optimal ratio for flight efficiency is similar for all young swifts regardless of brood size or maximum mass attained during the nestling period (Martins 1997, Wright et al. 2006).

### *Conclusion*

The results presented here of experimental mass manipulations in nestling Chimney Swifts seem to support the facultative adjustment hypothesis. Weighted nestlings were able to accelerate their rate of mass recession, so that they ultimately attained a wing loading ratio similar to that of other nestlings. However, the mechanism involved in this process is still unclear; parental provisioning rates were relatively constant throughout the nestling period, whereas percent begging time by nestlings tended to increase with nestling age. Given that individual nestlings could not be distinguished in my recordings, it is possible that weighted nestlings solicit less food from adults than control nestlings, allowing them to lose more mass. Additionally, weighted nestlings may have been more active, exercising more and thus losing more mass than controls. Finally, because weighted nestlings put on more mass (i.e., tissue), they had more water weight to lose. Any combination of these factors may have contributed to the differential mass recession by weighted, half-weighted, and control nestlings observed in my study. Regardless of the mechanism(s) driving mass recession by young Chimney Swifts, all nestlings converged at a similar wing loading ratio, suggesting that this was the optimal ratio for flight efficiency.

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# APPENDIX:

## Figures

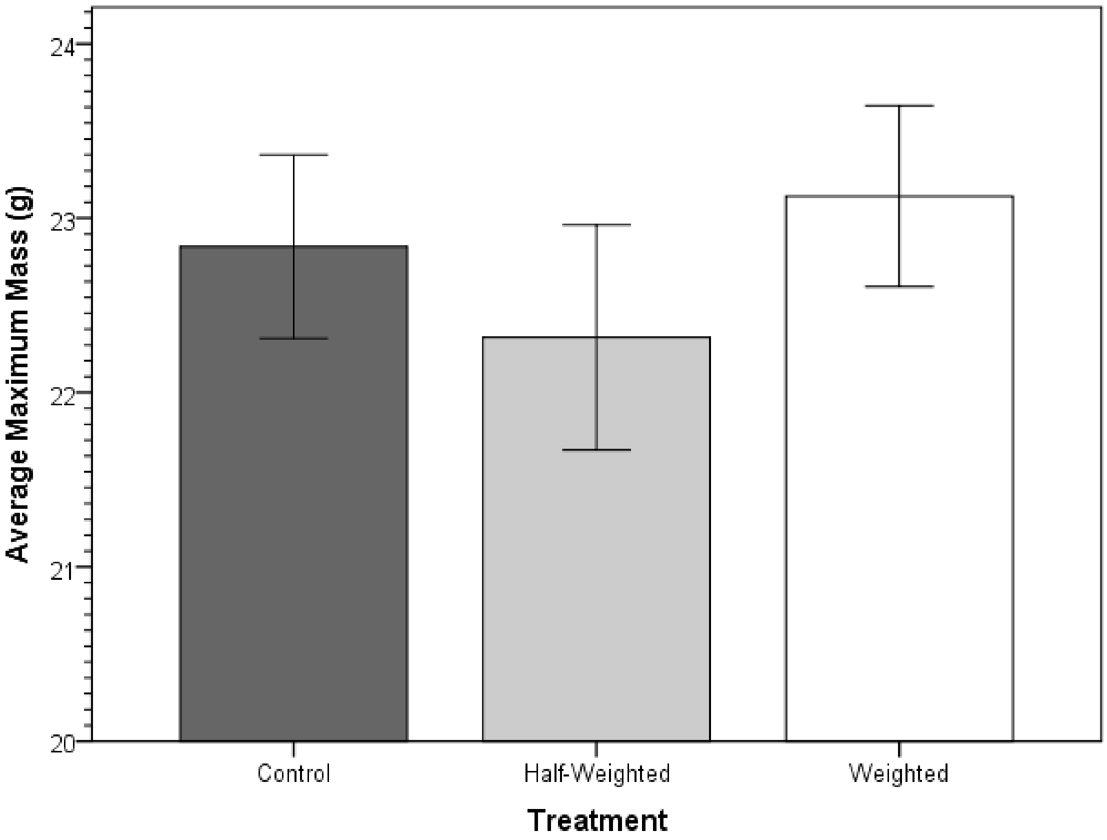


Figure 1. Average maximum mass of Chimney Swift nestlings in three experimental groups at the Bluegrass Army Depot (BGAD) in Madison County, KY, during the summer of 2012. Experimental groups included controls, half-weighted (a 0.6-g weight attached to the back), and weighted (a 1.2-g weight attached to the back). Error bars = 95% CI.

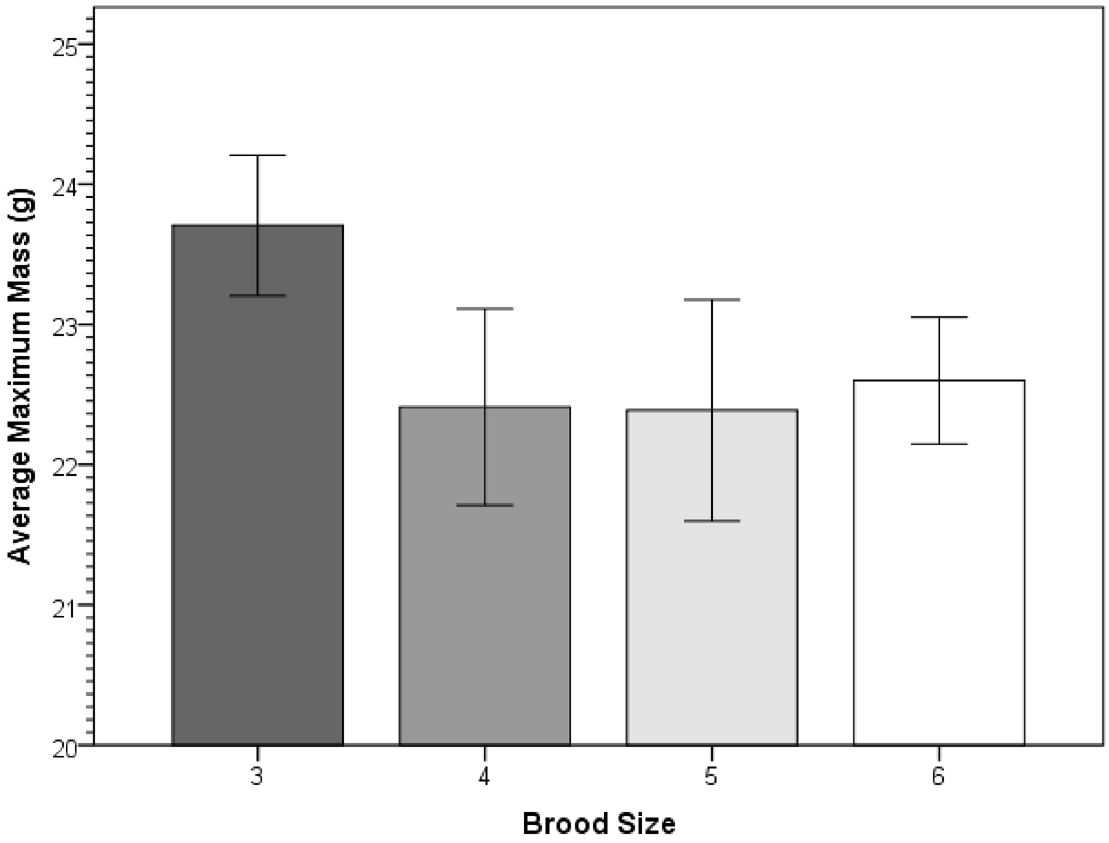


Figure 2. Average maximum mass of Chimney Swift nestlings in different-sized broods (3-6 nestlings) at the BGAD in Madison County, KY, during the summer of 2012. Error bars = 95% CI.

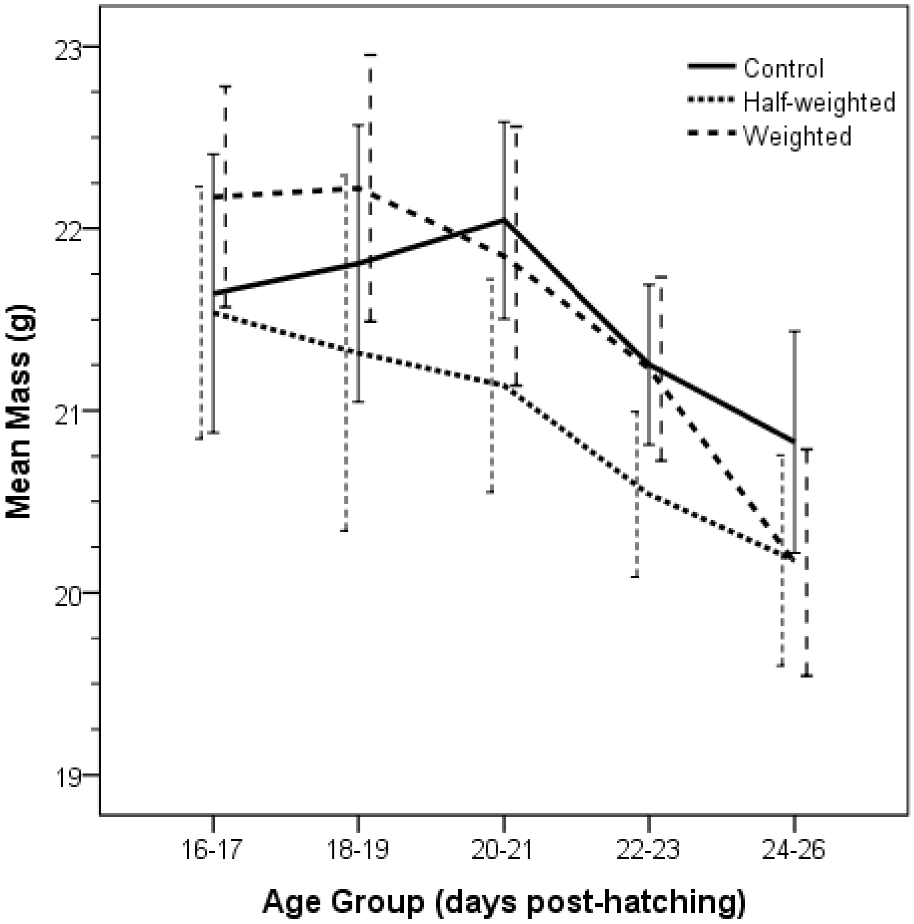


Figure 3. Average daily mass of Chimney Swift nestlings in three treatment groups throughout the experimental period (16-26 days post-hatching) at the BGAD in Madison County, KY, during the summer of 2012. Error bars = 95% CI.

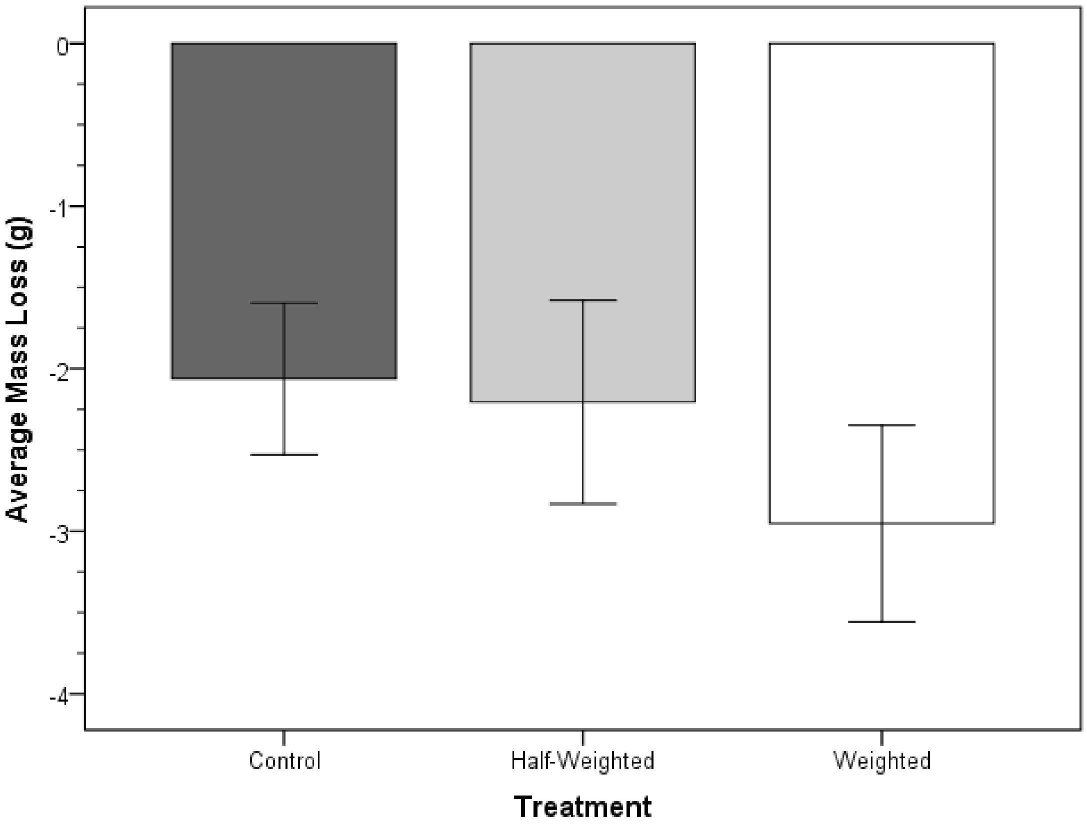


Figure 4. Average mass loss (maximum mass minus mass at time of last weighing) of Chimney Swift nestlings in three experimental groups at the BGAD in Madison County, KY, during the summer of 2012. Error bars = 95% CI.

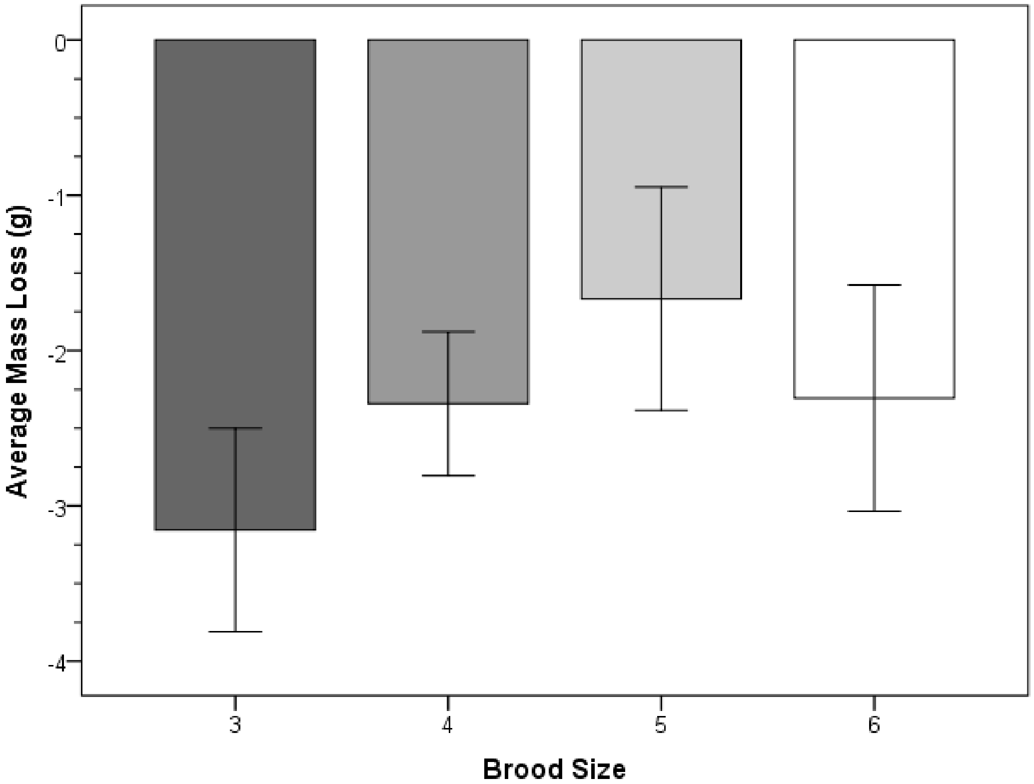


Figure 5. Average mass loss by Chimney Swift nestlings in different-sized broods at the BGAD in Madison County, KY, during the summer of 2012. Error bars = 95% CI.

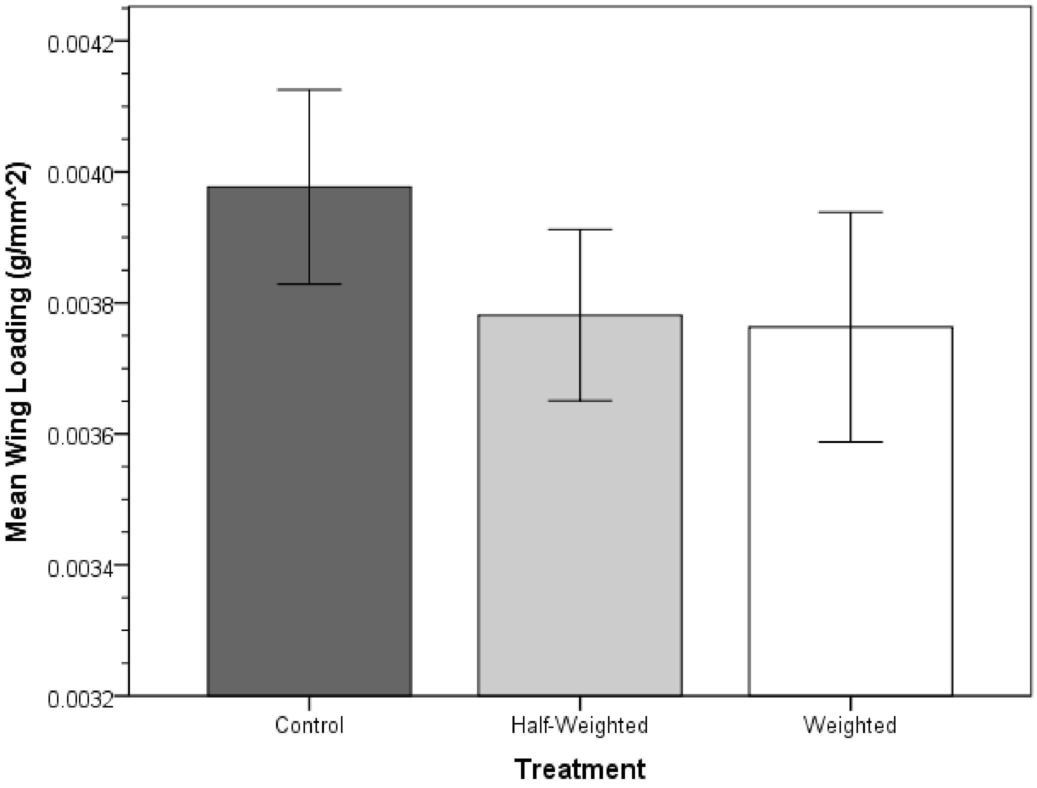


Figure 6. Average wing loading (g/mm$^2$) of Chimney Swift nestlings at end of the experimental period (24-26 days post-hatching) for three experimental groups at the BGAD in Madison County, KY, during the summer of 2012. Error bars = 95% CI.

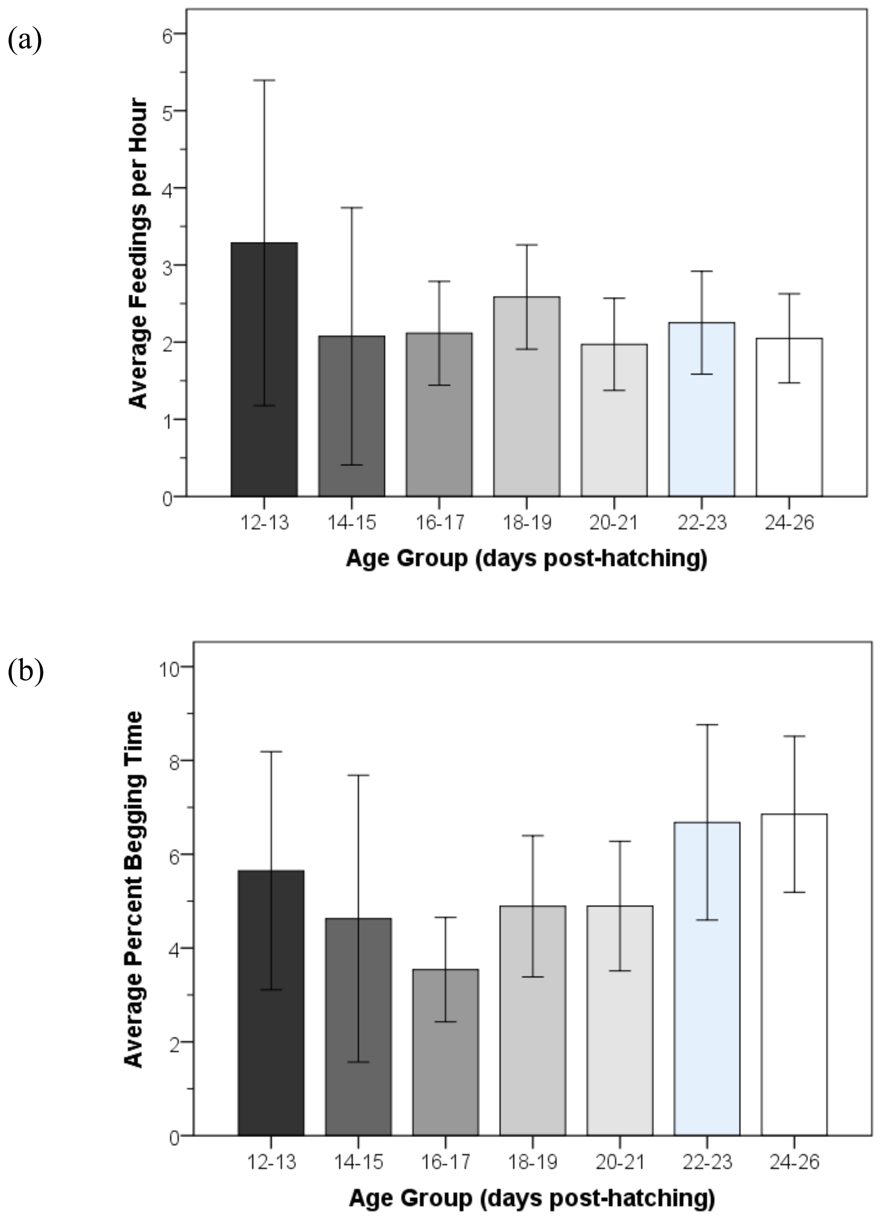
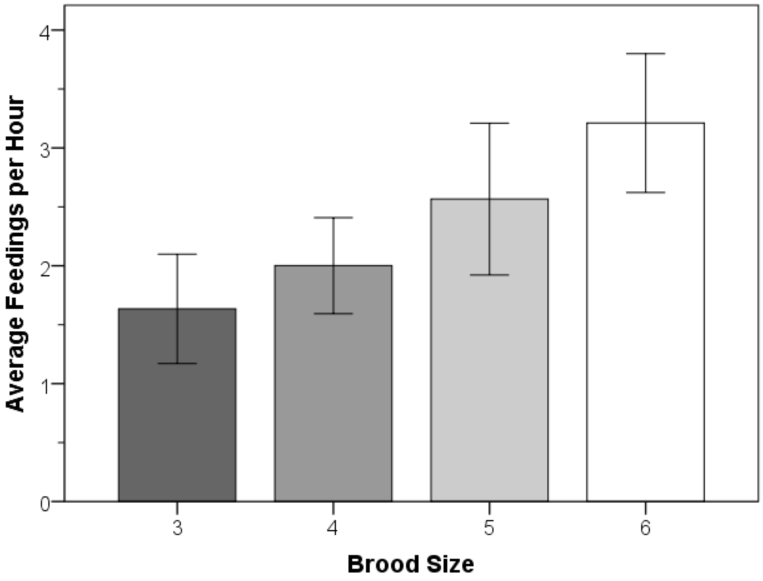


Figure 7. Changes in (a) adult provisioning rates and (b) percent time begging by nestlings throughout the nestling period for 18 Chimney Swift broods at the BGAD in Madison County, KY, during the summer of 2012. Error bars = 95% CI.

(a)



(b)

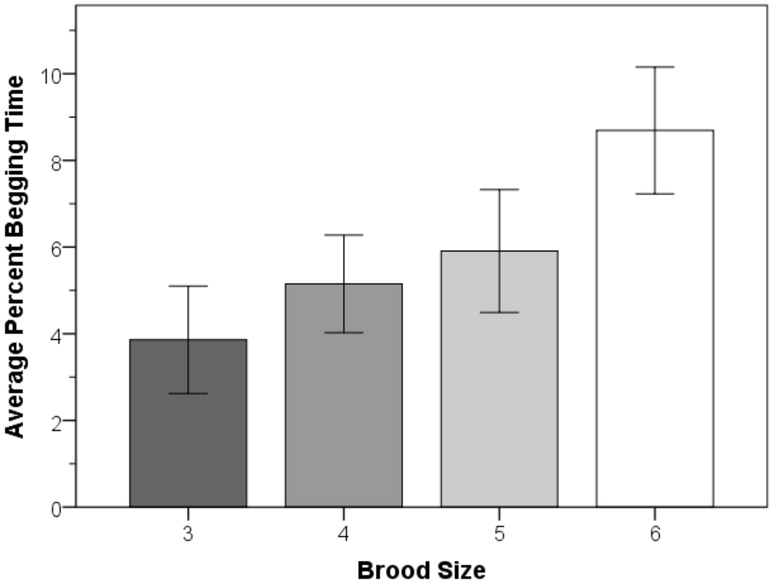


Figure 8. Variation in (a) provisioning rates of adults and (b) percent time spent begging by neslings in different-sized broods (3-6 nestlings) at the BGAD in Madison County, KY, during the summer of 2012. Error bars = 95% CI.

# VITA

Sagan Brianne Goodpaster (Kleinrichert) was born in Lagrange, IN on December 26, 1989. She later moved with her mother to West Liberty, KY. She graduated from Morgan County High School in May 2007 as the class valedictorian. In May 2011, she graduated *magna cum laude* with a Bachelor of Science in Biology from Morehead State University. She then went on to Eastern Kentucky University, where she became a member of the Phi Kappa Phi honor society, and graduated with a Master of Science in Biology in August 2013.

Sagan is currently employed as a biology instructor for Maysville Community and Technical College at the Rowan and Montgomery County campuses.