January 2018

Variation in mass and wing loading of nestling American Kestrels: possible effects of nestling behavior and adult provisioning behavior

Doug Mitchell
Eastern Kentucky University

Recommended Citation

Mitchell, Doug, "Variation in mass and wing loading of nestling American Kestrels: possible effects of nestling behavior and adult provisioning behavior" (2018). *Online Theses and Dissertations*. 542.
https://encompass.eku.edu/etd/542

VARIATION IN MASS AND WING LOADING OF NESTLING AMERICAN KESTRELS: POSSIBLE EFFECTS OF NESTLING BEHAVIOR AND ADULT PROVISIONING BEHAVIOR

By:

DOUG MITCHELL

THESIS APPROVED:

Chair, Advisory Committee

Member, Advisory Committee

Member, Advisory Committee

Dean, Graduate School

STATEMENT OF PERMISSION TO USE

In presenting this thesis in partial fulfillment of the requirements for a Master's degree at Eastern Kentucky University, I agree that the Library shall make it available to borrowers under rules of the Library. Brief quotations from this thesis are allowable without special permission, provided that accurate acknowledgment of the source is made. Permission for extensive quotation from or reproduction of this thesis may be granted by my major professor, or in [his/her] absence, by the Head of Interlibrary Services when, in the opinion of either, the proposed use of the material is for scholarly purposes. Any copying or use of the material in this thesis for financial gain shall not be allowed without my written permission.

Signature Doug Mitchell

Date March 30th 2018

VARIATION IN MASS AND WING LOADING OF NESTLING AMERICAN KESTRELS: POSSIBLE EFFECTS OF NESTLING BEHAVIOR AND ADULT PROVISIONING BEHAVIOR

BY
DOUG MITCHELL

Bachelor of Science
College of the Ozarks
Point Lookout, MO
2014

Submitted to the Faculty of the Graduate School of
Eastern Kentucky University
in partial fulfillment of the requirements
for the degree of
MASTER OF SCIENCE IN APPLIED ECOLOGY
May, 2018

ACKNOWLEDGMENTS

I would like to thank Dr. Gary Ritchison for providing the opportunity, guidance, and assistance on this project. Dr. Charles Elliott and Dr. Luke Dodd also provided advice and assistance. Thanks to the United States Army and Nathan White for allowing me to conduct field work at Blue Grass Army Depot. This project was also partially funded by the Kentucky Society of Natural History. I would also like to thank my family for their encouragement and support. The following students from Eastern Kentucky University were instrumental in helping me review the nest videos: John Abrams, Samantha Hoffman, Kevin Mardell, and Abby Newquist. I would also like to thank the following researchers and professors for their encouragement and for instilling in me a passion for studying nature: Dr. Jeff Rettig and Dr. Robert Snyder at College of the Ozarks, Andy Thomas at the University of Missouri Southwest Research Center, Dr. Paul Porneluzi with the Missouri Ozark Forest Ecosystem Project, and John Macey at Fort Hood DPW Natural Resources.

ABSTRACT

Among birds, the rapid growth rates of altricial young help reduce mortality by reducing the amount of time spent in the nest. However, in species where a high degree of maneuverability and speed is required (i.e. aerial insectivores), it is important that nestlings not gain excess weight. Nestlings in some species must attain an efficient wing loading just prior to fledging to facilitate mobility for hunting and evading predators. My objective was to examine the mass of nestling American Kestrels (*Falco sparverius*) during the mid- to late nestling period and specifically to determine the possible effects of attaching small lead weights (3gm and 6gm) to some nestlings. If wing loading at fledging is important for nestling kestrels, then the mass of nestlings with and without weights attached might differ at fledging whereas wing-loading values should be similar. My study was conducted during the 2016 breeding season at the Blue Grass Army Depot in Madison County, Kentucky. Nestling kestrels (n = 40) in 12 broods were divided into three treatment groups: control (n = 12), half-weighted (n = 14), and full-weighted (n = 14). At day 15 post-hatching, half-weighted nestlings received 3-g lead weights and weighted nestlings received 6-g weights, representing 2.5% and 5% of mean adult body mass. I used video recordings to monitor parental provisioning behavior and nestling begging behavior. After subtracting the mass of the lead weights, there were no differences among the treatment groups in mass or wing loading prior to fledging. Over the course of the nestling period, there was no change in the amount of prey biomass delivered per nestling per hour. However, there was a difference in the begging intensity, percent time begging, and activity levels by the nestlings in the days prior to fledging. These results suggest that the asymptotic mass of nestling kestrels is not due to parental behavior. Instead, a combination of physiological processes and nestling behavior may be influencing the asymptotic mass. The lack of difference in mass and wing loading among treatment groups may be due to the greater flexibility in wing loading required by predatory birds. These results also suggest that achieving optimum wing loading prior to fledging is less critical for American Kestrels than for smaller insectivorous birds.

TABLE OF CONTENTS

CHAPTER PAGE

LIST OF TABLES

LIST OF FIGURES

FIGURE PAGE

CHAPTER 1

INTRODUCTION

Nestlings of altricial species of birds grow at a rapid rate. This rapid growth can reduce nestling mortality rates by shortening the nestling period [1](Martin 1987). However, for species of birds where nestling mobility after fledging is important, nestlings must not gain too much mass during this period of rapid growth. Greater mass at fledging may result in young being less maneuverable and more susceptible to predation (Witter and Cuthill 1993). However, nestlings in many species of birds display a sigmoidal growth curve, such that mass gain ceases or mass may even decrease slightly just prior to fledging (Ricklefs 1968a). This leveling off or loss of mass prior to fledging may be due in part to water loss during feather development, but other factors such as changes in adult or nestling behavior might also influence nestling mass (Ricklefs 1968b).

The growth curves of nestling American Kestrels (*Falco sparverius*) are sigmoid in form, with mass increasing at the highest rate during the mid-nestling period and leveling off in the days prior to fledging (Roest 1957). In addition, studies to date suggest a tendency for nestling kestrels to attain similar masses prior to fledging. For example, nestling American Kestrels that were starved for short periods of time achieved similar asymptotic body mass as nestlings fed on a regular basis (Negro et al. 1994). Similarly, nestlings provided with supplemental food did not differ from control nestlings in either

---

[1] All figures and tables are presented in appendices at end of thesis

mass at fledging or survival rates after fledging (Dawson and Bortolotti 2002). Food-supplemented nestling Eurasian Kestrels (*Falco tinnunculus*) also had similar asymptotic mass and growth rates as control nestlings (Massemin et al. 2002). This tendency for nestling kestrels to achieve a similar mass and body condition despite differences in food availability suggests that some factor or factors help maintain or slightly reduce their mass during the days just prior to fledging.

The mass of nestlings prior to fledging may be influenced by the provisioning behavior of the parents. For example, adult Ferruginous Hawks (*Buteo regalis)* were found to deliver the most food to nestlings (grams/nestling/hour) at approximately the midpoint of the nestling stage. Similarly, adult Swainson's Hawks (*Buteo swainsonii*) delivered the most prey biomass to nestlings about three-quarters of the way through the nestling stage (Giovanni et al. 2007). Such results suggest that the amount of biomass delivered to nestling raptors may decrease in the days prior to fledging. However, the asymptotic sigmoid growth curves of nestlings may also result from changes in nestling behavior, e.g., an increase in energy use due to increasing activity of nestlings.

The sigmoidal growth curves of nestling American Kestrels, and specifically the leveling off or slight decline in mass just prior to fledging, may be important for achieving an efficient ratio of body mass to wing area, or wing loading. For example, nestling Common Swifts (*Apus apus*) fed at different rates due to experimentally manipulated brood sizes all achieved the same wing loading at fledging (Martins 1997). In another study, nestling Common Swifts fit with artificial weights lost more mass in the two weeks prior to fledging than did unweighted control nestlings (Wright et al. 2006). Weighted nestlings also fledged with wing-loading values that matched the control nestlings, suggesting that nestlings were able to sense the extra mass and facultatively adjust their mass to attain proper wing loading prior to fledging (Wright et al. 2006). Similar results were obtained in a study of nestling Chimney Swifts (*Chaetura pelagica*) fit with weights (Goodpaster and Ritchison 2014).

The extent to which changes in parental or nestling behavior may contribute to the sigmoidal growth curves of nestling American Kestrels and the factors that might favor a cessation in mass gain by nestlings just prior to fledging remain to be determined. Thus, my objectives were to: (1) examine the provisioning rates of adult kestrels and the begging behavior of nestlings to determine if changes in either adult or nestling behavior might contribute to changes in nestling mass (leveling off or declining) prior to fledging, and (2) compare the mass and wing loading of nestlings with and without small weights attached to their backs to determine if experimental manipulation of the ‘apparent mass’ of nestlings results in differences in actual mass and similar wing loading values just prior to fledging. Similar wing loading values of manipulated and non-manipulated (control) nestlings would provide support for the hypothesis that wing loading at fledging is important for young American Kestrels and that cessation of mass gain in the days prior to fledging is important in achieving wing-loading values that enhance the flying ability of newly fledged young.

Chapter 2

MATERIALS AND METHODS

My study was conducted at the Blue Grass Army Depot in Madison County, Kentucky, from March to July 2016. The Depot is comprised of 6014 ha of scattered woodlots, pasture, and ungrazed grassland. Thirty-three nest boxes were available for use by kestrels at the depot. Procedures related to the capture and handling of kestrels in my study were reviewed by Eastern Kentucky University's Institutional Animal Care and Use Committee and approved as Protocol #03-2016. I began monitoring nest boxes in early March 2016 to determine if kestrels were present near boxes, suggesting probable use for nesting. Beginning on 1 April, I checked nest boxes for eggs every three to five days using a small camera and monitor mounted on a pole (TreeTop Peeper, Sandpiper Technologies, Inc., Manteca, CA). The incubation period of American Kestrels is typically 29 to 31 days (Johnsgard 1990), so I began checking nest boxes with eggs daily about 28 days after the first egg was laid to ensure accurate determination of hatch day.

Nest boxes with eggs were modified for video recording. Nest boxes were designed so that the right side (when viewed from the front) could be rotated upward to allow access to the interior. That side was removed and, in its place, a new side of the same size was attached, but with a 10 cm x 10 cm opening covered with wire mesh (to keep nestlings in the nest box). Attached to the new side was a 12.5 cm x 12.5 cm x 38 cm-long, plastic 'camcorder box' with a removable top so camcorders could be inserted and removed. After installation of the camcorder box, a 'fake' camcorder (made of cardboard, but similar in size and color to a real camcorder) was inserted. By modifying nest boxes at least three or more days before recording began (and placing a 'fake' camcorder inside), adult and nestling kestrels were able to habituate to the altered appearance of their nest box and the presence of a camcorder. During video-recording, a real camcorder (Handycam HDR-XR 100, Sony, Tokyo, Japan) was placed in the camcorder box and its position adjusted to provide the best view of nestlings and the nest-box entrance.

I video-recorded at kestrel nests during the period from 1 May 2016 to 2 July 2016. Video-recording began when nestlings were nine days old and continued every day until fledging. Some nests were not recorded every day due to a limited number of camcorders, and I did not record during inclement weather or heavy winds. I video-recorded each nest for ≈4 hours between approximately 0800 and 1200 hours when kestrels usually deliver food at the highest rates (Smallwood and Bird 2002). Videos were later viewed to examine nestling begging behavior and adult provisioning rates. When an adult kestrel arrived at the box, I categorized nestling begging behavior as: 0 = no vocalizations/no response, 1 = vocalizing only, 2 = gaping, 3 = gaping with extended neck, and 4 = gaping with extended neck and flapping wings. I quantified nestling begging behavior by calculating the percent of time nestlings spent begging for every hour of video. I also quantified nestling activity levels (when adults were absent from the nest box) by counting the number of times a nestling flapped or jumped for every hour of video. A single jump was recorded any time a nestling tried to jump into the nest entrance or to jump up and cling to the walls of the box. A single flap was recorded when a nestling fully extended its wings and completed at least one complete wing stroke.

I quantified adult kestrel provisioning behavior as the number of food deliveries per hour as well as by the prey biomass delivered. Mass estimates for small mammalian prey were calculated using information from Barbour and Davis (1974) and from Kays and Wilson (2002). Estimates for reptile, amphibian, and bird prey items were calculated using information from Steenhof (1983). I estimated biomass of invertebrate prey items by conducting net sweeps near the study area and measuring the specimens and weighing them using a digital scale (± 0.001 gm; Mettler Toledo AL204). I then plotted the masses (gm) and lengths (mm) and calculated the slope. I generated mass estimates for prey items by entering their lengths (based on comparing its size to the ≈ 6mm wire mesh openings in the camera boxes) and solving for the mass in the slope equation.

After eggs hatched, I tied different-colored threads around the legs of nestling kestrels in each nest box to permit individual identification. When nestlings were large enough (about 10 days old), I removed the threads and banded each nestling with a colored plastic band. I weighed nestlings daily with a digital scale (± 0.1 gm). When nestlings reached 15 days old, the weight manipulation treatments began. I applied the weight treatments to nestlings randomly, but attempted to maintain an equal number birds per treatment and per sex. For the half-weighted treatment group, I used cyanoacrylate glue to attach a lead strip weighing 3 gm to feathers on the back of the nestling. Birds in the full-weighted treatment group received a lead strip weighing 6 gm.

The weight of these lead strips represented approximately 2.5% and 5% of the average mass of an adult American Kestrel (Balgooyen 1976). Weights representing these same percentages of the body mass of adults of other species have been used previously in similar studies (Wright et al. 2006, Goodpaster and Ritchison 2014). All other nestlings served as controls and were treated in the same manner as the weighted nestlings except that weights were not glued to their backs. I put control nestlings through a mock treatment equal to the amount of time required to weigh, band, and attach weights to treated nestlings. If a weight was lost and needed to be reattached to a nestling, I put all their siblings through an additional mock treatment.

I removed weights from birds when their flight feathers had little remaining sheath (≈ 26-28 days post-hatching), which is also about 2-4 days before nestling kestrels usually fledge (Smallwood and Bird 2002). I removed the weights by carefully trimming the glued body feathers with a scalpel. After removing weights, I also traced the right wing of each nestling on graph paper. Scanned images of the wing tracings were then re-traced using the program ImageJ (National Institutes of Health, Bethesda, Maryland). I traced each wing image in the program 5 times (scale: 39 pixels = 1 cm) and then averaged these values. I doubled this value to calculate the surface area of both wings. I calculated wing loading by dividing the birds mass on the day wings were traced by the surface area of the wings (gm/cm^2).

Statistical analyses

To determine the effect of the weights on kestrel nestlings, I compared the mass of weighted and control nestlings from day 9 post-hatching to the day the weights were removed. I also compared the wing loading of weighted and control nestlings. Two nestlings that displayed poor mass gain and feather development were not used in the mass and wing loading analyses. For nestling begging behavior and parental provisioning rates, I compared mean values for percent time begging, begging intensity, number of deliveries per hour, and prey biomass per hour. To assess nestling activity levels, I used the mean number of jumps and flaps per nestling per hour. I used the mean values of 11 two-day periods (days post-hatching 9 and 10 through days 29 and 30) for all analyses. Because the behavior of adults and nestlings at all nests were monitored over several days, I used repeated measures analysis of variance for all analyses. When differences were significant ($P<0.05$), I used post-hoc tests (Student-Newman-Keuls tests) to determine which means differed. All analyses were conducted using the Statistical Analysis System (SAS Institute, Inc., Cary, NC). Values are presented as means ± SE.

Chapter 3

RESULTS

Number of nests and clutch and brood sizes

Kestrels at the Blue Grass Army Depot began laying and incubating eggs in mid-March and the last clutch was completed in mid-May of 2016. Modal clutch size was five eggs (N = 98 eggs and 21 nests). Six nests were lost to predation, one nest with eggs was abandoned (the adult female may have been predated), eggs (N = 5) were incubated, but did not hatch at another nest, and one additional nest with four nestlings was abandoned after disappearance of the adult female (the adult male was observed nearby, but did not continue to provision the nestlings). A total of 12 remaining nests were used for this study.

Surviving nestlings fledged between 25 days and 36 days post-hatching. The average age at fledging was 30 days post-hatch. The first nestling fledged on 19 May 2016 and the last nestling fledged on 2 July 2016.

Nestling mass and wing loading

The mean mass of nestlings on the day of hatching was 10.94 ± 0.75 grams (N = 13). Nestlings grew rapidly until about day 20 post-hatching when mass changed little until fledging 5 to 10 days later (Table 1).

The mean age of nestlings when wings were traced and fledglings were weighed did not differ among treatment groups ($F_{2,14} = 0.5$, $P = 0.63$). The mass of nestlings including the mass of the weights (manipulated mass) on the last day they were weighed did not differ among treatment groups ($F_{2,14} = 1.6$, $P = 0.23$; Figure 1) and the interaction between treatment and sex was not significant ($F_{2,3} = 0.2$, $P = 0.79$).

I found no difference among treatment groups in wing loading (with weights still attached; $F_{2,14} = 2.9$, $P = 0.089$) and no interaction between treatment and sex ($F_{2,3} = 0.5$, $P = 0.96$). Wing surface area was also similar among treatments ($F_{2,14} = 0.7$, $P = 0.49$), with no interaction between treatment and sex ($F_{2,3} = 0.01$, $P = 0.92$). Similarly, the final mass of nestlings with weights removed (actual mass) did not differ among treatments ($F_{2,14} = 0.2$, $P = 0.81$; Figure 2), with no interaction between treatment and sex ($F_{2,3} = 0.3$, $P = 0.79$). In addition, I found no difference among treatments in wing loading after removal of weights ($F_{2,14} = 1.0$, $P = 0.38$), with wing loading values of 0.51 ± 0.02 g/cm^2 for control nestlings, 0.48 ± 0.01 g/cm^2 for half-weighted nestlings, and 0.50 ± 0.01 g/cm^2 for full-weighted nestlings.

Provisioning, begging behavior, and activity levels

Between days 9 and 30 post-hatching, parental provisioning rates (number of visits/nestling/hour) varied with nestling age ($F_{12,77} = 4.5$, $P < 0.0001$). However, a post-hoc test revealed that mean provisioning rates were generally similar throughout most of the nestling period (SNK tests, $P > 0.05$; Figure 3). Provisioning rates were significantly higher on days 29-30 post-hatching than during the rest of the nestling period (SNK, $P < 0.05$; Figure 3), but the mean for days 29-30 post-hatching was based on data collected on only five days at three nests. Finally, the amount of prey biomass delivered per nestling per hour did not vary with nestling age ($F_{10,77} = 0.7$, $P = 0.70$; Figure 4). Prey items included members of Orthoptera, Odonata, Coleoptera, Lepidoptera, Araneae, Rodentia, Squamata, Anura, and Passeriformes.

The proportion of time nestlings spent begging varied with nestling age ($F_{10,77}$ = 5.2, P < 0.0001); nestlings tended to spend more time begging between days 9 – 12 post-hatching than during the rest of the nestling period (SNK tests, Figure 5). Mean begging intensity also varied with nestling age ($F_{10,77}$ = 3.2, P = 0.0017), with intensity similar throughout most of the nestling period before declining during the last few days before fledging (SNK tests; Figure 6). The number of jumps per nestling per hour ($F_{10,77}$ = 6.1, P < 0.0001) and the number of flaps per nestling per hour ($F_{10,77}$ = 2.8, P = 0.0055) also varied with nestling age, with both jumping and flapping rates higher in the week prior to fledging (SNK tests; Figures 7 and 8).

Chapter 4

DISCUSSION

Experimentally increasing the mass of nestling American Kestrels by attaching weights to their backs had no effect on body mass prior to fledging, with no difference in the body masses of control, weighted, and half-weighted nestlings. Similarly, I found no difference among treatment groups in wing loading at fledging. In contrast, similar studies of nestling Common Swifts (Wright et al. 2006) and nestling Chimney Swifts (Goodpaster and Ritchison 2014) revealed facultative mass loss, with weighted nestlings losing more mass than control nestlings to achieve wing loading values similar to those of control nestlings. Several factors may have contributed to the lack of differences among weighted and control nestlings in mass and wing loading in my study. First, the 3- and 6-gram weights used in my study may not have been heavy enough to affect the mass and wing loading of young kestrels at fledging. American Kestrels prey on a wide variety of organisms and are able to carry captured prey up to about half of their own mass (Johnsgard 1990). Other raptors have also been reported to either carry relatively large prey or increase their own wing loading by increasing their mass. For example, Walter (1979) reported that Eleonora Falcons (*Falco eleonorae*) that weigh about 350 g were observed in flight carrying prey that typically weigh more than they do, including a Chukar Partridge (*Alectornix chukar*; typical adult mass = 390 g, Dunning 1993) and a Manx Shearwater (*Puffinus puffinus*; typical adult mass = 450 g, Dunning 1993). In addition, Eurasian Kestrels (*Falco tinnunculus*) may increase their body mass by as much as 15% during the day as they consume prey (Dijkstra et al. 1988). This suggests that, in contrast to aerial insectivores like swifts, attaining and maintaining a specific wing-loading is less important for American Kestrels.

Fledgling kestrels are dependent on the parents for about two weeks after fledging (Varland et al. 1991). Initially, adults deliver food to young, but fledglings begin flying to adults to obtain food by one or two weeks after fledging (Smallwood and Bird 2002). By three weeks after fledging, young kestrels no longer beg for food from adults as their ability to capture their own prey continues to improve (Varland et al. 1991). This dependence on parental provisioning by newly fledged American Kestrels suggests that, although flying sufficiently well to reach cover when they leave nests is likely important, they have at least two weeks to develop the ability and flying skill to begin hunting. This also suggests that, unlike young aerial insectivores like swifts, attaining a particular wing-loading at fledging is not as critical for young American Kestrels and for fledglings in other species of raptors that are fed by adults for several weeks after fledging, e.g., Merlins (*Falco columbarius*; Sodhi et al. 1992), Sharp-shinned Hawks (*Accipiter striatus*; Bildstein and Meyer 2000), and Red-shouldered Hawks (*Buteo lineatus*; Snyder and Wiley 1976, Jacobs and Jacobs 2002).

Weibe and Bortolotti (1994) monitored nestlings throughout the entire nestling period and found that provisioning rates of American Kestrels reached an asymptote about 18 days post-hatching when nestlings approached asymptotic mass. Nestlings in my study also reached asymptotic mass at about 18 days post-hatching (Figure 2). Although my observations of provisioning behavior did not begin until day 9 post-hatching, my results suggest that provisioning rates reached an apparent asymptote on days 11-12 post-hatching, with no significant differences among feeding rates from days 11-12 to days 27-28 post-hatching (Figure 3). One possible explanation for this difference between studies is that adult kestrels in my study were providing nestlings with more prey biomass and, therefore, did not need to increase their provisioning rates in the days prior to nestlings reaching asymptotic mass (i.e., days 11-12 to days 17-18 post-hatching). In support of this hypothesis, Anderson et al. (1993) examined the daily food consumption of 61 hand-fed kestrel nestlings in a captive population from days 2 to 29 post-hatching and found that, from day 9 to day 29 post-hatching (corresponding to the days when I video-recorded nests), the mean mass of food consumed by nestlings ranged from about 34.3 to 48.2 grams per 15-hour day (Figure 9). Extrapolating my results, i.e., mean amount of biomass delivered by adults/nestling/hour, to 15-hour days, adult American Kestrels in my study provided each nestling with more, and on some days much more, biomass than consumed by the captive kestrels (Figure 9).

Hand-raised nestling kestrels may use less energy than free-living nestlings because they did not have to compete with siblings for access to food. However, even taking this into account, the amount of prey biomass delivered to nestlings by adult American Kestrels in my study likely met or exceeded that required for their continued growth and development. If so, this may also explain why the time spent begging by nestlings in my study, as well as their begging intensity, exhibited little variation during the last two weeks of the nestling period (Figures 5 and 6). Even as nestlings in my study became more active in the days prior to fledging, with more energetically costly behavior such as jumping and wing-flapping, there was no increase in either time spent begging or begging intensity.

Studies of other raptors have revealed both within- and among-species variation in the effect of nestling age on provisioning rates and amount of biomass delivered. For example, some investigators have reported that provisioning rates of Cooper's Hawks continue to increase through the nestling period (Kennedy and Johnson 1986; Murphy et al. 1988), whereas others found that their provisioning rates decreased as nestlings approached fledging age (Meng 1959). Holthuijzen (1990) found that provisioning rates of Prairie Falcons reached an asymptote sometime between 21 to 27 days post-hatching, or about 7 to 14 days before fledging. The provisioning rates of male and female Eurasian Kestrels (*Falco tinnunculus*) were also found to decrease during the later stages of their approximately 4-week nestling periods (Steen et al. 2012). The effect of nestling age on the provisioning behavior of raptors can be influenced by a number of variables, including habitat quality and prey availability (Snyder and Snyder 1973, Estes and Mannan 2003). For example, Steen et al. (2012) found that the amount of prey biomass delivered to nestlings by adult Eurasian Kestrels peaked when nestlings were 16.7 days old, about halfway through the nestling period. However, the reason for this reduction in the amount of prey biomass provided to nestlings later in the nestling period was unclear, possibly due to a reduction in nestling food demand, a decrease in prey availability, or some combination of both (Steen et al. 2012). One possible explanation for the consistent delivery of similar amounts of prey biomass to nestlings from days 9-10 to days 29-30 post-hatching by adult American Kestrels in my study is that prey availability was relatively high throughout the nestling period.

Summary

In my study, the addition of artificial weight did not influence the mass or wingloading of nestling American Kestrels near fledging. The nestlings also exhibited very little variation in their begging efforts in the latter part of the nestling period. Adult kestrels also did not vary the amount of prey biomass they delivered to each nestling per hour over the majority of the nestling period. This is likely due to an abundance of prey and the parents' ability to consistently deliver more than enough food. Considering the nestling and parental behavior results, the lack of differences in mass and wing loading of American Kestrel nestlings near fledging appears to be an early indicator of the flexibility in wing loading required for predatory birds.

LITERATURE CITED

Anderson, D. J., J. Reeve, J. E. Martinez Gomez, W. W. Weathers, S. Hutson, H. V. Cunningham, and D. M. Bird. 1993. Sexual size dimorphism and food requirements of nestling birds. Canadian Journal of Zoology 71: 2541-2545.

Balgooyen, T. G. 1976. Behavior and ecology of the American Kestrel (*Falco sparverius* L.) in the Sierra Nevada of California. University of California Publications in Zoology 103: 1–83.

Barbour, R. W., and W.H. Davis. 1974. Mammals of Kentucky. University Press of Kentucky, Lexington, KY.

Bildstein, K. L., and K. D. Meyer. 2000. Sharp-shinned Hawk (*Accipiter striatus*). In: The Birds of North America (P. G. Rodewald, ed.). Cornell Lab of Ornithology, Ithaca, NY.

Dawson, R. D., and G. R. Bortolotti. 2002. Experimental evidence for food limitation and sex-specific strategies of American Kestrels (*Falco sparverius*) provisioning offspring. Behavioral Ecology and Sociobiology 52: 43–52.

Dijkstra, C., S. Daan, T. Miejer, A. J. Cave, and R. F. B. Foppen. 1988. Daily and seasonal variations in body mass of the kestrel in relation to food availability and reproduction. Ardea 76: 127-140.

Dunning, J. B., Jr. 1993. CRC handbook of avian body masses. CRC Press, Boca Raton, FL.

Estes, W. A., and R. W. Mannan. 2003. Feeding behavior of Cooper's Hawks at urban and rural nests in southeastern Arizona. The Condor 105: 107-116.

Giovanni, M. D., C. W. Boal, and H. A. Whitlaw. 2007. Prey use and provisioning rates of breeding Ferruginous and Swainson's hawks on the Southern Great Plains, USA. Wilson Journal of Ornithology 119: 558–569.

Goodpaster, S., and G. Ritchison. 2014. Facultative adjustment of pre-fledging mass recession by nestling Chimney Swifts *Chaetura pelagica*. Journal of Avian Biology 45: 247–252.

Holthuijzen, A. M. 1990. Prey delivery, caching, and retrieval rates in nesting Prairie Falcons. Condor 92: 415–484.

Jacobs, J. P., and E. A. Jacobs. 2002. Conservation assessment for Red-shouldered Hawk (*Buteo lineatus*): national forests of north central states. USDA Forest Service Eastern Region, Milwaukee, WI.

Johnsgard, P. A. 1990. Hawks, eagles, & falcons of North America: biology and natural history. Smithsonian Institution Press, Washington, D.C.

Kays, R. W., and D. E. Wilson. 2002. Mammals of North America. Princeton University Press, Princeton, NJ.

Kennedy, P. L., & Johnson, D. R. and D. R. Johnson. 1986. Prey-size selection in nesting male and female Cooper's Hawks. The Wilson Bulletin 98: 110-115.

Martin, T. E. 1987. Food as a limit on breeding birds: a life-history perspective. Annual Review of Ecology and Systematics 18: 453–487.

Martins, T. L. F. 1997. Fledging in the Common Swift, *Apus apus*: weight-watching with a difference. Animal Behaviour 54: 99–108.

Massemin, S., E. Korpimaki, V. Poyri, and T. Zorn. 2002. Influence of hatching order on growth rate and resting metabolism of kestrel nestlings. Journal of Avian Biology 33: 235–244.

Meng, H. 1959. Food habits of nestling Cooper's Hawks and Goshawks in New York and Pennsylvania. Wilson Bulletin 71:169-174.

Murphy, R. K., M. W. Gratson, and R. N. Rosenfield. 1988. Activity and habitat use by a breeding male Cooper's Hawk in a suburban area. Journal of Raptor Research 22: 97-100.

Negro, J. J., A. Chastin, and D. M. Bird. 1994. Effects of short-term food deprivation on growth of hand-raised American Kestrels (*Falco sparverius*). Condor 96: 749–760.

Ricklefs, R. E. 1968a. Weight recession in nestling birds. Auk 85: 30–35.

Ricklefs, R. E. 1968b. Patterns of growth in birds. Ibis 110: 419–451.

Roest, A. I. 1957. Notes on the American Sparrow Hawk. Auk 74: 1–19.

Smallwood, J. A., and D. M. Bird. 2002. American Kestrel (*Falco sparverius*) In: The Birds of North America Online (A. Poole, ed.). Cornell Lab of Ornithology, Ithaca, NY.

Snyder, N. F., and H. A. Snyder. 1973. Experimental study of feeding rates of nesting Cooper's Hawks. Condor 75: 461-463.

Snyder, N. F. R., and J. W. Wiley. 1976. Sexual size dimorphism in hawks and owls of North America. Ornithological Monograph, no. 20., American Ornithologists' Union, Washington, D.C.

Sodhi, N. S., P. C. James, I. G. Warkentin, and L. W. Oliphant. 1992. Breeding ecology of urban Merlins (*Falco columbarius*). Canadian Journal of Zoology 70:1477-1483.

Steen, R., G. A. Sonerud, and T. Slagsvold. 2012. Parents adjust feeding effort in relation to nestling age in the Eurasian Kestrel (*Falco tinnunculus*). Journal of Ornithology 153: 1087-1099.

Steenhof, K. 1983. Prey weights for computing percent biomass in raptor diets. Raptor Research 17: 15–27.

Varland, D. E., E. E. Klass, and T. M. Loughin. 1991. Development of foraging behavior in the American Kestrel. Journal of Raptor Research 25: 9–17.

Walter, H. 1979. Adaptations to prey and habitat in a social raptor. University of Chicago Press, Chicago, IL.

Wiebe, K. L., and G. R. Bortolotti. 1994. Energetic efficiency of reproduction: the benefits of asynchronous hatching for American Kestrels. Journal of Animal Ecology 63: 551-560.

Witter, M. S., and I. C. Cuthill. 1993. The ecological costs of avian fat storage. Philosophical Transactions of the Royal Society B 340: 73–92.

Wright, J., S. Markman, and S. M. Denney. 2006. Facultative adjustment of pre-fledging mass loss by nestling swifts preparing for flight. Proceedings of the Royal Society B 273: 1895–1900.

APPENDICES

APPENDIX A:

TABLES

Table 1. Mean daily mass (± SE) of nestling American Kestrels in three treatment groups (including added mass of lead weights) from day 9 to day 29 post-hatching at the Blue Grass Army Depot in Madison County, Kentucky, in 2016. Sample sizes (number of nestlings) are given in parentheses. There were too few nests with nestlings for statistical analysis for days 27 to 29 post-hatching.

Days Post-hatch		Treatment			Statistics	
	Control	Half-weighted[A]	Full-weighted[B]	*F*	df	*P*
9	76.7 ± 3.6 (15)	70.6 ± 3.1 (15)	71.6 ± 2.9 (15)	0.2	2,18	0.83
10	84.3 ± 4.2 (15)	78.6 ± 3.7 (15)	80.1 ± 2.7 (15)	0.1	2,18	0.87
11	92.2 ± 4.3 (15)	85.6 ± 3.3 (15)	86.4 ± 3.0 (15)	0.2	2,18	0.84
12	96.4 ± 4.7 (15)	90.2 ± 3.6 (15)	94.2 ± 2.8 (15)	0.3	2,18	0.75
13	104.1 ± 5.2 (15)	95.9 ± 4.3 (15)	98.9 ± 3.0 (15)	0.3	2,18	0.74
14	108.1 ± 5.0 (15)	103.3 ± 3.6 (15)	102.7 ± 3.3 (15)	0.3	2,18	0.73
15	110.6 ± 5.5 (15)	111.9 ± 4.7 (15)	112.1 ± 3.9 (15)	0.4	2,18	0.66
16	114.7 ± 6.4 (15)	108.9 ± 4.7 (15)	115.3 ± 4.1 (15)	0.5	2,18	0.60
17	116.5 ± 5.8 (15)	113.5 ± 5.0 (15)	117.8 ± 4.3 (15)	0.4	2,18	0.67
18	119.7 ± 6.0 (15)	115.8 ± 5.4 (15)	119.1 ± 4.7 (15)	0.1	2,18	0.94
19	119.6 ± 5.9 (15)	116.0 ± 5.5 (15)	119.9 ± 4.6 (15)	0.1	2,18	0.87
20	121.0 ± 5.4 (15)	118.3 ± 4.6 (15)	121.7 ± 4.0 (15)	0.2	2,18	0.83
21	124.0 ± 5.3 (15)	120.5 ± 4.2 (15)	124.6 ± 3.2 (15)	0.3	2,18	0.73
22	124.0 ± 4.5 (15)	120.9 ± 4.0 (15)	127.5 ± 3.0 (15)	1.2	2,18	0.33
23	126.8 ± 4.6 (15)	122.4 ± 4.2 (15)	127.4 ± 3.3 (15)	0.5	2,18	0.60
24	125.7 ± 4.4 (15)	123.0 ± 3.6 (15)	129.4 ± 2.5 (15)	0.4	2,18	0.37
25	124.0 ± 4.1 (15)	123.7 ± 4.8 (14)	127.4 ± 3.1 (14)	0.5	2,17	0.63
26	122.5 ± 4.1 (13)	122.0 ± 4.3 (14)	127.7 ± 3.9 (11)	0.7	2,17	0.50
27	121.9 ± 7.6 (7)	127.6 ± 7.1 (7)	128.7 ± 4.6 (7)	-	-	-
28	124.4 ± 11.5 (4)	120.3 ± 11.3 (4)	126.7 ± 4.8 (5)	-	-	-
29	131.8 ± 12.4 (3)	131.7 ± 11.0 (3)	126.0 ± 4.8 (2)	-	-	-

[A] Half-weighted = lead weight equal to 2.5% of peak mass (3g) attached to back feathers

[B] Full-weighted = lead weight equal to 5% of peak mass (6g) attached to back feathers

Table 2. Mean daily mass (± SE) of nestling American Kestrels in three treatment groups (not including added mass of lead weights) from day 9 to day 29 post-hatching at the Blue Grass Army Depot in Madison County, Kentucky, in 2016. Sample sizes (number of nestlings) are given in parentheses. There were too few nests with nestlings for statistical analysis for days 27 to 29 post-hatching.

Days Post-hatch	Treatment			Statistics		
	Control	Half-weighted [A]	Full-weighted [B]	*F*	df	*P*
9	76.7 ± 3.6 (15)	70.6 ± 3.1 (15)	71.6 ± 2.9 (15)	0.2	2,18	0.83
10	84.3 ± 4.2 (15)	78.6 ± 3.7 (15)	80.1 ± 2.7 (15)	0.1	2,18	0.87
11	92.2 ± 4.3 (15)	85.6 ± 3.3 (15)	86.4 ± 3.0 (15)	0.2	2,18	0.84
12	96.4 ± 4.7 (15)	90.2 ± 3.6 (15)	94.2 ± 2.8 (15)	0.3	2,18	0.75
13	104.1 ± 5.2 (15)	95.9 ± 4.3 (15)	98.9 ± 3.0 (15)	0.3	2,18	0.74
14	108.1 ± 5.0 (15)	103.3 ± 3.6 (15)	102.7 ± 3.3 (15)	0.3	2,18	0.73
15	110.6 ± 5.5 (15)	105.6 ± 4.6 (15)	106.1 ± 3.9 (15)	0.4	2,18	0.66
16	114.7 ± 6.4 (15)	108.9 ± 4.7 (15)	109.3 ± 4.1 (15)	0.5	2,18	0.60
17	116.5 ± 5.8 (15)	110.5 ± 5.0 (15)	111.1 ± 4.3 (15)	0.4	2,18	0.67
18	119.7 ± 6.0 (15)	112.8 ± 5.4 (15)	113.1 ± 4.7 (15)	1.1	2,18	0.35
19	119.6 ± 5.9 (15)	113.0 ± 5.5 (15)	113.9 ± 4.6 (15)	0.9	2,18	0.43
20	121.0 ± 5.4 (15)	115.3 ± 4.6 (15)	115.7 ± 4.0 (15)	0.8	2,18	0.45
21	124.0 ± 5.3 (15)	117.5 ± 4.2 (15)	118.6 ± 3.2 (15)	0.9	2,18	0.42
22	124.0 ± 4.5 (15)	117.9 ± 4.0 (15)	121.5 ± 3.0 (15)	0.5	2,18	0.64
23	126.8 ± 4.6 (15)	119.4 ± 4.2 (15)	121.4 ± 3.3 (15)	0.9	2,18	0.44
24	125.7 ± 4.4 (15)	120.0 ± 3.6 (15)	123.4 ± 2.5 (15)	0.3	2,18	0.75
25	124.0 ± 4.1 (15)	120.7 ± 4.8 (14)	121.4 ± 3.1 (14)	0.1	2,17	0.91
26	122.5 ± 4.1 (13)	119.0 ± 4.3 (14)	121.7 ± 3.9 (11)	0.2	2,17	0.82
27	121.9 ± 7.6 (7)	124.6 ± 7.1 (7)	122.7 ± 4.6 (7)	-	-	-
28	124.4 ± 11.5 (4)	117.3 ± 11.3 (4)	120.7 ± 4.8 (5)	-	-	-
29	131.8 ± 12.4 (3)	128.7 ± 11.0 (3)	120.0 ± 4.8 (2)	-	-	-

[A] Half-weighted = lead weight equal to 2.5% of peak mass (3 g) attached to back feathers

[B] Full-weighted = lead weight equal to 5% of peak mass (6 g) attached to back feathers

APPENDIX B:

FIGURES

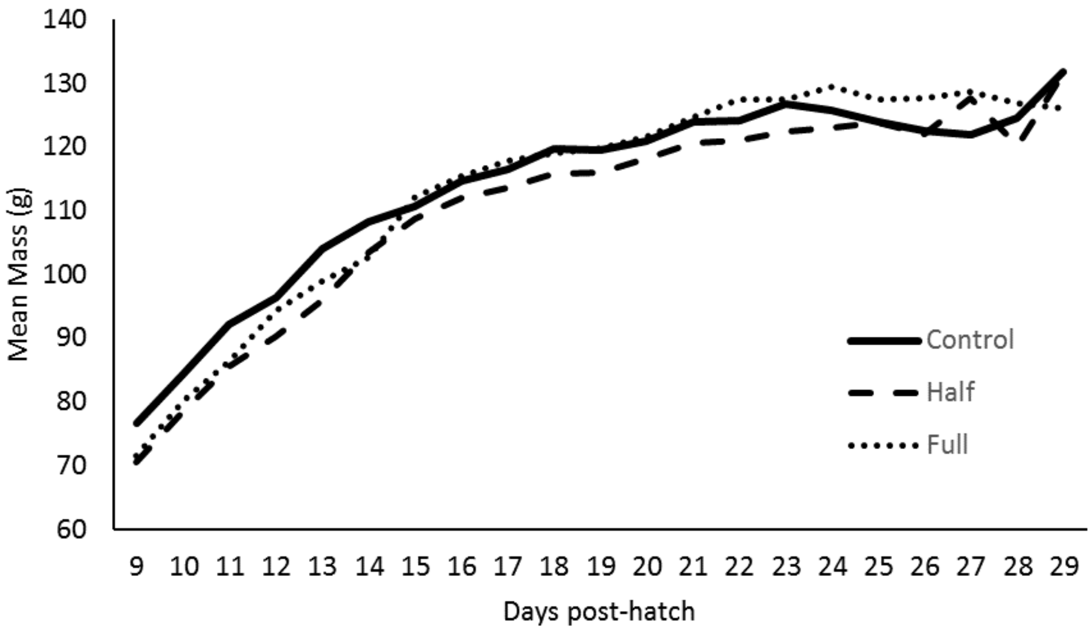

Figure 1. Mean daily mass of nestling American Kestrels in the three treatment groups including added mass of lead weights from day 9 to day 29 post-hatching at the Blue Grass Army Depot in Madison County, Kentucky, in 2016. Half-weighted nestlings had lead weight equal to 2.5% of peak mass (3 g) attached to back feathers, and full-weighted nestlings had lead weights equal to 5% of peak mass (6 g) attached to back feathers.

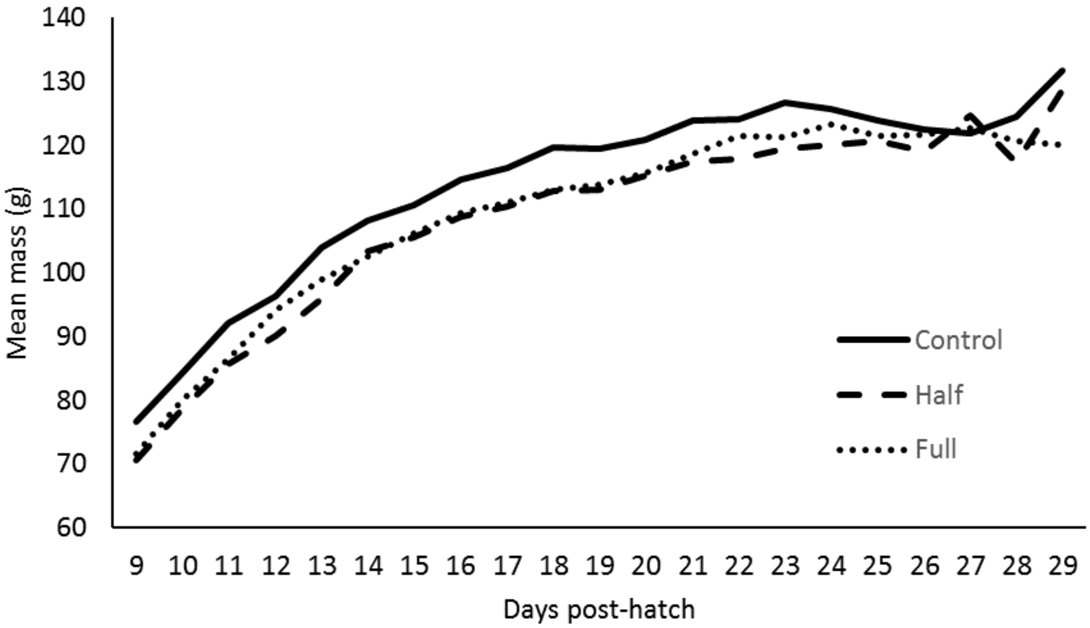

Figure 2. Mean daily mass of nestling American Kestrels in the three treatment groups without the added mass of experimentally added weights from day 9 to day 29 post-hatching at the Blue Grass Army Depot in Madison County, Kentucky, in 2016. Half-weighted nestlings had lead weight equal to 2.5% of peak mass (3 g) attached to back feathers, and full-weighted nestlings had lead weights equal to 5% of peak mass (6 g) attached to back feathers.

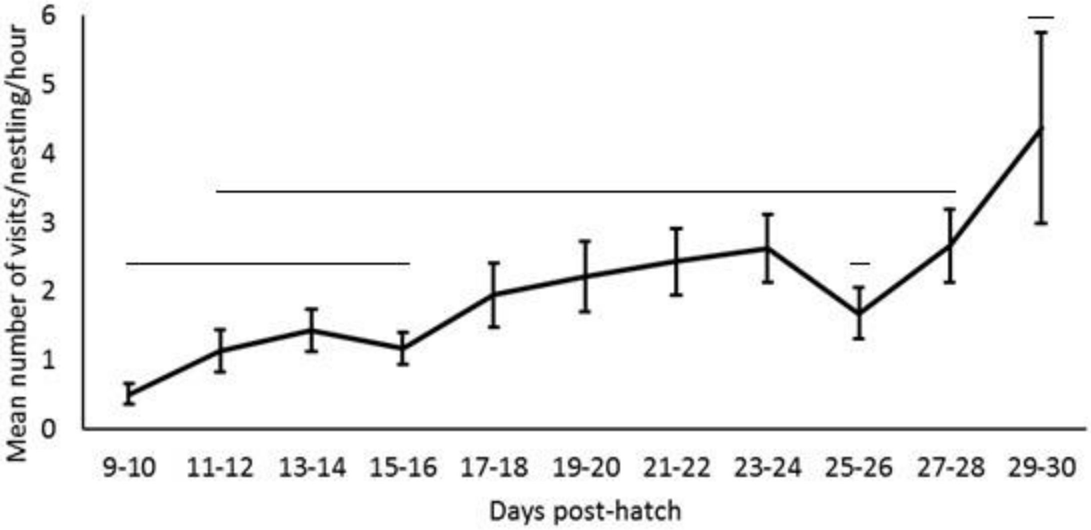

Figure 3. Mean daily number of visits per nestling per hour (± SE) by adult American Kestrels from day 9 to day 30 post-hatching at the Blue Grass Army Depot in Madison County, Kentucky, in 2016. Means under the same lines are not significantly different (SNK, $P > 0.05$).

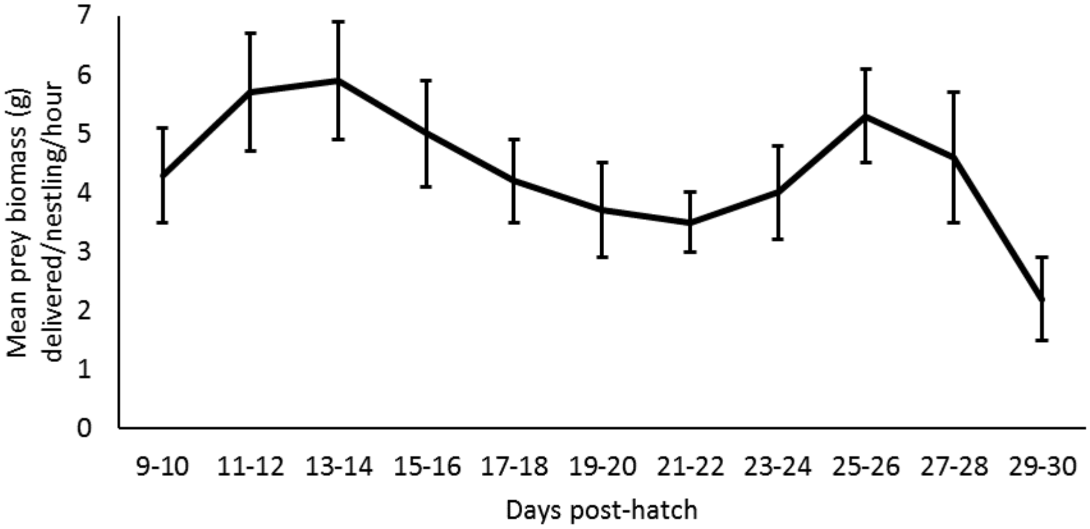

Figure 4. Mean daily prey biomass (grams) delivered per nestling per hour (± SE) by adult American Kestrels from day 9 to day 30 post-hatching at the Blue Grass Army Depot in Madison County, Kentucky, in 2016.

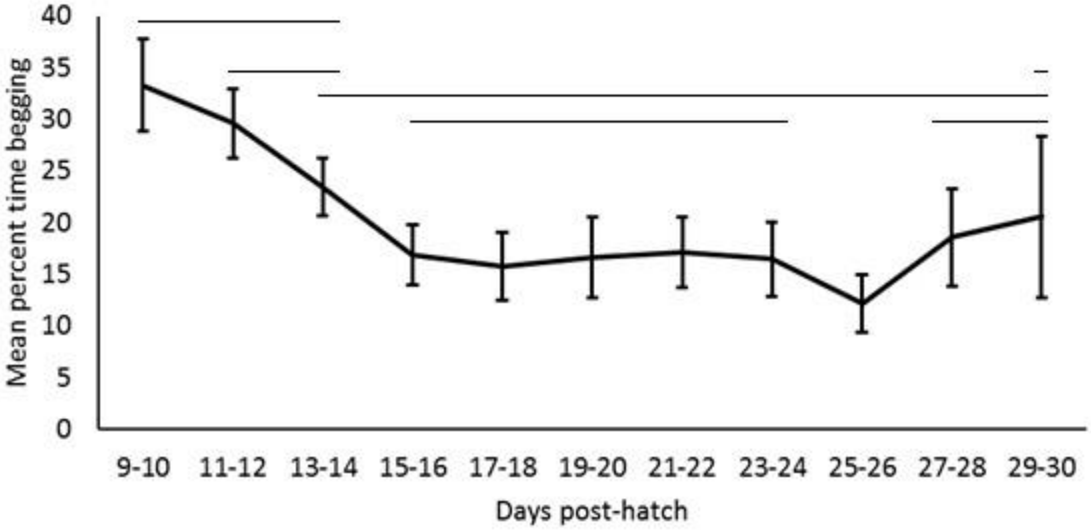

Figure 5. Mean daily percent time spent begging per hour (± SE) by nestling American Kestrels from day 9 to day 30 post-hatching at the Blue Grass Army Depot in Madison County, Kentucky, in 2016. Means under the same lines are not significantly different (SNK, P > 0.05).

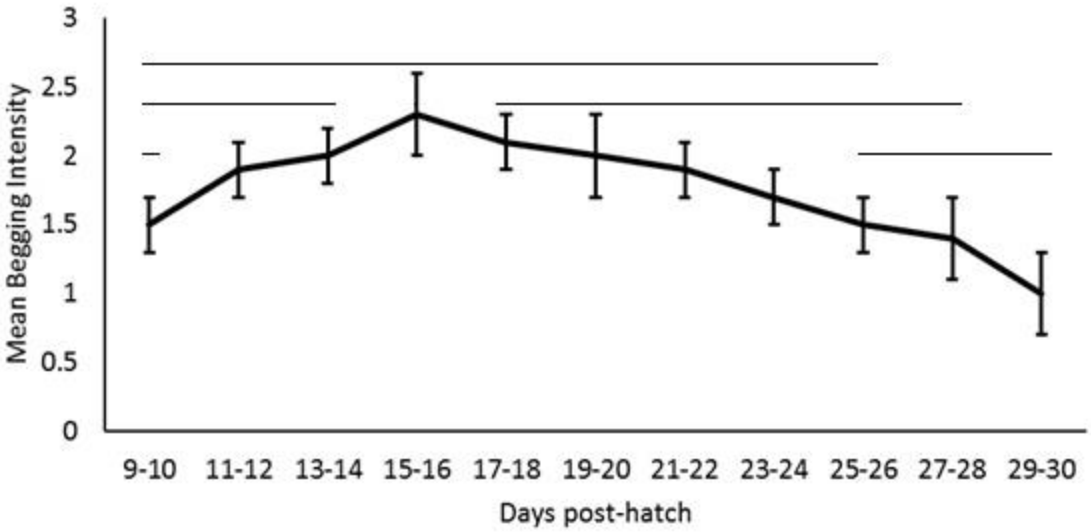

Figure 6. Mean daily begging intensity (± SE) during provisioning by nestling American Kestrels from day 9 to day 30 post-hatching at the Blue Grass Army Depot in Madison County, Kentucky, in 2016. Means under the same lines are not significantly different (SNK, P > 0.05).

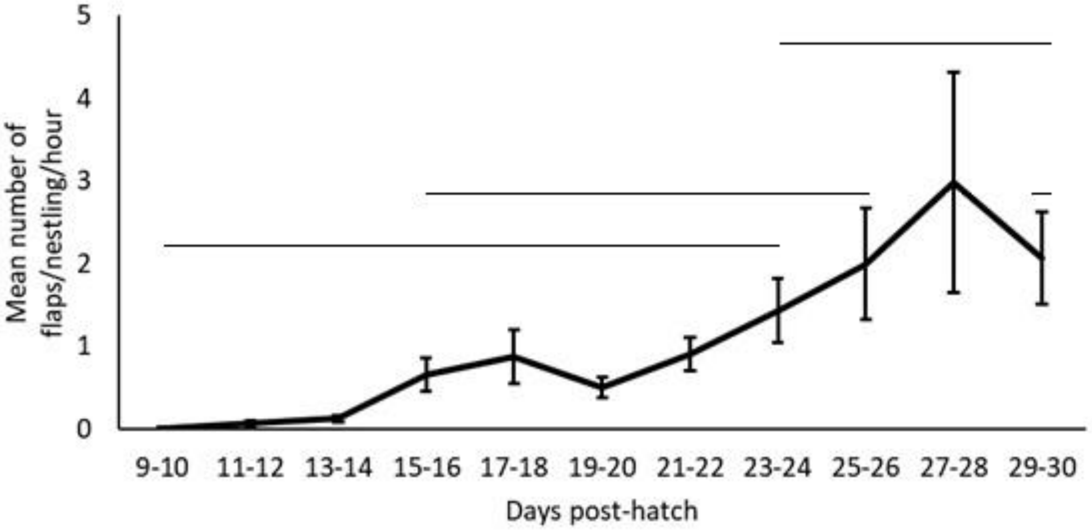

Figure 7. Mean number of wing flaps per nestling per hour (± SE) by nestling American Kestrels from day 9 to day 30 post-hatching at the Blue Grass Army Depot in Madison County, Kentucky, in 2016. Means under the same lines are not significantly different (SNK, $P > 0.05$).

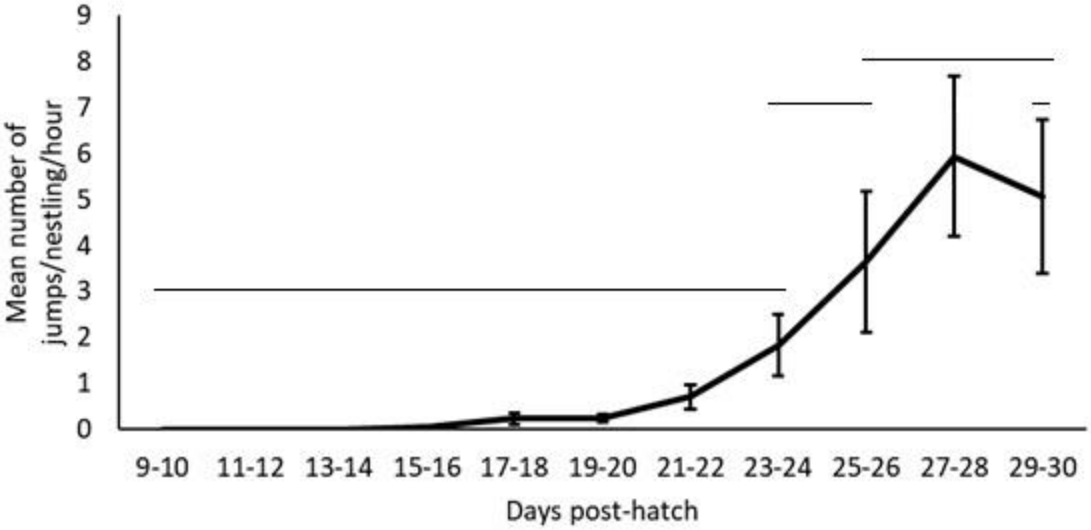

Figure 8. Mean number of jumps per nestling per hour (± SE) by nestling American Kestrels from day 9 to day 30 post-hatching at the Blue Grass Army Depot in Madison County, Kentucky, in 2016. Means under the same lines are not significantly different (SNK, P > 0.05).

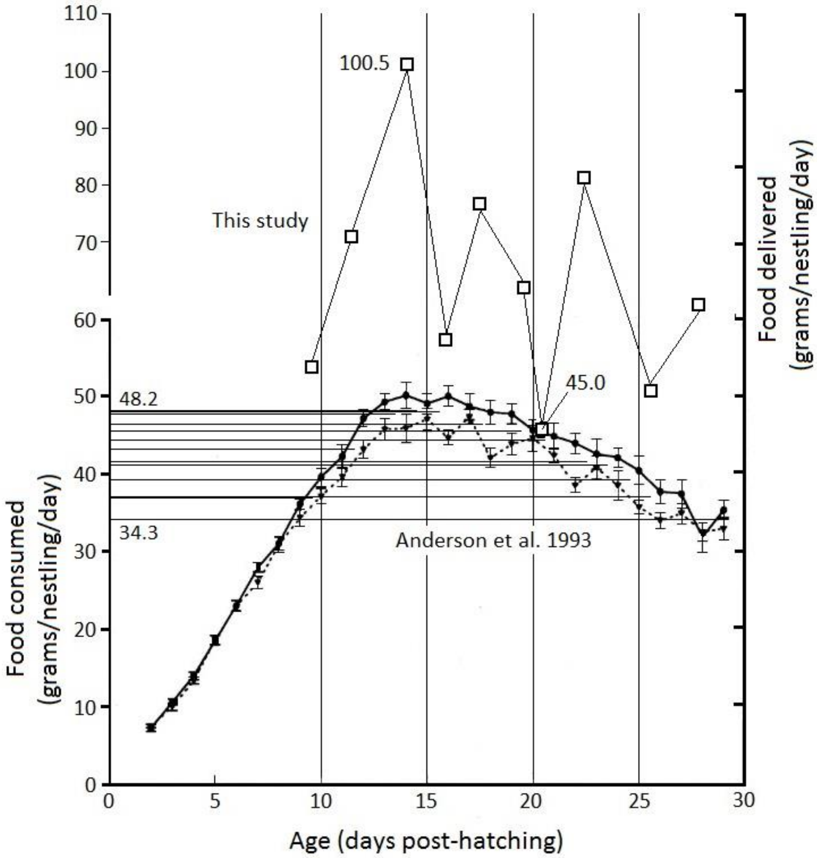

Figure 9. Comparison of the results of a study of food consumed per day by captive nestlings (Source: Anderson, D. J., J. Reeve, J. E. Martinez Gomez, W. W. Weathers, S. Hutson, H. V. Cunningham, and D. M. Bird. 1993. Sexual size dimorphism and food requirements of nestling birds. Canadian Journal of Zoology 71: 2541-2545.) and my study. Estimating the means for each two-day period (as in my study) for both females (solid line) and males (dotted line), captive nestlings consumed from about 34.3 to 48.2 grams of food per 15-hour day during the period from days 9-10 to day 29 post-hatching. In my study, extrapolating my results (biomass delivered/nestling/hour) to 15-hour days, adult American Kestrels provided nestlings with either as much biomass (days 20-31 post-hatching) or, for all other days, more biomass than consumed by the captive nestlings.