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Effect of variation in nestling hunger levels on the begging behavior of nestlings and the provisioning behavior of adult American Kestrels

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By

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By
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Bachelor of Science
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Eastern Kentucky University
in partial fulfillment of the requirements
for the degree of
MASTER OF SCIENCE
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DEDICATION

This thesis is dedicated to my father, who gave me the gifts of life, intelligence, passion, education, and a love of nature.

ACKNOWLEDGMENTS

I would like to thank my graduate advisor, Gary Ritchison, for his inspiration and guidance, and my committee members, David Brown and Charles Elliott, for their advice and assistance with this project. I appreciate the help of Mark Winland and Darcy Schueler in the field and Drew Harvey for reviewing drafts. Funding for my study was provided by the Kentucky Society of Natural History.

ABSTRACT

Little is known about how variation in nestling begging intensity influences the behavior of adult raptors and how responses of adult males and females to such variation might differ. My objective was to manipulate the begging intensity of nestling American Kestrels (*Falco sparverius*) and examine the responses of adult males and females. I studied 12 pairs of kestrels nesting in nest boxes from 1 March to 1 July 2014 at the Blue Grass Army Depot, Madison County, Kentucky. Nest boxes were modified with a separate compartment for a camcorder to record nestling behavior, and a second camcorder was placed outside of nests to monitor adult behavior. To manipulate nestling hunger levels, 12 to 26-day-old nestlings in six nests were deprived of food for 24 hours and those in the other six nests were fed until satiated. At each nest, I alternated control (no treatment) and treatment (fed or food-deprived) days (control, treatment, control, and treatment) over a four-day period to minimize the possible effect of nestling age on adult and nestling behavior. Each day, nestlings and adults were video-recorded for four hours. Recordings were subsequently reviewed and, to quantify begging behavior, I: (1) determined the proportion of nestlings in broods begging when adults arrived at and left nests, (2) categorized begging intensity of each nestling as 0 (no gaping), 1 (gaping), 2 (gaping with neck extended), or 3 (wings flapping vigorously) when adults arrived at and left nests, and (3) noted how long nestlings continued to utter begging calls after adults left nests. I also determined the provisioning rates of adult males and females. Analysis revealed that the proportion of nestlings begging when adults arrived at nests did not differ among treatments (food-deprived, fed, and control; $P = 0.057$), but did differ at adult departure ($P = 0.0002$), with a smaller proportion of nestlings in the fed-treatment nests begging after being fed. Nestling begging intensity differed among treatments both when adults arrived at ($P = 0.0011$) and left nests ($P < 0.0001$), with nestlings in food-deprived nests begging with greater intensity after food deprivation and those in fed-treatment nests begging with less intensity after being fed. In addition, food-deprived nestlings continued uttering begging calls longer ($P = 0.007$) after deprivation than during control periods. Adult male and female kestrels fed nestlings at similar rates ($P = 0.10$), and they fed nestlings (P = 0.0009) at higher rates after food deprivation than during control periods and at lower rates after fed treatments than during control periods. Adults provisioned food-deprived nestlings (mean = 4.2 visits/nestling/hour) at nearly four times the rate of satiated nestlings (mean = 1.1 visits/nestling/hour). My results suggest that the begging behavior of nestling American Kestrels varies with hunger level and is an honest signal of need, and that adult kestrels respond to changes in nestling hunger levels by adjusting provisioning rates. Although the responses of adult kestrels to variation in nestling begging behavior suggest that natural selection might favor ‘dishonest’ begging by nestlings, i.e., begging with greater intensity to obtain more food, the potential costs of ‘dishonest’ begging may outweigh any possible benefit, e.g., increased likelihood of attracting predators and loss of indirect fitness benefits if increased begging has negative impacts on the condition of siblings and parents

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Chapter 1

INTRODUCTION

The parental roles of males and females vary among species, but, among songbirds, both males and females typically provision nestlings, with the relative contributions of each sex varying among species (Houston et al. 2005, Cockburn 2006, Sonerud et al. 2014). Provisioning young is an essential, but costly, aspect of avian parental care, and parents must balance investment in their own survival and fecundity with investment in their young (Clutton-Brock 1991, Owens and Bennett 1994). At the same time, nestlings, also attempting to maximize their fitness, may seek care and provisioning rates at levels that could negatively impact adult fitness (Trivers 1974). If optimal provisioning rates for parents and nestlings differ (in terms of optimal fitness), then an evolutionary conflict (i.e., parent-offspring conflict) will result (Trivers 1974).

Nestlings solicit food from parents using conspicuous vocalizations and gaping behaviors (Kilner and Johnstone 1997, Johnstone and Godfray 2002). However, begging comes at the potential cost of attracting predators (Haskell 1994, Moreno-Rueda 2007, McDonald et al. 2009, Haff and Magrath 2011) and, in addition, energy expenditure due to excessive begging could reduce nestling growth rates and immunocompetence (Kilner 2001, Moreno-Rueda and Redondo 2011, Martín-Gálvez et al. 2012). As a result, some theoretical signaling models suggest that the potential costs of excessive begging for nestlings allow parents to interpret begging as an honest signal of need (Godfray 1995, Kilner and Johnstone 1997, Mock et al. 2011) and allocate food to nestlings accordingly.

However, because their investment in young may differ, adult males and females may respond differently to nestling begging. For example, Ottosson et al. (1997) found that male Pied Flycatchers (*Ficedula hypoleuca*) were more likely to increase provisioning rates in response to increased begging intensity than females. In contrast, Leonard and Horn (1998, 2001) found no difference between the responses of male and female Tree Swallows (*Tachycineta bicolor*) to variation in nestling begging intensity. Several factors may contribute to interspecific differences in the responses of males and females to nestlings, including certainty of parentage (Schwagmeyer et al. 1999), differences in the relative quality of males and females (DeMory et al. 2010, Mahr et al. 2012), food availability (Hoi-Leitner et al. 1999), habitat quality (Whittingham and Robertson 1994, Jenkins 2000), and time spent defending nests and territories (Markman et al. 1995).

Studies to-date that have focused on how parent birds respond to the begging behavior of nestlings have mostly involved songbirds (Order Passeriformes) (e.g., Bengtsson and Rydén 1983, Price and Ydenberg 1995, Ottosson et al. 1997, Leonard and Horn 1998, Price 1998, Grodzinski and Lotem 2007). Adults in other taxa also provision their altricial or semi-altricial young, including raptors. No one to-date, however, has examined how male and female raptors respond to variation in nestling begging intensity.

American Kestrels (*Falco sparverius*) are socially monogamous, cavity-nesting falcons and both males and females provision young, with provisioning rates of females generally higher than those of males (Smith et al. 1972, Balgooyen 1976, Liébana et al. 2009). Dawson and Bortolotti (2002) provided American Kestrels with supplemental food (whole mice [*Mus musculus*] placed in nest boxes every other day from hatching to fledging) and video-recorded adult provisioning at random times throughout the nesting period. They found that adult females reduced their provisioning rates, often removed supplemental food to consume or cache for future feedings, and were more likely than control females to return the following year, whereas the provisioning and return rates of adult males did not differ. Similarly, Wiehn and Korpimäki (1997) provided supplemental food (one to two rooster chicks [*Gallus gallus domesticus*] per nestling placed in nest boxes every other day from hatching to fledging) to nesting Eurasian Kestrels (*Falco tinnunculus*). To determine provisioning behaviors, they observed nest boxes for 6-8 hours per adult immediately after food supplementation and again 24 hours after supplementation when nestlings were 13-16 days post-hatching. They found that females reduced their provisioning rates when provided with supplemental food (females fed most of the supplemental food to nestlings, but also removed and cached some food), but, compared to controls, males did not alter their provisioning rates (males were not observed feeding supplemental food to nestlings) (Wiehn and Korpimäki 1997).

Although these results suggest that providing supplemental food can influence the provisioning rates of adult kestrels, the extent to which changes in provisioning rates might be due to changes in nestling begging behavior and, in addition, how adult male and female kestrels might differ in their responses to changes in nestling behavior remains to be examined.

Available evidence suggests that the begging intensity of nestling songbirds varies with hunger level and that this variation can influence adult provisioning behavior. However, less is known about the possibility that adult males and females might differ in their responses to changes in nestling begging intensity. In addition, the possible effect of variation in hunger levels on the begging behavior of nestling raptors has not been examined. Thus, my objectives were to determine (1) the effect of variation in hunger level on the begging intensity of nestling American Kestrels and, (2) if hunger level does affect begging intensity, how such variation influences the provisioning behavior of adult males and females.

Chapter 2

METHODS

Fieldwork was conducted from 1 March – 1 July 2014 at the Blue Grass Army Depot (BGAD) in Madison County, Kentucky. The BGAD encompasses 6014 ha of pastures, ungrazed grasslands, and scattered woodlots. For an unrelated study, 21 American Kestrel (hereafter kestrels) nest boxes were placed throughout the BGAD in 2012 and 2013. An additional eight nest boxes were put up at the BGAD in February 2014. Beginning in early March, nest boxes were checked weekly to monitor their use by kestrels, e.g., single birds or pairs observed near boxes. Because female kestrels typically begin egg-laying during the period from late March through April (Smallwood and Bird 2002), the contents of nest boxes were checked every two or three days beginning on 1 April with a TreeTop Peeper (Sandpiper Technologies, Inc., Manteca, CA) for the presence of eggs. Nests that had eggs for 20 days were then checked every one to two days for hatching, and date of first hatching was recorded to estimate age of nestlings during experiments. Although nestlings often hatched asynchronously, I used day of first hatching to identify age of broods for recordings. I continued to monitor all nest boxes at BGAD until all nestlings fledged or nests failed. 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 #04-2014.

Video-recording and treatments

To examine adult provisioning rates and the effect of experimental treatment on adult and nestling kestrels, nests were video-recorded over a period of four to eight days (typically four, but with additional days resulting from foster events [see Nestling removal and replacement below] or inclement weather, e.g., rain or strong wind). During this period, I alternated control (no treatment) and treatment (fed or food-deprived) days (control, treatment, control, and treatment) to minimize the possible effect of nestling age on adult and nestling behavior. Each nest was randomly assigned a single treatment, which was repeated to increase sample size. Video-recording occurred when nestlings were 12 to 26 days post-hatching (young kestrels typically fledge from nests 28 to 31 days post-hatching, Smallwood and Bird 2002).

At least three days prior to the beginning of video recording, nest boxes were modified. Nest boxes were designed so that one side could be rotated upward to allow access to the interior. That side was removed and, in its place, I attached a new side that had 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 container to hold the camcorder. Containers had a 10 cm x 10 cm opening aligned with the opening on the side and a hinged top so camcorders could be inserted and removed and would be protected from sunlight and rain. After attaching the new side, a 'mock' camcorder (made of cardboard, but similar in size and color to a real camcorder) was placed in the plastic container for three days to allow kestrels to habituate to the altered appearance of their nest box and the presence of a camcorder. During video recording, a camcorder (Handycam HDR-XR 100, Sony, Tokyo, Japan) was placed in the container and adjusted for the best possible view of nestlings and the nest box entrance. An additional camcorder mounted on a tripod was placed on the ground 5-10 m from the box, facing up and focusing on the entrance hole of the next box, to record the sex of visiting adults. The sex of adult kestrels was determined by plumage differences; males have bluish wings and an unbarred tail, and females are rufous with barred wings and tail (Smallwood and Bird 2002). When the sex of an adult could not be determined due to poor lighting, the sex of the visitor was recorded as unknown.

To manipulate nestling hunger levels and begging intensity, I used methods and treatments similar to those of Leonard and Horn (1998), with all nestlings fed to satiation in some broods (fed treatment) and all nestlings deprived of food for 24 hours in other broods (deprived treatment). All video-recording occurred during the periods from 0830 to 1200 hours and 1530 to 1930 hours when adult kestrels typically provision at the highest rates (Smallwood and Bird 2002). During each recording session, I noted the nest box number, number and age of nestlings, and time of day recordings were made.

On treatment days, all nestlings in a brood were removed from their nest boxes and placed in a cardboard box lined with cedar shavings. Nestlings in the fed treatment (N = 6 nests) were fed pieces of chicken hearts and gizzards (known to be readily eaten by young kestrels, G. Ritchison, pers. observ.) for one hour. Nestlings were fed at about 10-min intervals during the hour and, during the last 10 min, were fed until they no longer responded to the approach of food (held in forceps) by holding their heads up and gaping. Nestlings in broods subjected to the deprived treatment (N = 6 nests) were food deprived for about 24 hours by keeping them in the cardboard box in a dark, quiet room overnight. After the periods of feeding and deprivation, respectively, nestlings were returned to their nest boxes and video-recorded for four hours.

Nestling removal and replacement

To reduce disturbance to adult kestrels and insure that they did not abandon nests, two or more nestlings of similar age and size from another kestrel nest were temporarily removed and placed in nest boxes after nestlings in focal nests had been removed for treatment. The number of ‘foster’ nestlings placed in nests varied with availability, but an attempt was made to use the same number of replacements as there were nestlings in the brood that was removed. At least one nestling from foster broods was left in their respective nest box to insure that those adults did not abandon their nests. Nestlings in eight nest boxes (23 total nestlings) were used as foster nestlings for other nest boxes during my study. Adult kestrels willingly care for foster nestlings (Dawson and Bortolotti 2000, 2008), and kestrels have even been reported to raise broods of other species after they have lost a nest (Smallwood and Bird 2002).

Video review and analysis

Videos were subsequently viewed on a computer and, for each video recording, I noted the nest box number, date, time of day the recording was made, and whether it was a control day or treatment day. On treatment days, I also noted the type of treatment (fed or deprived). I noted the number of nest box visits by each adult sex and divided those numbers by the duration of the recording (in hours) and then by number of nestlings to determine provisioning rates per hour per nestling. I used the time from the first nest visit by an adult to the end of recording period in calculating provisioning rate.

For the inside-nest-box videos, I noted the type of food delivered (if possible), the proportion of nestlings begging, the maximum begging intensity of each nestling upon arrival and departure of parent, and the amount of time nestlings continued to utter begging calls after adults left the nest. Begging was defined as the conspicuous gaping and calling used by nestlings to elicit food from parents (Wright and Leonard 2002). The proportion of nestlings begging was defined as the number of nestlings gaping when an adult arrived at and departed from a nest box (determining which nestlings were vocalizing was not possible because gaping nestlings do not always call and vocalizing nestlings may not gape). Begging intensity was scored for each nestling as: (0) no gaping, (1) gaping, (2) gaping with neck extended upward, or (3) same as 2 with wings flapping vigorously. I did not include sitting or standing in scores because, after about 15-17 days post-hatching, nestlings stand almost constantly. Individual scores were averaged to produce an overall mean begging intensity for each adult arrival and departure. For each provisioning visit, I also recorded the amount of time that nestlings continued to utter begging calls after an adult left because adults may be able to hear begging calls when perching and hunting near nest boxes (Maurer et al. 2003).

Statistical analysis

Following Leonard and Horn (1998), nests, rather than individual feedings or nestlings, were the unit of replication. Data (i.e., differences between treatment types and treatment and control periods in adult provisioning rates, mean proportion of nestlings begging, mean nestling begging intensity, and mean time nestlings continued uttering begging calls after adults left nests) were analyzed using completely randomized block analysis of variance, with adult sex (male or female) and treatment category (fed-control, fed-treatment, deprived-control, and deprived-treatment) as fixed factors. Because I video-recorded each nest on multiple days, I used nest box number as a block in the models to account for variation among nests. I also blocked on nestling age to account for measurements taken on successive days. Blocking factors were effective in strengthening all models. If a model was found significant ($P < 0.05$), I performed a Tukey's HSD post-hoc examination to find statistical differences between the means of each treatment and its respective control.

To satisfy normality and variance assumptions, percentage data (proportion of nestlings begging) were arcsine-square root transformed and numerical data (adult provisioning rate and begging intensity scores) were natural log transformed prior to analysis. Begging time did not require transformation. Adult sex was initially included as a fixed factor, but was removed to simplify the models ($P > 0.1$ in all models). For final analysis, I pooled the visits of adult males and females with visits of adults of unknown sex. When estimating variation in nestling vocalizations in absence of a parent, I originally found that the "adult sex" factor was approaching significance ($F_{1,57} = 3.5$, $P = 0.068$), unlike other models. I found a significant outlier in the data that was three times the next-highest residual, so I experimentally removed the outlier and found that adult sex was no longer a significant factor ($F_{1,56} = 2.4$, $P = 0.13$), consistent with other models. I then simplified the model to only include treatment and blocking factors. The lack of two videos (see Results below) and nestling data where an adult male did not provision during the time period were treated as missing values in the analysis. All means and 95% confidence intervals reported for the models that required transformation are based on least-squared means of transformed data (natural log or arcsine-square root transformed) that have been back-transformed (exponent or sine-squared, respectively) to reflect the original scale of the data. Back-transformed 95% confidence limits are included in figures. Values are presented as means ± SE. All analyses were conducted using the Statistical Analysis System (SAS Institute, Inc., Cary, NC).

Chapter 3

RESULTS

Twenty-one pairs of kestrels initiated nests. Eggs failed to hatch at four nests that were subsequently abandoned, and six nests were predated during the breeding season. Mean clutch size was 4.6 ± 0.1 eggs, mean brood size was 3.7 ± 0.3, and the mean number of fledglings per nest was 3.6 ± 0.3 with a fledging success of 75%. Six nestlings at four nests died (apparently, based on their small size, due to starvation) within a few days of hatching. All nests with broods older than 10 days-post-hatching were used for experiments (12 of 29 nest boxes) to maximize sample size (N = 6 fed and 6 food-deprived treatments). Nestlings were predated at one nest in the fed group after the first treatment recording, so only two videos were used for analysis instead of four. Thirty-nine nestlings fledged from 11 experimental nests, including 14 males (36%) and 25 females (64%).

Nestling begging behavior

Comparing treatment categories (deprived, fed, and the control periods for kestrel nests in each treatment), the difference in the proportion of nestlings begging when an adult arrived at a nest approached significance ($F_{2,19} = 3.3$, $P = 0.057$), with a tendency for a larger proportion of nestlings to beg after the food-deprivation treatment and a smaller proportion begging after the fed treatment (Fig. 1a). Differences among treatments in the proportion of nestlings begging when adults left nests were significant ($F_{2,19} = 13.8$, $P = 0.0002$), with a smaller proportion of nestlings in the fed-treatment nests begging after the fed treatment than during control periods (Tukey's test, $P < 0.05$; Fig. 1b). The difference between treatment and control periods for nestlings at nests in the food-deprived treatment was not significant (Tukey's test, $P > 0.05$, Fig. 1b).

Mean begging intensity (scores based on begging posture) differed significantly among treatments both when adult kestrels arrived at ($F_{2,19} = 9.9$, $P = 0.0011$) and left ($F_{2,19} = 16.0$, $P < 0.0001$) nests. Both when adults arrived at and left nests, nestlings in

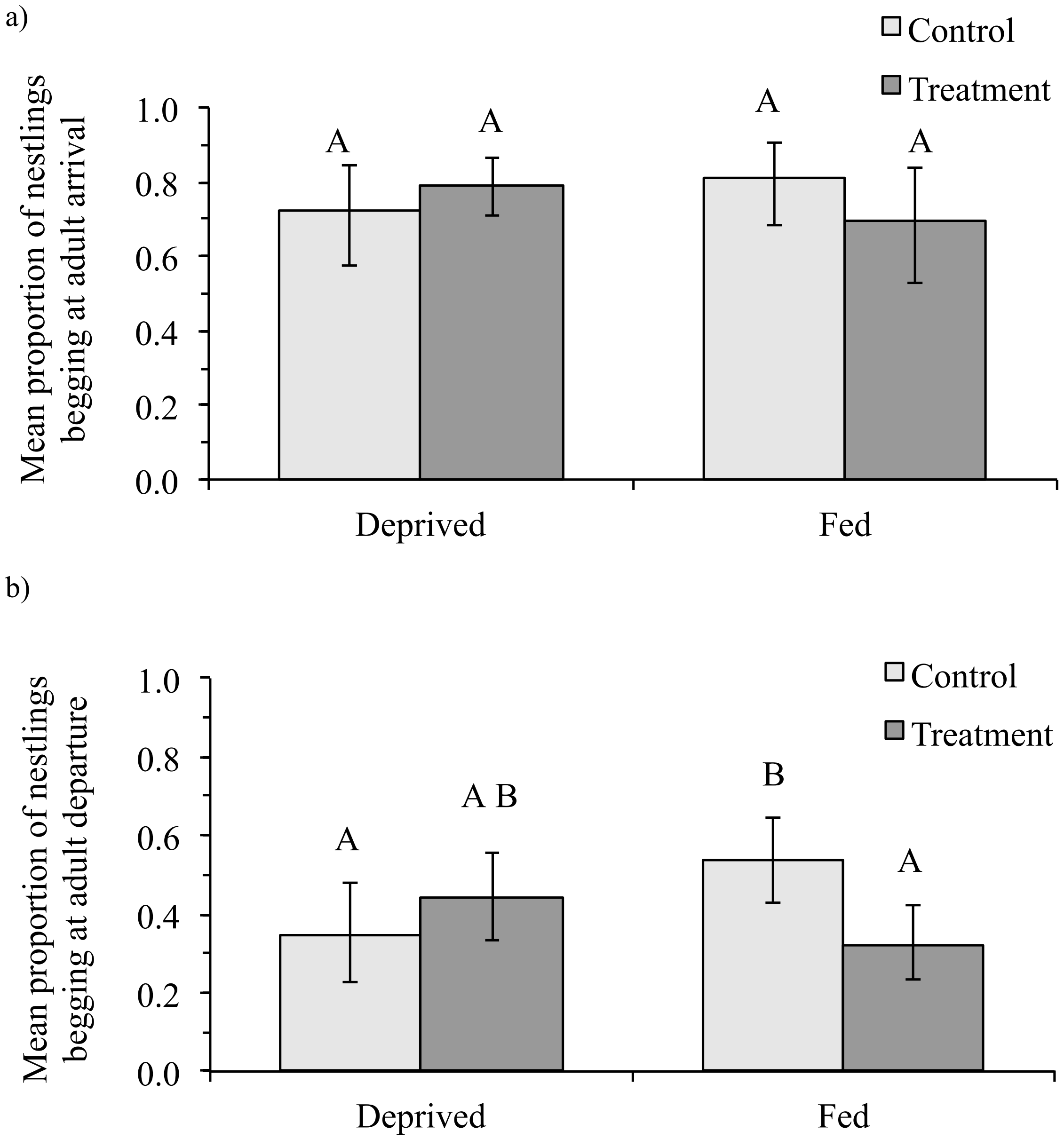

Figure 1. Mean (± SE) percentage of American Kestrel nestlings that made conspicuous begging behaviors (gaping) when an adult first arrived at (a) and then left (b) nests. Nestlings were subjected to food deprivation (Deprived) or were fed to satiation (Fed), and were video recorded prior-to (Control) and after treatment application (Treatment). Bars represent back-transformed 95% confidence limits, and different letters indicate statistically significant differences (Tukey's test, $P < 0.05$).

deprived nests begged with significantly greater intensity after food-deprivation treatment than during control periods (Tukey's test, $P < 0.05$; Fig. 2a, b), whereas nestlings in fed-treatment nests begged with significantly less intensity after being fed than during control periods (Tukey's test, $P < 0.05$; Fig. 2a, b). The mean time that nestlings continued to utter begging calls after adults left nests also differed among treatments ($F_{2,19} = 6.4$, $P = 0.0073$), with nestlings in deprived-treatment nests calling longer after food deprivation than during control periods (Tukey's test, $P < 0.05$; Fig. 3). The difference between the fed-treatment and control periods in time spent begging after adults left fed-treatment nests was not significant (Tukey's test, $P > 0.05$; Fig. 3).

Adult provisioning rates

Overall, the provisioning rates of adult male and female American Kestrels did not differ ($F_{1,57} = 2.8$, $P = 0.10$). For adult males and females combined, provisioning rates (visits/nestling/hour) did, however, differ significantly among treatment categories ($F_{2,19} = 10.4$, $P = 0.0009$), with adults at deprived nests provisioning nestlings at significantly higher rates after nestlings were food-deprived than during control periods, and adults at fed nests provisioning nestlings at significantly lower rates after the fed treatment than during control periods (Tukey's tests, $P < 0.05$; Fig. 4). Adults returned to nests an average of 37.3 min (range = 7 to 115 min) after video recording began, suggesting that, at least at some nests, my presence at nest boxes influenced subsequent adult behavior.

Prey delivered to nests by adults

Most prey items delivered to nestlings by adult kestrels could not be identified (63.1%, Table 1) because of poor camera angles, feedings so quick that I was unable to identify prey items, nestlings blocking my view of adults, and nestling taking prey items from adults when reaching outside the nest-box entrance hole. Most or all unidentified prey were likely small invertebrates because vertebrate prey delivered by adults to nestlings were larger and more easily seen and identified. Vertebrate prey deliveries

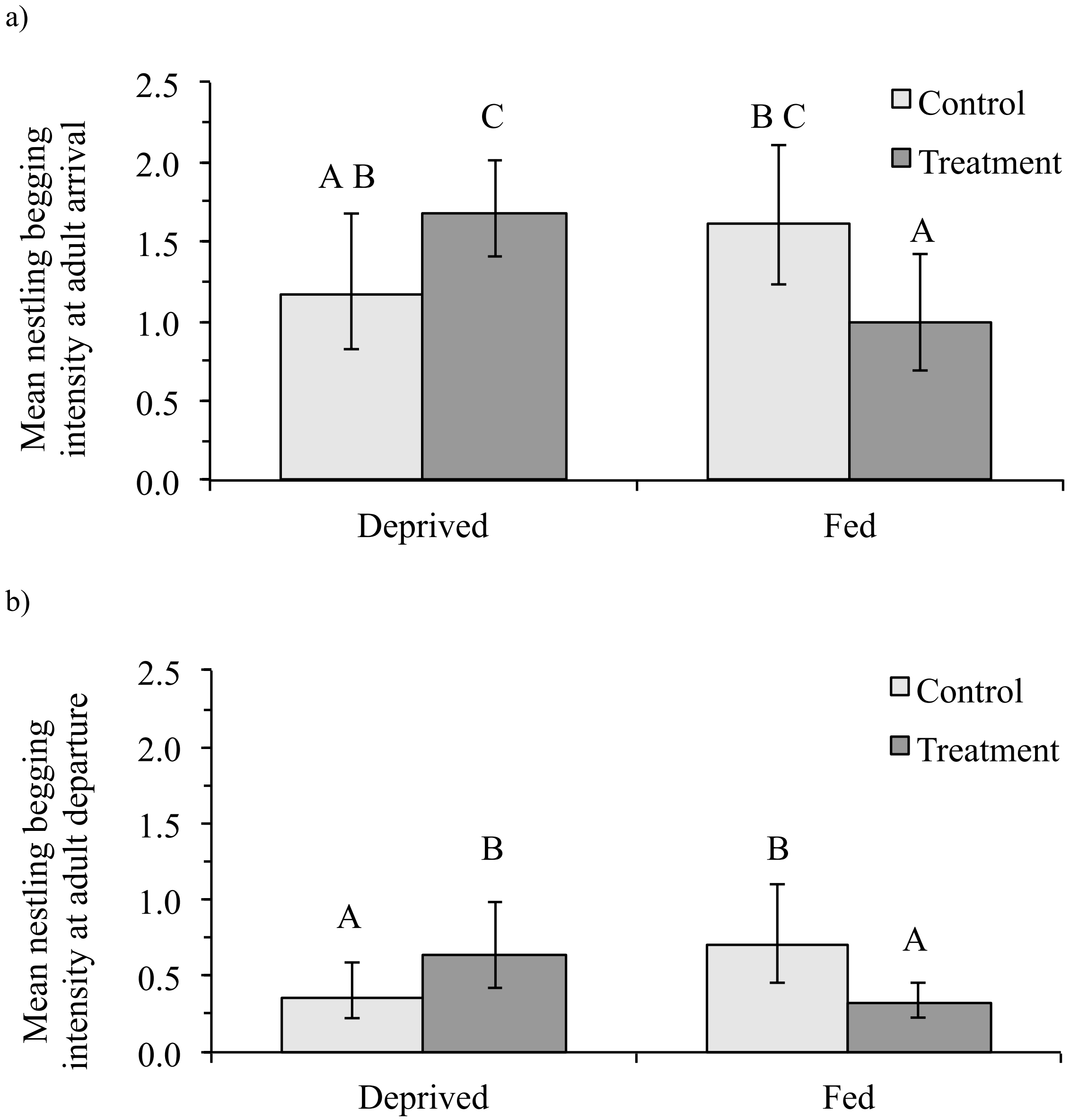

Figure 2. Mean (±SE) begging intensity of nestling American Kestrels when an adult first arrived at (a) and then left (b) a nest. Nestlings were subjected to food deprivation (Deprived) or were fed to satiation (Fed), and were video recorded prior-to (Control) and after treatment application (Treatment). Begging intensity was scored for each nestling as: (0) no gaping, (1) gaping, (2) gaping with neck extended, and (3) wings flapping vigorously. Bars represent back-transformed 95% confidence limits, and different letters indicate statistically significant differences (Tukey's test, $P < 0.05$).

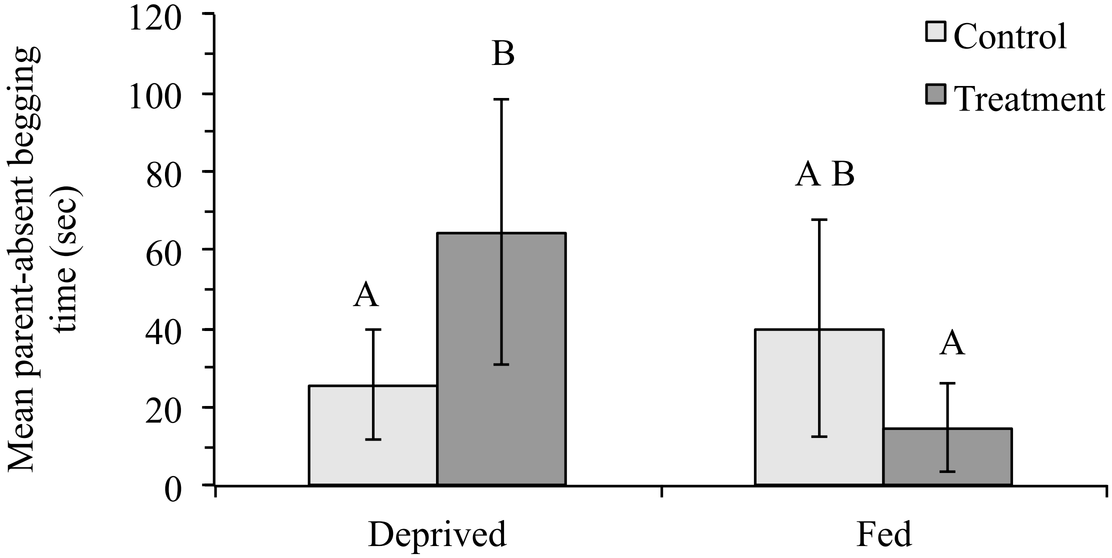

Figure 3. Mean (± SE) amount of time (seconds) that American Kestrel nestlings uttered begging calls when an adult was not at the nest box. Nestlings were subjected to food deprivation (Deprived) or were fed to satiation (Fed), and were video recorded prior-to (Control) and after treatment application (Treatment). Bars represent 95% confidence limits, and different letters indicate statistically significant differences (Tukey's test, $P < 0.05$).

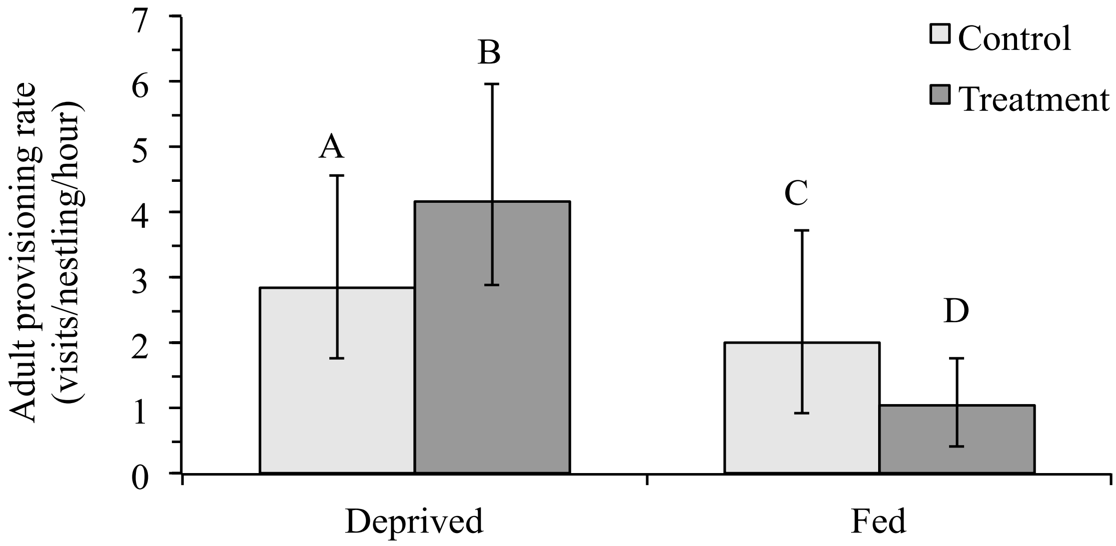

Figure 4. Mean (± SE) provisioning rates of adult American Kestrels during control and treatment periods at nests where nestlings were either food-deprived or fed to satiation. Means are back-transformed from natural log transformation, bars represent back-transformed 95% confidence limits, and different letters signify statistically significant differences (Tukey's test, $P < 0.05$).

Table 1. Prey items delivered to nestlings by adult male and female American Kestrels at 12 nests from May to June 2014 at the Blue Grass Army Depot in Madison County, Kentucky. Percentages are a ratio of number of prey items to total adult visits.

Prey type	**Number**	**%**
Invertebrates	**505**	**33.1**
Cricket	128	8.4
Grasshopper	29	1.9
Dragonfly	7	0.4
Wasp	5	1.0
Moth	4	0.3
Spider	4	0.3
Caterpillar	2	0.1
Beetle	2	0.1
Butterfly	1	0.1
Fly	1	0.1
Unidentified	322	21.1
Vertebrates	**58**	**3.8**
Rodent	40	2.6
Bird	8	0.5
Snake	2	0.1
Unidentified	8	0.5
Unknown	963	63.1
Total prey delivered	1526	100.0

made up 3.8% of total adult visits and included rodents, birds, and snakes (Table 1). If unknown prey items are assumed to have been small invertebrate prey, then about 96.2% of prey items fed to nestlings were invertebrates. In general, adult males and females brought similar types of prey to nestlings, but females provided nestlings with 44 vertebrate prey items (30 rodents, 5 birds, 1 snake, and 8 unidentified), whereas males delivered only 12 vertebrate prey items (8 rodents, 3 birds, and 1 snake).

Chapter 4

DISCUSSION

Responses of nestlings to treatments

Nestling American Kestrels in this study begged more vigorously after food deprivation and less vigorously when satiated (fed treatment). Similar results have been reported for several species of songbirds (Bengtsson and Rydén 1983, Redondo and Castro 1992, Kilner 1995, Price and Ydenberg 1995, Leonard and Horn 1998, Wright et al. 2010, Martín-Gálvez et al. 2012). This behavioral plasticity, along with potential costs of excessive begging, including attracting predators (Haskell 1994, Moreno-Rueda 2007, McDonald et al. 2009, Haff and Magrath 2011) and expending energy that may result in reduced growth rates and weakened immune systems (Kilner 2001, Moreno-Rueda and Redondo 2011, Martín-Gálvez et al. 2012), suggest that begging by nestling American Kestrels is, as has also been reported for nestlings in several other species of birds, an honest signal of need (Godfray 1995, Kilner and Johnstone 1997, Johnstone and Kilner 2011).

I found that the begging behavior of American Kestrel nestlings in the food-deprived and fed treatments differed, with food-deprived nestlings begging more vigorously (both in terms of proportion of nestlings in a brood begging and begging intensity) after food deprivation and fed nestlings begging much less vigorously after being fed. Similar results have been reported in a variety of avian taxa, including many passerines (e.g., Bengtsson and Rydén 1983, Redondo and Castro 1992, Leonard and Horn 1998), plus species in the orders Psittaciformes (Krebs and Magrath 2000), Strigiformes (Hofstetter and Ritchison 1998), Procellariiformes (Hamer et al. 2006), and Columbiformes (Mondloch 1995).

Food-deprived nestling kestrels in my study also continued begging significantly longer after adults left nests than they did during their control periods and significantly longer than nestlings in the fed-treatment after being fed to satiation. The possible costs associated with excessive begging are presumably greater in the absence of a parent because excessive energy expenditure that does not result in increased resources may reduce nestling growth (Kilner 2001, Moreno-Rueda and Redondo 2011, Martín-Gálvez et al. 2012) and the risk of attracting predators is greater if a parent is not nearby to defend the nest (Haskell 1994, Moreno-Rueda 2007, McDonald et al. 2009, Haff and Magrath 2011), but those costs may be mediated if nearby adults can hear the continued begging calls of nestlings and respond by increasing their provisioning rates (Budden and Wright 2001). Budden and Wright (2001) suggested that cavity-nesting species might have evolved a higher incidence of parent-absent begging because a lower risk of predation incurs a reduced cost to begging behaviors. Price (1998) placed speakers near nests of Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*) and played back nestling begging calls after adults left the nests. Adult Yellow-headed Blackbirds responded by doubling their nestling-provisioning efforts and, as a result, their nestlings grew faster than those in control nests where begging calls were not played back (Price 1998). Maurer et al. (2003) found that food-deprived nestling White-browed Scrubwrens (*Sericornis frontalis*) continued to utter begging calls when parents were not present at the nests, and suggested that this begging allowed nearby parents to assess nestling need without visiting nests, thereby reducing unnecessary visits or the risk of alerting predators to nest location.

Continued begging after adult birds leave nests may function in intrabrood communication. Romano et al. (2013) found nestling Barn Swallows (*Hirundo rustica*) that continued begging after adults left nests tended to increase their begging intensity when a parent next arrived with food and prior-fed siblings tended to beg with less intensity. As a result, nestlings that had continued begging in the absence of parents were more likely to receive food. This suggests intrabrood communication, with hungry siblings signaling their hunger and likelihood of begging vigorously during the next parental visit and less-hungry nestlings responding by begging less vigorously and increasing the likelihood that their siblings will be fed (Romano et al. 2013). After food deprivation, Romano et al. (2013) found that continued begging by nestling Barn Swallows after adults left the nests had no apparent effect on the behavior of siblings; all deprived nestlings begged vigorously.

Responses of adult kestrels to treatments

Adult kestrels in this study responded to the increased begging intensity of food-deprived nestlings by increasing provisioning rates and to the reduced begging intensity of fed nestlings by decreasing provisioning rates, supporting theoretical predictions that adults respond to variation in nestling begging behavior and adjust their provisioning efforts accordingly. Similar results have been reported in a variety of avian taxa, including many passerines (Bengtsson and Rydén 1983, Redondo and Castro 1992, Price and Ydenberg 1995, Leonard and Horn 1998, Budden and Wright 2001), plus species in the orders Psittaciformes (Krebs and Magrath 2000), Procellariiformes (Hamer et al. 2006), and Columbiformes (Mondloch 1995).

Adult male and female kestrels in this study responded similarly to experimentally manipulated changes in nestling begging intensity, with both sexes increasing provisioning rates to vigorously begging food-deprived nestlings and decreasing provisioning rates to satiated nestlings that begged with less vigor. Similar results, with adult males and females responding similarly to changes in nestling begging intensity (either due to investigators feeding or starving nestlings or playing back begging calls at nest sites), have been reported for several species of songbirds (Price and Ydenberg 1995, Leonard and Horn 1998, Hinde 2005, Tarwater et al. 2009). However, in other species, adult provisioning rates either did not vary in response to changes in nestling begging intensity or adult males and females responded differently to such changes. For example, Masman et al. (1988) experimentally increased hunger levels and begging intensity of nestling Eurasian Kestrels and found the adult males did not respond by increasing provisioning rates (data for adult females were not provided). Similarly, Sasvári and Hegyi (2010) increased nestling begging rates by experimentally increasing brood sizes of Tawny Owls (*Strix aluco*) during the early nestling period, when females remained in nest cavities, and found that males did not increase provisioning rates. Among some species, males have been found to be more responsive to variation in nestling begging intensity than females, e.g., Budgerigars (*Melopsittacus undulates*; Stamps et al. 1985), Pied Flycatchers (Ottosson et al. 1997), and Superb Fairy-wrens

(*Malurus cyaneus*; MacGregor and Cockburn 2002). In other species, females are more responsive to variation in nestling begging intensity, e.g., Manx Shearwaters (*Puffinus puffinus*; Quillfeldt et al. 2004).

Several factors can potentially contribute to differences among species and between adult males and females in how parent birds respond to variation in nestling begging intensity. In some cases, food availability may limit the extent to which parents can respond to increases in nestling begging intensity. For example, in response to increased nestling begging intensity, male Eurasian Kestrels did not provide nestlings with more prey, but did spend more time hunting (Masman et al. 1988). This suggests that, despite increased male effort, reduced availability of their most common prey (common voles, *Microtus arvalis*; 92% of prey captured) may have prevented male Eurasian Kestrels from providing nestlings with additional prey. In contrast, American Kestrels in my study fed nestlings a wide variety of vertebrate and invertebrate prey. A less-specialized diet makes it more likely that sufficient prey will be available if an increase in nestling begging intensity indicates the need for additional food.

Differences among avian species in average lifespan may also contribute to differences in adult responses to nestling begging. Sasvári and Hegyi (2010) found that male Tawny Owls did not increase provisioning rates in response to increases in the frequency of nestling begging calls (that resulted from experimental increases in brood sizes). However, for long-lived birds like Tawny Owls, reproductive success in a single breeding season is less important than surviving to breed in the future and maximize lifetime reproductive success. As such, selection should favor behaviors that increase the likelihood of survival. Because investing more time and energy to provide prey for nestlings could negatively impact body condition and reduce their likelihood of survival, male Tawny Owls, and perhaps adults in other species of long-lived birds (e.g., Sæther et al. 1993, Mauck and Grubb 1995), may benefit more in terms of fitness by limiting their investment in offspring to some ‘fixed’ level (Sasvári and Hegyi 2010). In contrast, shorter-lived species, like American Kestrels and most songbirds, may benefit more by increasing investment in their current offspring.

Sex-specific differences in avian parental roles may also contribute to differences between males and females in their responses to variation in nestling begging intensity. For example, during the early nestling period, female in many species must brood young that are not yet able to thermoregulate and, as a result, only males can respond to changes in nestling begging intensity. Ottosson et al. (1997) used small speakers at nests to increase begging frequency and intensity of nestling Pied Flycatchers and found that males, but not females, increased provisioning rates when nestlings were 3 to 6 days old. However, when nestlings were 7 to 10 days old, males again increased their provisioning rates and, in addition, the increase in female provisioning rates approached significance (P = 0.09). Ottosson et al. (1997) suggested the responses of female Pied Flycatchers likely changed with increasing nestling age because they spend much of their time brooding when nestlings are small, but spend less time brooding older nestlings. Such results suggest that responses by adult male and female birds to variation in nestling begging intensity may vary with nestling age. I examined the responses of adult American Kestrels to variation in nestling begging intensity when nestlings were 12 to 26 days old, when females do not brood and are provisioning young. Experimentally altering the begging intensity of nestling kestrels when they are younger, and when adult females must spend time brooding and adult males do most of the provisioning (Smallwood and Bird 2002), might yield results more similar to those reported by Ottosson et al. (1997) than those in my study.

Male and female American Kestrels increased provisioning rates in response to increases in nestling begging intensity, and similar results have been reported in many other species of birds. Martín-Gálvez et al. (2011) used an appetite stimulant to increase the begging intensity of nestling Black-billed Magpies (*Pica pica*) and found the nestlings received more food from their parents and were in better condition as they approached fledging age than control nestlings. These results suggest that natural selection should favor ‘dishonest’ begging by nestlings. However, the potential costs of ‘dishonest’ begging may outweigh any possible benefit, e.g., increased likelihood of attracting predators and loss of indirect fitness benefits if increased begging has negative impacts on the condition of siblings and/or parents (Martín-Gálvez et al. 2011).

Adult provisioning during control periods

I found that male and female American Kestrels provisioned young at similar rates during days 12 to 22 post-hatching. Similarly, Dawson and Bortolotti (2000) examined the provisioning rates of adult kestrels with nestlings that were 16 to 25 days old and found no difference between males and females. Other investigators have reported that female kestrels provision nestlings at higher rates than males (Smith et al. 1972, Coonan 1986, Dawson and Bortolotti 2002, 2003, 2008, Liébana et al. 2009). One possible explanation for different in the provisioning rates of males and females is that, particularly during the early nestling period when females are brooding young, male kestrels sometimes provide females with prey, and females then provide the prey to nestlings (Smith et al. 1972). Liébana et al. (2009) observed that male kestrels delivered 65.2% of their prey to females, and Dawson and Bortolotti (2002) noted that some prey delivered to young by females may have been captured by males. Studies that differ in the timing (e.g., entire nestling period or just early or later portions of the nestling period) and location (e.g., at nest sites and noting only nest visits vs. closely monitoring adult hunting behavior away from nests) of observations may provide differing results concerning the respective roles of male and female kestrels in provisioning nestlings. However, my results and those of Dawson and Bortolotti (2000) suggest that, during the post-brooding period when nestlings are able to thermoregulate and feed themselves (especially small prey like invertebrates), male and female kestrels provision nestlings at similar rates.

Most prey items provided to nestlings by adult American Kestrels in my study were invertebrates (96.2% invertebrate prey and 3.8% vertebrate prey). Investigators have reported that kestrels prey primarily on invertebrates during the breeding season (Rudolph 1982, Sarasola et al. 2003, Liébana et al. 2009), but others have noted that kestrels prey primarily on vertebrates, either small mammals (Gard and Bird 1990, Bortolotti et al. 1991, Dawson and Bortolotti 2000) or birds (Craig and Trost 1979), during the breeding season. When adults provide nestlings with more invertebrate than vertebrate prey items, vertebrate prey may contribute more of the total biomass consumed by nestlings than the invertebrate prey (Smith et al. 1972, Sarasola et al. 2003, this study). American Kestrels are opportunistic predators (Sarasola et al. 2003) and their choice of prey varies with availability (e.g., Gard and Bird 1990) and accessibility (e.g., Toland 1987, Dawson and Bortolotti 2000). However, given the energy demands of growing nestlings, the biomass provided by vertebrate prey, even if relatively few in number compared to invertebrates, appears to be an important factor in kestrel nesting success (Sarasola et al. 2003).

Although most prey items provided to nestlings by both male and female kestrels in my study were invertebrates, females delivered more vertebrate prey to nestlings than males (44 vs. 12). The extent to which this indicates a possible difference between the sexes in hunting strategies is unclear because, as noted above, males sometimes provide prey to females who then deliver it to nestlings. Sonerud et al. (2013) video-recorded nests of Eurasian Kestrels and found that females delivered more large prey to nestlings than males. However, observations of adults revealed that males selectively delivered larger prey items like birds and mammals to females who then fed nestlings. Thus, analysis of video-recordings suggested that females delivered more large prey to nestlings than males, but observations revealed no difference between adult males and females in the sizes of prey captured (Sonerud et al. 2013). Although American Kestrels exhibit reversed size dimorphism, with females generally larger than males, there is considerable overlap in size, e.g., male mass typically ranges from 80-143 g and female mass from 86-165 g (Smallwood and Bird 2002). Thus, unlike larger raptors, particularly bird-eating raptors in the genus *Accipiter* where females are significantly larger than males and tend to take larger prey (e.g., Storer 1966), male and female American Kestrels exhibit less variation in body size and prey selection and both can be characterized as being carnivorous (preying on small vertebrates) and insectivorous (Jaksić et al. 1981).

Nest success and brood reduction

Mean clutch size (4.6 eggs), brood size (3.7 nestlings), number of fledglings/brood (3.6 nestlings), and fledging success (75%) in my study were similar to those reported for American Kestrels in other parts of their breeding range (Smallwood and Bird 2002). For example, in Pennsylvania, clutch sizes of kestrels ranged from 4.3 to 4.8 eggs, brood sizes from 2.3 to 3.7 nestlings, and fledging success from 58 to 83% (Valdez et al. 2000). In Argentina, Liébana et al. (2009) reported that kestrels had a mean clutch size of 4.3 eggs, mean hatching success of 73%, and mean fledging success of 61%. Variation in food availability can influence annual variation in clutch sizes and nest success, especially for raptors that prey on rodents with fluctuating populations (Lack 1947).

Six nestlings in my study died within a few days after hatching, reducing brood sizes at four nests. Nestling mortality varies among species, locations, and years and can be influenced by food availability (Lack 1954, Gard and Bird 1990), weather (Dawson and Bortolotti 2000, 2003), parental experience (Viñuela 2000), sibling aggression and siblicide (Estes et al. 1999, Simmons 2002), infanticide (Bortolotti et al. 1991), and predation (Nilsson 1984, Christman and Dhondt 1997). Brood reduction occurs in species of birds with asynchronous hatching when food availability is insufficient to support all young and typically affects the youngest and smallest nestling(s) (Lack 1954, Bortolotti 1986, Estes et al. 1999, Viñuela 2000, Simmons 2002). Brood reduction has been reported previously in American Kestrels (Gard and Bird 1990, Anderson et al. 1993, Dawson and Bortolotti 2000, 2002, 2003). Adult kestrels in my study tended to give food items to nestlings closest to the nest box entrance (pers. observ.) so larger and older nestlings would likely obtain more food, potentially resulting in starvation of the youngest and smallest nestling(s). As the larger sex, female nestlings can potentially outcompete males in scramble competition in broods of American Kestrels (Anderson et al. 1993), leading to skewed fledgling sex ratios (Smith et al. 1972, Anderson et al. 1993, Liébana et al. 2009, this study). Lack (1947, 1954) suggested that hatching asynchrony and facultative brood reduction is adaptive when food supplies are unpredictable. Although adult raptors tend to reduce provisioning rates after a reduction in number of young, surviving nestlings may receive more resources than they would have if no reduction had occurred, giving evidence to an adaptive advantage for the siblings (Bortolotti 1986, Simmons 2002). Brood reduction may also improve the fitness of adult birds by reducing their workload so they can better provide for themselves and their remaining nestlings (Bortolotti 1986, Simmons 2002, Mock et al. 2011).

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VITA

Katheryn Watson was born in Houston, Texas in 1987. She attended grade school in Spring, Texas and graduated in May 2006. The following two years she attended Lone Star Community College and Austin Community College, and then entered Texas State University where she earned a Bachelor's of Science in Wildlife Biology in May 2013. She was president of the student chapter of The Wildlife Society and vice president of the Bobcat Botany Club. She conducted undergraduate research by monitoring raptor and vulture populations in south-central Texas, and published an article of her findings in the Bulletin of the Texas Ornithological Society in 2014. She also volunteered with several research projects, including endangered Anegada Iguana restoration and territory mapping of the endangered Golden-cheeked Warbler.

After earning her B.S., she moved to Kentucky to work with Dr. Gary Ritchison studying raptors at Eastern Kentucky University, where she earned her Master of Science degree in Biology. She plans to enter a Ph.D. program and hopes to one day earn a position as a university professor studying ornithology. She continues to volunteer with bird-related research in her spare time.