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Effects of Variation in Hunger Levels on Begging Behavior of Nestlings and the Provsioning Behavior of Male and Female Eastern Phoebes

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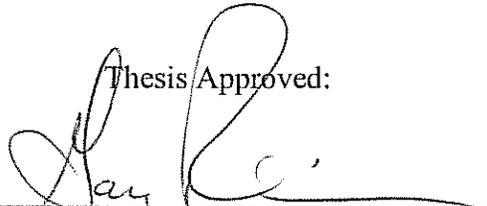
EFFECTS OF VARIATION IN HUNGER LEVELS ON BEGGING BEHAVIOR OF
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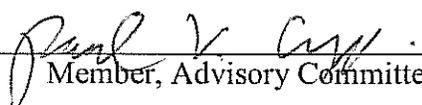
By

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NESTLINGS AND THE PROVISIONING BEHAVIOR OF MALE AND FEMALE
EASTERN PHOEBES

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

This thesis is dedicated to Rebecca.

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I would like to thank my advisor, Dr. Gary Ritchison, for his time, advice, and assistance, both in the field and in preparing this thesis. I would also like to thank my committee members, Dr. Charles Elliott and Dr. Paul Cupp, for their assistance during my tenure at ECU, as well as the Blue Grass Army Depot for access to the field site. In addition, I thank my fellow graduate assistants, friends, and family for their encouragement.

ABSTRACT

Nestling birds solicit food from their parents using conspicuous vocalizations and visual begging displays and there is considerable empirical evidence suggesting that nestling begging represents honest signals of need, and that adults use these signals to determine provisioning rates. Less is known about how males and females may differ in their response to changes in nestling begging behavior as a result of variation in hunger levels, or how nestling begging and adult provisioning may be influenced by brood number (i.e., first versus second broods). To examine these parent-offspring interactions, I first manipulated hunger levels of whole broods of nestling Eastern Phoebes (*Sayornis phoebe*) during the 2011 breeding season at the Blue Grass Army Depot in Madison Co., KY, to determine if nestling begging was positively correlated with hunger. Both first and second broods were divided into three treatments: (1) hand-feeding to satiation all nestlings in a brood (fed treatment, N = 12), (2) depriving all nestlings of food (deprived treatment, N = 16), and (3) feeding some nestlings in a brood and depriving the others (some deprived/some fed treatment, N = 14). Nestling begging and adult provisioning behavior was videotaped both before and after treatments were administered to analyze responses to experimental manipulation of nestling hunger level. Nestling begging behavior varied significantly among treatments, but there was no significant interaction between brood and treatment, and the begging behavior of nestling phoebes was not affected by the sex of the visiting adult. When broods were food-deprived, nestling begging intensity increased. Conversely, when whole broods were fed, both begging intensity and proportion of nestlings begging decreased. For some deprived/some fed broods, the change in begging intensity after treatment was between that of fed and

deprived broods. Thus, adult Eastern Phoebes adjusted their provisioning rates in response to changes in the begging intensity of nestlings, provisioning food-deprived nestlings at higher rates and nestlings in fed and some fed/some deprived broods at lower rates. These results suggest that nestling begging is an honest signal of need and that parents respond to variation in nestling begging by adjusting their provisioning behavior, consistent with predictions of signaling models. Although the overall provisioning rates of male and female phoebes did not differ, post-treatment responses of adults to changes in the begging behavior of nestlings differed for first and second broods. For both first and second broods, adult phoebes reduced provisioning rates to nestlings in fed and some fed/some deprived broods. However, food-deprived nestlings in first broods were fed at similar rates before and after treatment, whereas food-deprived nestlings in second broods were provisioned at much higher rates after treatment. Differences in the provisioning of first and second broods by adult phoebes may be a result of environmental factors, including weather and prey availability, or may represent a trade-off between investment in current and future reproduction.

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Chapter I

INTRODUCTION

Provisioning young is an essential aspect of avian parental care, but doing so requires time and energy and, therefore, can be costly for parents (Clutton-Brock 1991, Owens and Bennett 1994). As a result, each parent must balance their investment in offspring with the need to maximize their own lifetime reproductive success (Williams 1966), which can lead to differences between the sexes in the amount of parental care provided (Houston et al. 2005), including provisioning rates (Trivers 1972, Davies 1991). Factors that may contribute to sex-related differences in parental care include a skewed sex ratio with corresponding differences in potential reproductive rate and opportunities to engage in extra-pair copulations (Maynard Smith 1977, Breitwisch et al. 1986, Møller and Cuervo 2000, Chuang-Dobbs et al. 2001) which may impact an individual's potential lifetime fitness. Parents should attempt to fledge as many reproductively successful young as possible at the lowest cost to self-maintenance, whereas young, attempting to maximize their own fitness, may demand more care than adults are selected to provide (Trivers 1974). Several theoretical models have demonstrated this difference between parents and offspring in the optimum level of parental resource distribution (Macnair and Parker 1978; Parker and Macnair 1978, 1979; Godfray and Parker 1992, Godfray and Johnstone 2000). This parent-offspring conflict most commonly arises over the amount of food provided by parents.

Nestlings solicit food from parents by signaling their need using conspicuous begging behaviors, including vocalizations and gaping (Kilner and Johnstone 1997,

Wright and Leonard 2002). These conspicuous vocalizations can be costly via increased predator attraction (Leech and Leonard 1996, McDonald et al. 2009, Haff and Magrath 2011) and depressed immune responses (Moreno-Rueda 2010), and Kilner (2001) suggested that excessive begging could reduce growth rates. Some theoretical signaling models propose that extravagant begging by nestlings is a way to manipulate parents to provide more resources (Macnair and Parker 1978, Parker and Macnair 1978, 1979, Godfray 1995) or a means by which individual nestlings obtain more food than their siblings (Macnair and Parker 1979, Mock and Parker 1997). Furthermore, some models suggest that nestlings may escalate their own begging rates in response to their siblings (Stamps et al. 1978, Macnair and Parker 1979) and therefore extravagant begging may be a result of nestling competition (Harper 1986, Rodríguez-Gironés et al. 1996). Although the results of some studies indicate that nestling begging is unaffected by the begging intensity of siblings (Kacelnik et al. 1995, Cotton et al. 1996, Leonard and Horn 1996), others have found that chicks do adjust their begging to the effort of nestmates (Muller and Smith 1978, Smith and Montgomerie 1991, Leonard and Horn 1998, Leonard et al. 2000).

Other theoretical signaling models suggest that costly begging displays provide parents with accurate and honest indications of nestling need (Godfray 1991, Maynard Smith 1991, Godfray 1995, Johnstone and Godfray 2002), allowing parents to allocate food accordingly. The results of several studies provide support for these models, with the begging intensity of nestlings found to increase with food deprivation (Smith and Montgomerie 1991, Kilner 1995, Price and Ydenberg 1995, Leonard and Horn 1998) and decrease when young are provided with supplemental food by investigators (Litovich and

Power 1992, Redondo and Castro 1992, Price and Ydenberg 1995). Theoretical models (Godfray 1991, 1995, Godfray and Johnstone 2000) also indicate that parental responsiveness to nestling begging (costly or not) is adaptive, suggesting that responsive parents gain more fitness than non-responsive parents. Grodzinski and Lotem (2007) provide evidence suggesting that indeed, responsiveness to begging is adaptive because it reduces time wasted by returning too soon to feed satiated nestlings and the risk of overlooking hungry nestlings when compared to a random, non-responsive strategy. Empirical evidence also indicates that parents adjust provisioning rates to whole broods (Ottooson et al. 1997, Leonard and Horn 1998, Price 1998, Kilner et al. 1999) and to particular nestlings in broods (Kacelnik et al. 1995, Kilner 1995, Leonard and Horn 2001) based on variation in begging intensity. However, few investigators have examined the possibility that males and females might differ in their responses to variation in nestling begging intensity.

Because males and females may differ in how much they invest in parental care, they may also respond differently to variation in nestling begging intensity. For example, Ottooson et al. (1997) found that the responses of male and female Pied Flycatchers (*Ficedula hypoleuca*) to changes in nestling begging intensity differed, with males more likely to increase provisioning rates in response to increased begging than females. In contrast, Leonard and Horn (1998, 2001) found that male and female Tree Swallows (*Tachycineta bicolor*) did not differ in their responses to variation in the intensity of begging by nestlings and provisioned nestlings at similar rates. Factors that might contribute to differences in the response of males and females to variation in the begging intensity of nestlings include differences between the sexes in the certainty of parentage

(Møller and Birkhead 1993, Dixon et al. 1994, Sheldon et al. 1997, Møller and Cuervo 2000, but see Bennet and Owens 2002, Kvarnemo 2006), skewed breeding-adult sex ratios (Breitwisch et al. 1986, Westneat et al. 1990), or additional mating opportunities (Magrath and Komdeur 2003). Differences in relative quality of males and females (i.e. differential allocation) might also contribute to differences in parental response to nestlings (Sheldon 2000, Limbourg et al. 2004, Rutstein et al. 2005, DeMory et al. 2010, Mahr et al. 2012). Food availability (Hoi-Leitner et al. 2009), habitat quality (Whittingham and Robertson 1994), and time spent mate guarding or defending the nest (Markman et al. 1995) may also contribute to differences between the sexes in their responses to variation in nestling begging intensity.

The effect of variation in nestling begging intensity on adult provisioning rates may also differ among or between broods in multi-brooded species. Some studies have revealed that adults feed nestlings in second broods less than first broods (Royama 1966, Goodbred and Holmes 1996, Barba et al. 2009, García-Navas and Sanz 2011), whereas the results of other studies (Johnson and Best 1982, Veiga 1993, MacColl and Hatchwell 2003) indicate that provisioning rates do not differ between broods. Previous studies of Eastern Phoebes (*Sayornis phoebe*) have revealed conflicting results. Horn (2009) found that provisioning rates of adult phoebes did not differ for first and second broods, whereas Underwood (2011) found that adults fed second broods at significantly lower rates than first broods. Second broods may not be as valuable to adults because young in second broods may be less likely to survive to breed (Winkler 1987, Naef-Daenzer et al. 2001); adults, therefore, may be less responsive to variation in nestling begging intensity. Adults may also reduce investment in second broods, and be less responsive to variation

in begging intensity, because they must conserve energy for molting (Svensson and Nilsson 1997) or migration later in the breeding season.

Although previous studies have revealed that the intensity of begging by nestling songbirds may vary with hunger level and that the provisioning behavior of adults may be influenced by such variation, less is known about the possibility that nestling responses to variation in hunger levels might be influenced by season (brood number) or that the responses of adults to variation in nestling begging intensity might vary with sex or season. Thus, my objectives were to examine the (1) effect of variation in hunger level on the intensity of begging by nestling Eastern Phoebes in first and second broods, and (2) effect of variation in begging intensity by nestlings in first and second broods on the provisioning behavior of adult males and females.

Chapter II

METHODS

Study site

Fieldwork was conducted from 5 April – 31 July 2011 at the Blue Grass Army Depot (BGAD) in Madison County, Kentucky. The BGAD encompasses 5906 ha and consists primarily of pastures, ungrazed grasslands, and scattered woodlots of various sizes. Small concrete shelters (~ 2.5 x 5 x 2.5 m; N = 57) distributed throughout the depot to provide protection in case of emergencies also provided nesting sites for Eastern Phoebes. These shelters were monitored at least once every three days beginning in early April for nesting activity and the status of any nests recorded. At shelters with active nests, adults were captured and banded with a USGS numbered, aluminum band and a unique combination of three colored-plastic bands. Adults were captured and banded after eggs hatched to decrease chances of abandonment. The sex of each captured phoebe was determined using the presence of either a cloacal protuberance (males) or brood patch (females).

Video recording and treatments

To establish baseline provisioning rates of male and female phoebes, nests were video-taped over two consecutive days for two hours per day before treatments began. Pre-treatment taping occurred when nestlings were 7 - 11 days old. During taping, a camcorder (Handycam HDR-XR 100, Sony, Tokyo, Japan) was mounted on a tripod

placed 2 m from nests and adjusted for the best possible view of nestlings. In a study conducted with the same population of phoebes, Horn (2009) found that provisioning rates of adult phoebes did not differ significantly during the period when nestlings were 7 to 15 days old.

To manipulate the begging intensity of nestlings, I used methods similar to those used by Leonard and Horn (1998) including: (1) feeding to satiation all nestlings in a brood (fed treatment), (2) depriving all nestlings of food (deprived treatment), and (3) feeding some nestlings in a brood and depriving the others (some deprived/some fed treatment). For treatment (3), two nestlings were fed and two deprived for broods of four (N = 6). For half of the broods of 3 (N = 2) or 5 (N = 6), the extra nestling was fed; for the other half, the extra nestling was deprived. Treatments were comprised of broods with three nestlings (N = 9), four nestlings (N = 15), and five nestlings (N = 18).

Experimental trials were conducted on two consecutive days for each nest, with all taping occurring between 8:00 and 17:30. During each taping session, the shelter number, identity of the adults, brood number, number and age of nestlings, taping period, and time of day was noted. Any nest by a pair of phoebes that was not preceded by a nesting attempt where eggs hatched (and the nest may have subsequently failed or young may have fledged) was considered the first nest or brood. First broods (N = 22) were video-recorded during the period from (5 May – 23 June). Second nests or broods followed previous nesting attempts by the same pair of phoebes where eggs hatched. Second broods (N = 20) were video-recorded during the period from (9 June – 18 July).

Nestlings in broods subjected to the fed and some deprived/some fed treatments were removed from nests for one hour. Nestlings in broods subjected to the deprived treatment were food deprived for 1.5 – 2 hours, with the exact time determined by the gaping of all nestlings in response to slight movement of their container, simulating the arrival of an adult at a nest. Nestlings were either fed or sham-fed (deprived) depending on the treatment. For the some deprived/some fed treatment, nestlings were randomly assigned to one category or the other. Feeding consisted of opening the bill and placing small (<1gm) pieces of cat food (Pet Pride, Menu Foods, Streetsville, ON, Canada) in the nestlings' mouth using a forceps. Nestlings were fed until satiated (i.e., they no longer open their bills when presented with food). Food was presented to nestlings approximately every 10 minutes during the one hour removal period. The last 10 minutes was used to ensure that all nestlings that were fed were satiated and no longer accepted food when it was presented. Sham-feeding consisted of opening the bills of nestlings an equal number of times while the forceps were placed on the gape to simulate feeding. After one hour, nestlings in the fed and some deprived/some fed treatments were returned to their nest and nests were then video-taped for one hour.

Nestling removal and replacement

To reduce disturbance to adult phoebes and ensure that they did not abandon nests, one or more nestlings of similar age and size from another phoebe nest were temporarily removed and placed in nests after nestlings in focal nests were removed and treatments were conducted. The number of 'substitute' nestlings placed in nests varied

with availability and ranged from one to three. At least one nestling from replacement broods was left in the nest to ensure that those adults did not abandon their nests.

Replacement nestlings sometimes came from broods that were also used in my experiments. However, 'replacement nests' were not subjected to treatments on the same day that nestlings were used as replacements. Parents and nestlings do not recognize each other at this age (Leonard et al. 1997), and Leonard and Horn (1998) found that adult Tree Swallows fed replacement nestlings at the same rate they fed their own nestlings.

Video review and analysis

Videos were subsequently viewed and, for each recording session, I noted the shelter number, date, time of day, and whether it was a pre-treatment or post-treatment recording. For post-treatment recordings, I also noted the type of treatment. For each visit to a nest, sex of the visiting adult, the proportion of nestlings begging, and the maximum begging intensity of each nestling upon adult arrival and departure was recorded. Begging was defined as conspicuous gaping and vocalizations used by offspring to elicit food from parents (Wright and Leonard 2002). The proportion of nestling begging was defined as the number of nestlings gaping when an adult arrived at the nest (determining which nestlings were vocalizing was not possible given the quality of the video/audio). Leonard et al. (2003) suggest that posturing and gaping (henceforth referred to as begging intensity) may be a more reliable indicator of nestling hunger than calling. Begging intensity was scored for each nestling based on the following scale: (0)

head down, no gaping, (1) head up and gaping, (2) same as 1, but with neck extended upward, and (3) same as 2, but body elevated. Individual scores were then averaged to produce an overall mean begging intensity for each visit to the nest by an adult.

Statistical analysis

Following Leonard and Horn (1998), nests rather than individual feedings or nestlings, were the unit of replication, i.e., for each visit to a nest by an adult, the begging intensity of nestlings was determined based on the behavior of all nestlings (proportion of nestlings begging and average scores for begging intensity). For each treatment period, I determined the provisioning rate of each adult (visits per nestling per hour). I also determined the mean proportion of nestlings begging based on nestling behavior for all adult visits during that period, and the mean begging intensity of nestlings when an adult arrived at a nest and when they left. Because I was interested in examining possible effects of treatment on the behavior of adults and nestlings, I determined the difference in mean values for pre-treatment and treatment periods for each nest. Data (i.e., differences between pre-treatment and post-treatment period in adult provisioning rates, mean proportion of nestlings begging, and mean nestling begging intensity) were analyzed using two-way ANOVA, with adult sex (male and female) as a fixed factor, the difference between pre-treatment and post-treatment periods as a within-subject (i.e., within nest) effect, and treatment (fed, deprived, and some deprived/some fed) as a between-subject (i.e., between nest) effect. To satisfy normality assumptions, percentage data (proportion of nestlings begging) were arcsine-square root transformed prior to

analysis. When differences among treatments were significant, a post-hoc test (Tukey's) was used to determine differences among and between treatments. If nestling behavior differed significantly among treatments, then a significant interaction between adult sex and treatment would show that males and females responded differently. All analyses were conducted using the Statistical Analysis System (SAS 2004).

Chapter III

RESULTS

During the 2011 breeding season, 45 shelters and 61 nests were monitored. Of the 45 breeding pairs observed during my study, 16 successfully raised two broods. Excluding broods with fewer than three nestlings and, after randomly selecting one brood for pairs that successfully raised two broods, my sample consisted of 42 nests, including 22 first broods and 20 second broods. Of these 42 broods, all nestlings were fed in 12 broods, some nestlings were fed and some were food-deprived in 14 broods, and all nestlings were food-deprived in 16 broods. Of 22 first broods, all nestlings were fed in five broods, some nestlings were food-deprived and some fed in eight broods, and all nestlings were food-deprived in nine broods. Of 20 second broods, all nestlings were fed in seven broods, some nestlings were food-deprived and some fed in six broods, and all nestlings were food-deprived in seven broods.

Overall, mean brood size did not differ either among the three treatments ($F_{2,39} = 0.1, P = 0.92$) or between broods ($F_{1,40} = 0.2, P = 0.63$). Mean brood size was 4.36 ± 0.20 ($N = 22$) for first broods and 4.25 ± 0.16 ($N = 20$) for second broods. In addition, mean brood size did not differ among treatments for either first broods ($F_{2,19} = 0.8, P = 0.47$) or second broods ($F_{2,17} = 0.3, P = 0.74$).

Nestling begging behavior

Comparison of the begging behavior of nestling phoebes during pre-treatment and post-treatment periods revealed significant differences among treatments in begging the change in intensity scores both when adults arrived at and left nests and in the change in proportion of nestlings begging when adults arrived at and left nests (Table 1, Figures 1 and 2)¹. Post-hoc analysis indicated that changes in begging intensity of nestlings between pre- and post-treatment periods differed among all three treatments (Tukey's tests, all $P < 0.05$), with the begging intensity of food-deprived nestlings increasing after treatment (both when adults arrived at nests and left). The begging intensity of nestlings in the fed and some deprived/some fed treatments decreased after treatment (Figure 1), with a significantly greater decrease for nestlings in the fed treatment than the some deprived/some fed treatment (Tukey's test, $P < 0.05$; Figure 1).

Changes in the proportion of nestlings begging between pre- and post-treatment periods also differed significantly among treatments. The change for nestlings in the fed treatment differed significantly from that for nestlings in the deprived and some deprived/some fed treatments (Tukey's test, $P < 0.05$; Figure 2), with the proportion of nestlings begging declining for nestlings in the fed treatment. Changes in the proportion of nestlings begging did not differ between nestlings in the deprived and some deprived/some fed treatments (Tukey's test, $P > 0.05$; Figure 2).

The responses of nestling phoebes to treatment did not differ between broods, with no significant interaction between brood and treatment (Table 1). In addition, the

¹ All tables and figures located in appendix.

begging behavior of nestling phoebes was not affected by the sex of the visiting adult (Table 1), and this was true regardless of the type of treatment because the interaction between adult sex and treatment was not significant (Table 1).

Adult provisioning

Overall, male and female phoebes provisioned nestlings at similar rates and did so regardless of treatment, with no significant interaction between sex and treatment (Table 2). Differences between pre- and post-treatment provisioning rates of adult phoebes did, however, differ significantly among treatments (Table 2). Post-hoc tests indicated that differences between pre- and post-treatment periods in the provisioning rates of adult phoebes of fed and some deprived/some fed broods did not differ (Tukey's test, $P > 0.05$), with provisioning rates decreasing after treatment in both cases (Figure 3). However, the difference in provisioning rates for nestlings in the food-deprived treatment differed significantly from those for nestlings in the fed and some deprived/some fed treatments (Tukey's test, $P < 0.05$), with food-deprived nestlings fed at higher rates after treatment (Figure 3).

I found a significant interaction between brood and treatment (Table 2), suggesting that the effect of treatment on adult provisioning rates differed between first and second broods. For first broods, differences between pre- and post-treatment provisioning rates differed among treatments (Figure 4), with adults reducing provisioning rates to similar degrees (Tukey's test, $P > 0.05$) for nestlings in the fed and some deprived/some fed treatments (Figure 4). In addition, the difference between pre-

and post-treatment provisioning rates of fed and deprived nestlings differed significantly (Tukey's test, $P < 0.05$), with fed nestlings fed at lower rates and deprived nestlings fed at similar rates during pre- and post-treatment periods. However, the difference between deprived and some deprived/some fed treatment was not significant (Tukey's test, $P > 0.05$).

For second broods, the difference between pre- and post-treatment provisioning rates of adult phoebes also differed significantly among treatments (Figure 4). As with first broods, adult provisioning rates exhibited similar declines (Tukey's test, $P > 0.05$) after treatment for nestlings in the fed and some deprived/some fed treatments (Figure 4). However, the difference between pre- and post-treatment provisioning rates of food-deprived nestlings differed significantly from those for nestling in the fed and some deprived/some fed treatments, with provisioning rates increasing for food-deprived nestlings (Figure 4).

Chapter IV

DISCUSSION

Nestling begging and effects of treatment

I found that the begging behavior of nestling Eastern Phoebes varied in response to experimentally altered hunger levels. When whole broods were food-deprived, nestling begging intensity increased. Conversely, when whole broods were fed, both begging intensity and proportion of nestlings begging decreased. For some deprived/some fed broods, the change in begging intensity after treatment was between that of fed and deprived broods. Similar results, with a positive correlation between hunger level and begging intensity, have been reported for other species of songbirds (Smith and Montgomerie 1991, Litovich and Power 1992, Redondo and Castro 1992, Kilner 1995, Price and Ydenberg 1995, Leonard and Horn 1998, Leonard et al. 2003) and provide empirical evidence supporting theoretical signaling models that suggest nestling begging provides parents with a reliable signal of need (Godfray 1991, 1995).

My results also suggest that my attempt to satiate nestling Eastern Phoebes influenced their begging behavior more than 1.5 to 2 hours of food deprivation. Although I found significant differences among treatments in the responses of nestlings, fed nestlings exhibited the greatest change in the two measures of begging intensity in my study (proportion of nestlings in broods begging and begging intensity scores). For example, comparing pre- and post-treatment means for fed broods, the proportion of young begging when an adult first arrived at the nest decreased by 50.8% and the mean begging intensity score decreased by 60%, and those differences were greater when

adults left nests (68.8% and 81.0%, respectively). By contrast, these percentages for the some deprived/some fed and for deprived broods were 12.2% (decrease) and 9.5% (increase), respectively, for proportion begging and 16.1% (decrease) and 5.4% (increase), respectively, for begging intensity scores. Such results suggest that adult phoebes in my study provisioned nestlings at sufficiently high rates and with sufficient food to prevent hunger levels (as indicated by begging intensity) from increasing more than about 5-16% even after 1.5 to 2 hours of food deprivation. In addition, however, my results suggest that the begging intensity of satiated (or nearly satiated) nestling phoebes declines dramatically. Given the potential costs of begging for nestlings (e.g., predator attraction, Haff and Magrath 2011), dishonest begging (i.e., begging when satiated) would likely be selected against. Furthermore, because increased food intake by nestlings may reduce digestive efficiency (e.g., Konarzewski et al. 1996, Lepczyk et al. 1998, Grodzinski et al. 2009), reduced begging intensity when nestlings are satiated, and a corresponding decline in adult provisioning rates, would be beneficial for both nestlings and parents (Grodzinski et al. 2009).

Nestling begging and adult sex

The begging behavior of nestling phoebes in my study was not influenced by the sex of the visiting adult. These results suggest that, for nestling phoebes, the fitness benefits of begging from adult males and females are similar. In contrast, for species where the fitness benefits of begging from male and female parents differ, nestlings may respond differently to their feeding visits. For example, if adult males and females use

different provisioning rules, e.g., females are more likely to feed nestlings that beg most vigorously or males are more likely to feed the nearest nestling, then nestlings would benefit by adjusting their begging behavior, or position, in a nest, accordingly. The possibility that nestlings might respond differently to provisioning visits by male and female parents has rarely been examined. In one of the few such studies to date, Roulin and Bersier (2007) found that nestling Barn Owls (*Tyto alba*) begged more intensely in the presence of adult females than males. However, these authors could provide no clear explanation for this difference.

Differential begging by nestlings in response to adult males and females implies that nestlings can determine the identity of each parent and, to my knowledge, only the study by Roulin and Bersier (2007) has demonstrated such apparent recognition. Other studies have revealed differences in the responses of nestlings to male and female parents, but those responses appeared to depend on differences in the position of males and females when they arrived at nests. For example, Kolliker et al. (1998) found that food-deprived nestling Great Tits (*Parus major*) begged with greater intensity toward females than males, but adult male and female Great Tits fed nestlings from different locations on nests and food-deprived nestlings tended to position themselves near where females typically fed nestlings. As such, apparent differences in responses of nestling Great Tits to adult males and females may have resulted from differential positioning, with nestlings simply begging more when an arriving adult was closer (Kolliker et al. 1998). Similarly, Dickens et al. (2008) found that begging displays of nestling Blue Tits (*Cyanistes caeruleus*) were not influenced by the sex of the visiting adult, but, because males and females typically fed nestlings from different locations and males were more

likely to feed the closest nestling when they arrived at nests, food-deprived nestlings moved toward where males typically arrived at nests. Although not quantified in my study, my observations suggest that male and female Eastern Phoebes exhibited no apparent differences in where they were located on nests when they fed young.

The results of studies of several species of birds also suggest that nestlings that start begging first are more likely to be fed (Hofstetter and Ritchison 1998, Budden and Wright 2001, Roulin 2001, Porkert and Spinka 2006), conferring an advantage to rapid response to adult arrival. As a result, many stimuli, including vibrations of nest substrates when adults arrive, can cause nestlings to initiate begging, making selective begging problematic (Leonard et al. 2005). Responding quickly to both appropriate and inappropriate stimuli may be more advantageous than waiting to determine the identity of a visiting adult and potentially losing a chance to be fed (Dor et al. 2007).

Provisioning rates in response to nestling begging

Adult Eastern Phoebes in my study adjusted their provisioning rates in response to changes in the begging intensity of nestlings, provisioning food-deprived nestlings that begged with greater intensity at higher rates and nestlings in fed and some fed/some deprived broods at lower rates. Such results suggest that adult phoebes are sensitive to changes in the begging behavior of nestlings and that, as predicted by signaling models (Godfray 1991, 1995, Maynard Smith 1991), they use signals of need to allocate resources to nestlings as needed. By responding to changes in nestling begging intensity, adult Eastern Phoebes may avoid unnecessarily foraging for and attending to satiated

nestlings (Grodzinski and Lotem 2007). The results of previous studies provide additional evidence that adults in several species of birds adjust provisioning rates to broods and individual nestlings in response to changes in nestling begging intensity (Bengtsson and Ryden 1983, Ottosson et al. 1997, Kolliker et al. 1998, Leonard and Horn 1998, 2001, Price 1998, Villaseñor and Drummond 2007, Krauss and Yasukawa 2013).

Leonard and Horn (1998) found that adult Tree Swallows (*Tachycineta bicolor*), like the adult Eastern Phoebes in my study, responded to changes in nestling begging intensity (posturing and gaping) by increasing provisioning rates to food-deprived broods and provisioning fed broods at lower rates. Similarly, Kolliker et al. (1998) found that adult Great Tits (*Parus major*) increased provisioning to food-deprived nestlings and fed satiated (hand-fed) nestlings at lower rates than both food-deprived and control (unmanipulated) nestlings, and Villaseñor and Drummond (2007) found that adult Blue-footed Boobies (*Sula nebouxii*) adjusted provisioning rates to chicks based on chick body condition and food deprivation. The results of studies where playback of nestling vocalizations was used to simulate increased nestling demand for food have also demonstrated that enhanced nestling begging calls elicit an increase in adult provisioning (Ottosson et al. 1997, Price 1998). My results and those of previous studies, therefore, provide considerable empirical evidence that nestling begging intensity influences adult provisioning rates of whole broods and for allocation of food within broods.

I found that the begging intensity of nestling Eastern Phoebes in the three treatments differed significantly from each other. For the pre- to post-treatment change in the proportion of young in a brood begging, I also found a significant difference among treatments, but, whereas the change for fed broods was significantly different from that of

the other two treatments (i.e., significant reduction in the proportion begging), the extent of change for nestlings in the deprived and some fed/some deprived treatments was less pronounced (decreasing slightly for the some fed/some deprived treatment and increasing slightly for the deprived treatment) and did not differ between treatments. Such results provide further evidence that satiating nestling phoebes had a greater effect on their begging behavior than did depriving them of food. The proportion of nestlings in broods in the some fed/some deprived and the deprived treatments that begged was little affected by 1.5 to 2 hours of either total (whole brood) or partial (part of the brood) food deprivation, suggesting that, as noted above, adult phoebes provisioned nestlings at sufficiently high rates and with sufficient food to prevent hunger levels, and the proportion of nestlings begging, from changing substantially after a short period (1.5 to 2 hours) of food deprivation.

Nestlings in fed treatments begged at significantly lower intensities (postural and gaping scores) than nestlings in some fed/some deprived broods, yet the change in adult provisioning rates (pre-treatment vs. post-treatment) did not differ between fed and some fed/some deprived broods. One aspect of nestling begging that has been shown to have a significant impact on the provisioning behavior of adults is nestling vocalizations, which were not analyzed in this study. Several investigators have found that vocal cues appear to be more important in determining the overall level of brood provisioning whereas visual cues (e.g., gaping, neck-stretching, and jostling for position) may play a larger role in parental allocation of food within broods (Bengtsson and Ryden 1983, Leonard and Horn 2001, Glassey and Forbes 2002). Nestling vocal cues could have played a significant role in the provisioning responses of adult Eastern Phoebes in my study.

Nestling phoebes in fed broods may have vocalized at similar levels compared to nestlings in some fed/some deprived broods, therefore eliciting a similar provisioning response in adults.

Provisioning rates and adult sex

Overall, male and female Eastern Phoebes in my study provisioned nestlings at similar rates. In contrast, other investigators have reported that female Eastern Phoebes provisioned nestlings at higher rates than males (Conrad and Robertson 1993, Horn 2009). Differences between my results and those previous studies are likely due to differences in the timing of observations. I examined provisioning rates of nestling phoebes that were 7 – 13 days old, whereas Conrad and Robertson (1993) monitored provisioning behavior at days 2, 3, 6, 9, 11, and 14 days post-hatching and Horn (2009) from days 1 – 17 post-hatching. Although Horn (2009) found that provisioning rates of male and female phoebes differed over the entire nestling period, their provisioning rates during the period when nestlings were 7 – 13 days old were similar. Male phoebes may increase provisioning rates to levels similar to that of females during the mid-nestling period (7 – 13 days post-hatching) in order to meet the high metabolic needs of nestlings during this stage. Eastern Phoebes have relatively long nestling periods, with young typically fledging 16-18 days post-hatching (Weeks 2011), but the rate of increase in mass and tarsus length of nestling phoebes reaches an asymptote at about 13-14 days post-hatching (Murphy 1981). Thus, nestlings are typically growing fastest during the mid-nestling period, necessitating higher provision rates, while the metabolic needs of

nestlings reaching the fledging stage (15- 18 days post-hatching) may be lower. Both Horn (2009) and Conrad and Robertson (1993) found that provisioning rates of adult Eastern Phoebes typically increase with nestling age until around days 7-11 post-hatching, then leveled off before declining a few days before fledging.

Conrad and Robertson (1993) and Horn (2009) suggested that opportunities for extra-pair copulations may contribute to the lower overall provisioning rates of male Eastern Phoebes. Horn (2009) also noted that, although the costs of foraging for male and female Eastern Phoebes are currently unknown, differential costs of foraging could result in lower provisioning rates for males if they forage further from nests than females while patrolling territory boundaries (Morse 1968, Robins 1971, Franzreb 1983, Petit et al. 1990) or if preferred foraging habitat differs between the sexes (e.g., Black Phoebes, *Sayornis nigricans*; Wolf 1997). Investigators examining provisioning rates of other species during different stages of the nestling period have reported variation in the respective contributions of males and females. For example, Neudorf et al. (2013) found that male Carolina Wrens (*Thryothorus ludovicianus*) provisioned at higher rates than females early in the nestling period, likely in response to the reduced provisioning rates of brooding females. In contrast, Carey (1990) found that male Field Sparrows (*Spizella pusilla*) provisioned young nestlings less than females. Males may contribute less parental care to young nestlings because metabolic needs are lower in the earliest stages of the nestling period, allowing males to engage in alternative activities without reducing the chances of nestling survival and therefore male reproductive success (Westneat 1988, Carey 1990).

Male and female Eastern Phoebes in my study responded similarly to changes in nestling begging behavior (i.e., begging intensity). Similarly, Conrad and Robertson (1993) found that, although female phoebes made more provisioning trips per nestling, the provisioning rates of both males and females increased as broods aged, and their responses to increased nestling demand was similar. Males and females have also been reported to respond similarly to variation in nestling begging intensity in other species of birds, including, Tree Swallows (*Tachycineta bicolor*; Leonard and Horn 1998, 2001) and Great Tits (*Parus major*; Hinde 2006).

In contrast, Christie et al. (1996) found that, in broods of Great Tit infested with ectoparasites, nestlings more than doubled their total begging (gaping behavior) time per hour and, in response, males increased the frequency of feeding trips by over 50%, whereas females did not adjust their feeding rates. Christie et al. (1996) suggested that differences between males and females in their response to changes in nestling begging may be a result of sex-related differences in the trade-off between current and future reproduction, with males favoring current broods and females favoring future broods. Christie et al. (1996) cited previous studies of Great Tits (Linden 1991) and Blue Tits (Dhondt and Adriansen 1994) where females often divorced males after low breeding success or breeding failure, and concluded that such behavior indicates that females put a higher premium on future broods and males, attempting to avoid divorce, invest more in current broods. However, previous studies have revealed that divorce among Eastern Phoebe pairs is uncommon both within and between years, and the probability of divorce does not appear to be influenced by previous reproductive success (Beheler et al. 2003). Other factors may also contribute to differences in the provisioning rates of male and

females. For example, Ottosson et al. (1997) found that playing back nestling begging calls during visits to the nests by Pied Flycatchers (*Ficedula hypoleuca*) resulted in an increase in provisioning rates by males, but female provisioning rates remaining relatively constant. Ottosson et al. (1997) suggested that the response of female Pied Flycatchers may have been constrained by the time spent brooding young and also noted that, more generally, sex-related differences in parental effort might arise from different optimal responses to nestling begging due to variation in individual quality, opportunity for additional matings, or certainty of paternity.

One factor that may have contributed to the similar responses of male and female Eastern Phoebes to variation in nestling begging intensity during the mid-nestling period (7 – 13 days post-hatching) in my study is that, in contrast to younger nestlings, females need not spend as much time brooding 7 – 13 day old nestlings. Stoner (1939) found that the body temperatures of young phoebes were nearly constant after day 7 post-hatching (increasing only about one degree after that), whereas Mahan (1964) suggested that young phoebes were capable of regulating body temperature by day 10 post-hatching. Females that are no longer constrained by the need to brood young are likely better able to respond to the increased demands of nestlings. Male phoebes may be able to respond to variation in nestling begging intensity because, although Eastern Phoebes do sometimes engage in extra-pair copulations, most pairs are socially and genetically monogamous (Conrad et al. 1998, Beheler et al. 2003). Conrad et al. (1998) reported that 12% of the nestlings in an Ontario population were extra-pair, and Beheler (2001) found that 5.1 % of nestlings in a population in Indiana were extra-pair young. Given these relative low rates of extra-pair activity, limited opportunities for additional matings and

higher certainty of paternity for males in my study population may help explain the ability of males to respond to variation in the begging intensity of nestlings.

Effect of brood number on adult provisioning behavior

The responses of adult Eastern Phoebes to changes in the begging behavior of nestlings post-treatment differed for first and second broods. For both first and second broods, adult phoebes reduced provisioning rates to nestlings in fed and some fed/some deprived broods. However, food-deprived nestlings in first broods were fed at similar rates before and after treatment (mean increase after treatment was only 0.22 visits/nestling/hr), whereas, in second broods, food-deprived nestlings were provisioned at much higher rates after treatment (mean increase = 6.7 visits/nestling/hr).

Eastern Phoebes have one of the earliest arrival dates of migratory songbirds (Weeks 1994) and may begin nesting in suboptimal conditions (i.e., lower temperatures). Lower temperatures early in the breeding season may necessitate increased brooding by females, thereby reducing adults' ability to meet the increased begging by food-deprived broods (Wiebe and Elchuk 2003). Also, several studies have noted that insect abundance and flight are positively influenced by ambient temperature and precipitation (Williams 1961, Robins 1970, Bryant 1975, Davies 1977, Blancher and Robertson 1987) and that provisioning rates of some insectivorous songbirds (e.g., Northern Wheatears, *Oenanthe oenanthe*) are correlated with ambient temperature (Low et al. 2008). Adult phoebes may be unable to meet the demands of hungry nestlings in first broods if prey availability is low. However, increasing temperatures and growth of vegetation may increase the

availability of insect prey later in the breeding season (e.g., Sutter and Ritchison 2005) and enhance the foraging efficiency of adult phoebes, allowing them to increase provisioning rates of nestlings later in the breeding season.

Provisioning food-deprived nestlings in second broods at higher rates than nestlings in first broods may also represent a trade-off between current and future reproduction. In environments with unpredictable conditions, increasing the number of breeding attempts may provide a better strategy to maximize fecundity (Gill 2007), and parents should allocate time and energy to both broods accordingly to maximize their lifetime reproductive success (Williams 1966). Multi-brooded parents therefore face a trade-off between the amount of parental care provided to first broods, including provisioning, and the potential success of a second brood (Grüebler and Naef-Daenzer 2008, Naef-Daenzer et al. 2011). Stodola et al. (2009) suggested that female Black-throated Blue Warblers (*Setophaga caerulescens*) reduced provisioning rates to first broods to potentially save energy for second broods, and Grüebler and Naef-Daenzer (2008) found that adult Barn Swallows (*Hirundo rustica*), attempting to optimize pre- and post-fledging timing decisions, provisioned fledglings of first broods less than those of second broods, possibly to shorten the inter-clutch interval. Adult phoebes may be less responsive to the begging of hungry nestlings in first broods as a means of conserving energy for investing in second broods.

Conclusions

The results of my study provide additional empirical support for theoretical signaling models that suggest nestling begging is an honest signal of need, positively correlated with hunger, and that parents use variation in visual (i.e., gaping) begging intensity to determine provisioning rates. Although further study is needed to determine the influence that vocal begging intensity may have on the provisioning behavior of adult phoebes, the variation in begging intensity by nestling phoebes in response to experimentally manipulated hunger levels elicited similar provisioning responses from both males and females. Male and female Eastern Phoebes reduced provisioning to satiated broods and increased provisioning to food-deprived broods as predicted by signaling models. However, whereas adult phoebes did not increase provisioning rates to food-deprived first broods, they did increase provisioning rates to food-deprived second broods. This difference may represent a trade-off between investment in current versus future reproduction or may have been due to temporal changes in environmental conditions and prey abundance. Additional study is needed to understand the impact prey availability and potential sex-related differences in foraging behavior may have on the provisioning of first versus second broods.

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APPENDIX: TABLES AND FIGURES

Table 1. Comparison of mean (\pm SE) nestling begging intensity and mean proportion of nestling Eastern Phoebes begging plus differences between pre- and post-treatment periods (post-treatment minus pre-treatment) both when adults arrived and departed from nests during pre- and post-trial period and analysis (ANOVA) of effects of treatment, sex, and interactions on provisioning rates on differences between post- and pre-treatment periods. SF/SD = some nestlings fed and some deprived.

Treatment	Proportion Begging (%)				Begging Intensity			
	Adult Arrival		Adult Departure		Adult Arrival		Adult Departure	
	Pre	Post	Pre	Post	Pre	Post	Pre	Post
Fed (N = 12)	59 \pm 2	29 \pm 3	32 \pm 2	10 \pm 3	0.80 \pm 0.04	0.32 \pm 0.04	0.42 \pm 0.04	0.08 \pm 0.02
SF/SD (N = 14)	49 \pm 2	43 \pm 3	26 \pm 2	21 \pm 2	0.62 \pm 0.03	0.52 \pm 0.04	0.32 \pm 0.03	0.24 \pm 0.03
Deprived (N = 16)	63 \pm 2	69 \pm 2	37 \pm 2	41 \pm 2	0.93 \pm 0.03	0.98 \pm 0.04	0.52 \pm 0.04	0.57 \pm 0.04

Mean differences (post-treatment minus pre-treatment)

Fed	-30 \pm 4	-22 \pm 3	-0.48 \pm 0.05	-0.34 \pm 0.03		
SF/SD	-6 \pm 3	-5 \pm 3	-0.10 \pm 0.04	-0.08 \pm 0.03		
Deprived	6 \pm 2	4 \pm 2	0.05 \pm 0.04	0.05 \pm 0.04		
Source	df	F	P	df	F	P
Treatment	2	14.2	<0.0001	2	36.6	<0.0001
Sex	1	1.0	0.71	1	0.5	0.50
Brood*Treatment	2	0.1	0.94	2	2.1	0.13
Sex*Treatment	2	1.1	0.36	2	0.2	0.81
Error				2	25.0	0.0001

Table 2. Mean provisioning rates (\pm SE) of adult Eastern Phoebes in response to variation in nestling begging intensity by first and second broods during pre- and post-trial periods plus analysis (ANOVA) of effects of treatment, sex, and interactions on differences in provisioning rates. SF/SD = some nestlings fed and some deprived.

Treatment	Provisioning Rates (visits/hr/nestling)			
	Brood 1 ^a		Brood 2 ^b	
	Pre	Post	Pre	Post
Fed	9.47 \pm 2.04	5.59 \pm 1.37	8.66 \pm 1.18	3.79 \pm 0.59
SF/SD	10.07 \pm 1.51	8.33 \pm 1.85	10.74 \pm 2.05	4.71 \pm 1.08
Deprived	11.20 \pm 1.85	11.42 \pm 1.72	11.48 \pm 1.84	18.18 \pm 3.95

Mean differences (post-treatment minus pre-treatment)

	Brood 1	Brood 2
Fed	-3.88 \pm 2.18 (N = 10)	-4.87 \pm 1.12 (N = 14)
SF/SD	-1.74 \pm 1.00 (N = 16)	-6.03 \pm 2.17 (N = 12)
Deprived	0.22 \pm 1.32 (N = 18)	6.70 \pm 2.95 (N = 14)

Source	df	F	P value
Treatment	2	2.7	< 0.0001
Sex	1	0.2	0.67
Brood*Treatment	2	4.9	0.0099
Sex*Treatment	2	1.1	0.35
Error	35		

^aSample sizes for Brood 1: Fed (N = 5), SF/SD (N = 8), and Deprived (N = 9)

^bSample sizes for Brood 2: Fed (N = 7), SF/SD (N = 6), and Deprived (N = 7)

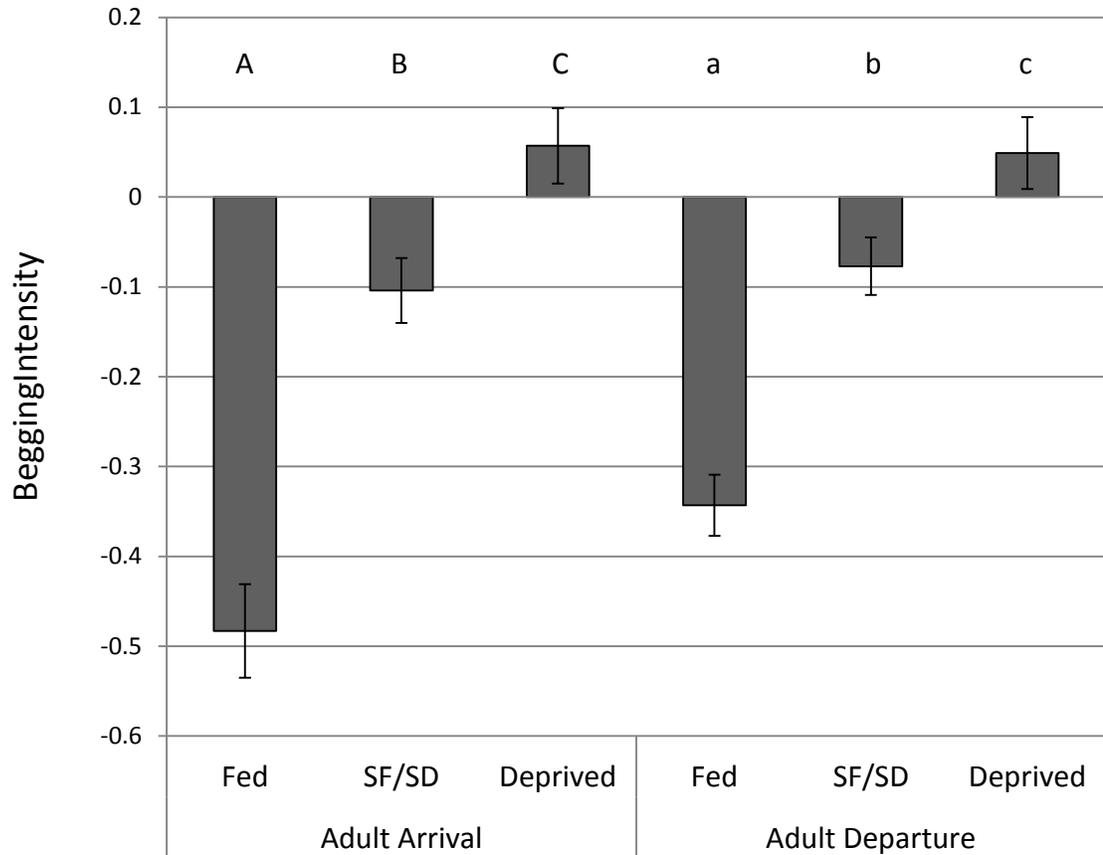


Figure 1. Mean differences (\pm SE) between pre- and post-trial periods in mean begging intensity scores of broods of Eastern Phoebes both when adults arrived and departed from nests for all three treatments. Letters above bars represent the results of a post-hoc test (Tukey's); means (bars) with different letters are significantly different ($P < 0.05$). SF/SD = some nestlings fed and some deprived.

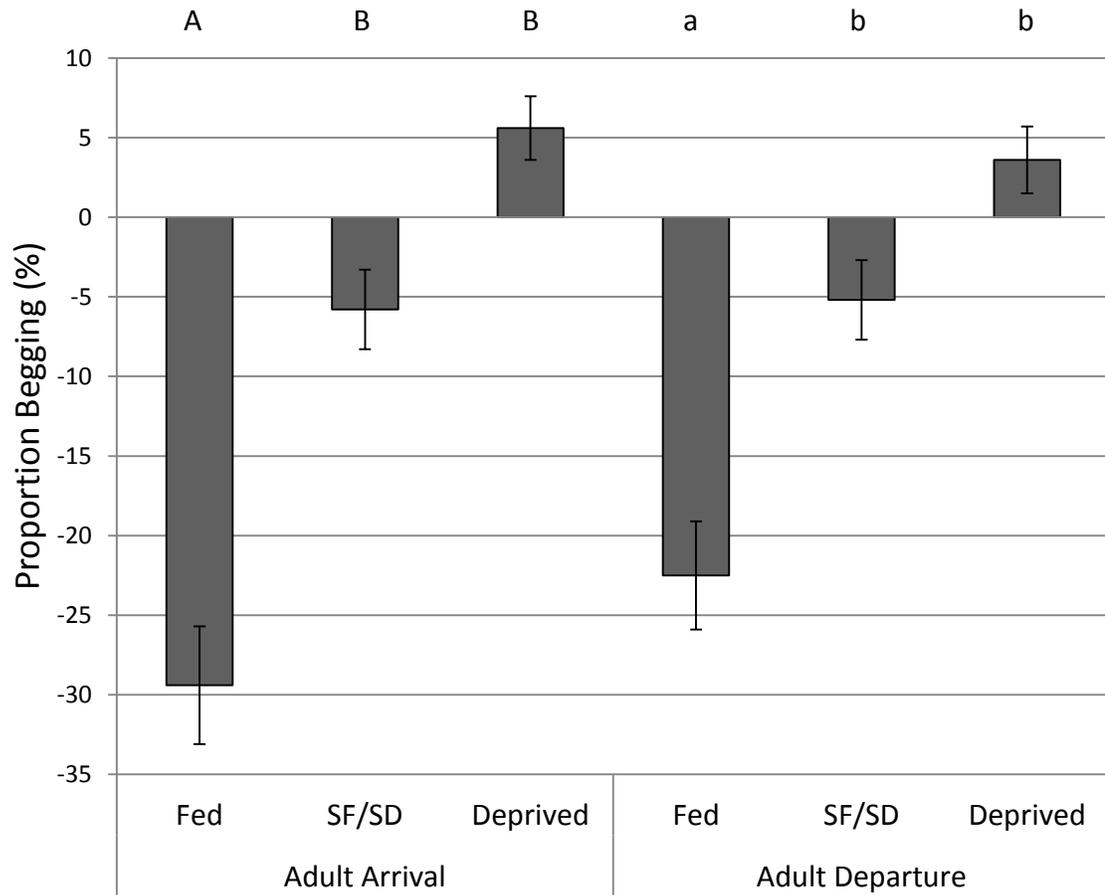


Figure 2. Mean differences (\pm SE) between pre- and post-trial periods in the proportion of nestling Eastern Phoebes begging both when adults arrived and departed from nests for all three treatments. Letters above bars represent the results of a post-hoc test (Tukey's); means (bars) with the same letter are not significantly different ($P > 0.05$). SF/SD = some nestlings fed and some deprived.

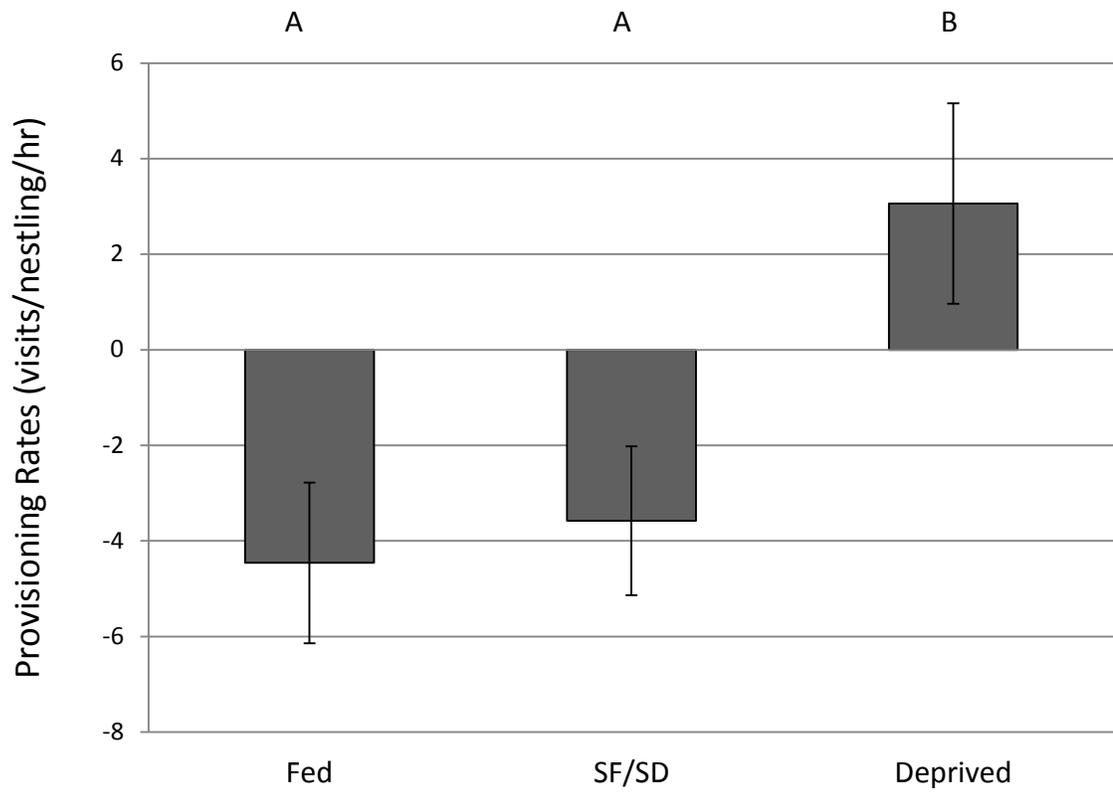


Figure 3. Mean differences (\pm SE) between pre- and post-trial periods in provisioning rates of adult Eastern Phoebes in response to changes in nestling begging intensity for all three treatments. Letters above bars represent the results of a post-hoc test (Tukey's); means (bars) with the same letter are not significantly different ($P > 0.05$). SF/SD = some nestlings fed and some deprived.

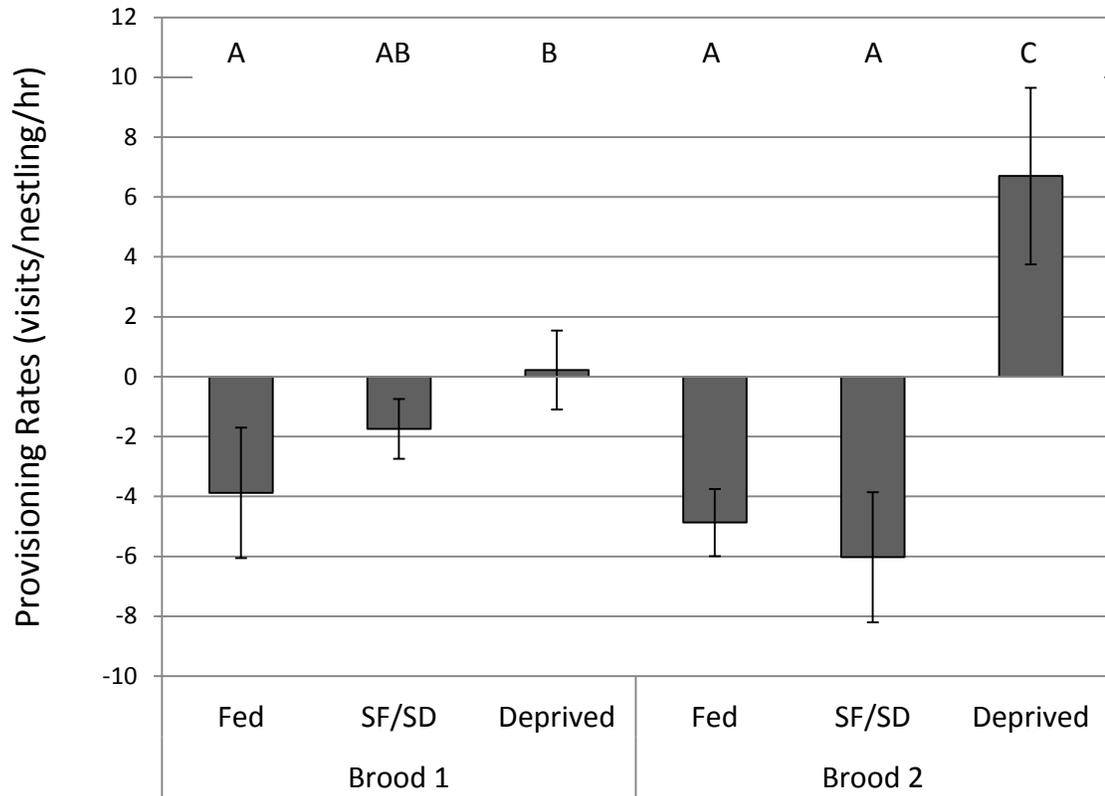


Figure 4. Mean differences (\pm SE) between pre- and post-trial periods in provisioning rates of adult Eastern Phoebes in response to changes in nestling begging intensity of first and second broods for all three treatments. Letters above bars represent the results of a post-hoc test (Tukey's); means (bars) with the same letter are not significantly different ($P > 0.05$). SF/SD = some nestlings fed and some deprived.