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Possible Role Of Breeding Phenology, Brood Size, And Male Parental Care On The Number Of Nesting Attempts By Female Eastern Bluebirds, A Facultatively Multibrooded Species

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POSSIBLE ROLE OF BREEDING PHENOLOGY, BROOD SIZE, AND MALE PARENTAL CARE ON THE NUMBER OF NESTING ATTEMPTS BY FEMALE EASTERN BLUEBIRDS, A FACULTATIVELY MULTIBROODED SPECIES

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Possible role of breeding phenology, brood size, and male parental care on the number of nesting attempts by female Eastern Bluebirds, a facultative multibrooded species

by

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DEDICATION

This manuscript is dedicated to my family and my wife, Rachel, for their unyielding love and support.

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ABSTRACT

To maximize reproductive output, several species of songbirds attempt to raise two or more broods in a single breeding season. The results of previous studies have revealed much variation among species in the factors that influence the likelihood of female songbirds attempting to raise multiple broods during a breeding season. As such, additional studies are needed to better understand the roles of early breeding, brood sizes, and, especially, male parental care in determining the likelihood of having multiple broods. My objective, therefore, was to examine the possible effects of breeding initiation date, brood size, and male provisioning behavior on the number of nesting attempts by female Eastern Bluebirds (*Sialia sialis*) during a single breeding season. My study was conducted at the Blue Grass Army Depot in Madison County, Kentucky, from mid-March to mid-August 2018. I monitored the nests of 39 first broods, 34 second broods, and eight third broods during my study. Bluebirds were captured in mist-nets and banded with unique combinations of color bands. Adult provisioning behavior was monitored with video-recorders placed from 1.5 – 3 m from nest boxes, and each nest was recorded at least every other day until nestlings fledged. Recordings were subsequently reviewed to quantify the provisioning behavior of male and female Eastern Bluebirds. The combined provisioning rates of male and female Eastern Bluebirds were similar for first, second, and third broods. For first and second broods, males provisioned young at higher rates than females during the first 5-6 days post-hatching, likely because females brooded nestlings during this period. Males did not provision young at higher rates than females during the first 5-6 days post-hatching for third broods, possibly reducing their investment in young in broods late in the breeding season. For broods one and two, the

combined provisioning rates of males and females were lower during the first four days post-hatching than for older nestlings, likely because the lower energy requirements of young during the first few days post-hatching. The number of young in broods did not affect the provisioning rates of male and female Eastern Bluebirds (in terms of feeding visits per nestling), with nestlings fed at similar rates regardless of the number of nestlings in a brood. One possible explanation for such results is that young in larger broods have, collectively, less exposed surface area, are better able to thermoregulate, and, therefore, require less food. I found that differences in initiation dates (laying of the first egg), clutch sizes, and brood sizes of first broods did not influence the likelihood of pairs having second and third broods during the breeding season. Rather, differences in individual quality among male and female Eastern Bluebirds may explain differences among pairs in the number of broods they attempt to raise in a breeding season.

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I. Introduction

To optimize reproductive output, several species of songbirds at temperate latitudes are multi-brooded, often attempting to raise two or more broods during a single breeding season (Hoffmann et al. 2015, Cornell and Williams 2016). However, the time, energy, and resources available for reproduction during a single breeding season are limited, potentially affecting the likelihood of more than one nesting attempt. For example, the probability of attempting a second brood may decline with the increasing size of the first clutch (Verboven and Verhulst 1996, Nagy and Holmes 2005, Siefferman and Hill 2008), suggesting possible constraints on the amount of energy that can be allocated to reproduction in a single breeding season (Hoffmann et al. 2015).

Among species of birds that are facultatively multi-brooded, the number of broods attempted per breeding season varies among females and pairs. For example, the number of breeding attempts per breeding season by female Black Redstarts (*Phoenicurus ochruros*) in a population in the Swiss Alps ranged from one to three (Weggler 2006). Similar variation among females and pairs in the number of breeding attempts per breeding season has been reported for many other species of songbirds (e.g., Mallord et al. 2008, Sim et al. 2012, García-Navas and Sanz 2012, Carro et al. 2014, Cornell and Williams 2016). Investigators have found that a number of factors can influence the number of breeding attempts in a season by females. For example, some investigators have found that females that begin breeding earlier in the season are more likely to be multi-brooded (e.g., Weggler 2006, Sim et al. 2012, Carro et al. 2014), but others have reported no relationship between the date of the first breeding attempt and the likelihood of being multi-brooded (e.g., Nagy and Holmes 2005, Mallord et al. 2008).

The number of broods attempted per breeding season can also be influenced by clutch size and the number of young that fledge from nests earlier in the breeding season. For example, the interval between successive nests was found to increase when clutches of Great Tits (*Parus major*) were experimentally enlarged (Slagsvold 1984, Tinbergen 1987), potentially reducing the likelihood to re-nesting. In contrast, when clutch sizes in first nests of Great Tits were experimentally reduced, the likelihood of attempting second nests increased (Tinbergen and Daan 1990, Verhulst et al. 1995). Investigators have also reported positive correlations between natural brood size (i.e., not experimentally manipulated) and interbrood intervals in House Sparrows (*Passer domesticus*, McGillivray 1983) and Song Sparrows (*Melospiza melodia*, Smith and Roff 1980). In contrast, the results of other studies have revealed no relationship between the clutch or brood size of earlier nests and the number of nesting attempts by multi-brooded species of birds (e.g., Finke et al. 1987, Nagy and Holmes 2005, Jacobs et al. 2013).

Another variable that can potentially influence the likelihood of multiple breeding attempts is the provisioning behavior of males. Few investigators have examined the possible role of males in multibrooded species of songbirds, perhaps because females decide whether or not to initiate another brood (Nomi et al. 2018). However, given the energetic costs associated with multibrooding, the contributions of males in provisioning young may reduce female reproductive effort and allow them to allocate more energy to later broods. This hypothesis, referred to as the enhanced fecundity hypothesis (Tallamy 2000) or load-lightening hypothesis (West and Capellini 2016), has been tested in some insects and mammals, but few investigators have tested this hypothesis with songbirds. Among the few studies to date, Wolf et al. (1990) examined the effect of removing males on the reproductive success of Dark-eyed Juncos (*Junco hyemalis*) and found no effect on the likelihood of females attempting multiple broods. In contrast, Nomi et al. (2018) found that the contributions of male Japanese Tits (*Parus minor*) in provisioning nestlings were positively correlated with the probability of females attempting multiple broods.

The results of previous studies have revealed much variation among species in the factors that influence the likelihood of females attempting multiple broods during a breeding season. As such, additional studies are needed to better understand the roles of early breeding, brood sizes, and, especially, male parental care in determining the likelihood of having multiple broods. Female Eastern Bluebirds (*Sialia sialis*) are known to exhibit much variation in the tendency of attempt multiple broods. For example, over a seven-year period in a population in South Carolina, 53.8% of 923 successful females had one nest/season, 36.5% had two, 9.4% had three, and 2% had four (Gowaty and Plissner 2015). However, no one to date has examined the factors that might contribute to this variation. Thus, the objective of my study was to examine the possible effects of the timing of breeding, clutch and brood sizes, and male provisioning behavior on the number of nesting attempts by female Eastern Bluebirds during a single breeding season.

II. Methods

My study was conducted from 1 March to 25 August 2018 at the Blue Grass Army Depot (BGAD) in Madison County, Kentucky. BGAD encompasses 6070 ha and consists of a matrix of pastures, open fields, and woodlots (Sutter and Ritchison 2005, Adler and Ritchison 2011). Approximately 2100 ha of BGAD are grazed by cattle (Sutter and Ritchison 2005), providing habitat suitable for Eastern Bluebirds. Nest boxes (N = 71) used by Eastern Bluebirds in previous studies were already available at the BGAD (Kieffer 2011).

Beginning in mid-March, nest boxes were checked at least weekly for signs of nesting activity (i.e., nest material in boxes). Nest boxes with nests were monitored at least twice a week to determine the date when the first egg was laid and clutch sizes; nest boxes with eggs were monitored every two days so the date of hatching could be determined. If incubation began before a nest box was checked, the date the first egg was laid was estimated by subtracting the mean number of incubation days (14 days) and a rate of one egg laid per day from the hatch date (Gowaty and Plissner 2015). When nestlings were at least seven days old (when females are no longer brooding young; Gowaty and Plissner 2015), adults were captured using mist-nets (using playback of the distress calls of nestling bluebirds to lure them into nets). Captured bluebirds were banded with a U. S. Geological Survey aluminum band and a unique combination of three, color bands to permit identification of individuals. For unbanded pairs of Eastern Bluebirds initiating nests in late April and into May, nest initiation dates were categorized to estimate likely brood numbers. Nests initiated prior to 14 May were considered first broods, those initiated from 20 May to 3 July were considered second broods (after a successful or unsuccessful first nesting attempt), and nests initiated between 11 and 26 July were considered third broods.

To monitor the provisioning behavior of male and female Eastern Bluebirds, plastic containers (60 cm x 30 cm x 30 cm) were attached to the top of 1.5-m high wooden posts and placed 1.5 – 2 m from nest boxes during the late incubation period and approximately 2 – 3 days before the anticipated hatch date. Prior to attaching the container, one end was removed to provide a clear view of nest-box entrances for video-recording. Once containers are were in place, a ‘decoy’ camcorder (small cardboard box similar in size and color to the camcorder that will be used) was placed inside so adults could habituate to its presence.

The provisioning behavior of adult bluebirds was recorded using digital camcorders (Handycam HDR-XR 100 and FDR-AX33, Sony Corp., Tokyo, Japan). Prior to video-recording, the number of nestlings was be noted, and the ‘decoy’ camcorder was removed and replaced with a real camcorder. Each nest was recorded at least every other day (depending on the number of active nests and availability of camcorders [N = 12], nests were sometimes video-recorded daily). Nests were video-recorded for 90-min periods during the period from 07:00 to 11:30 from the day after hatching until nests failed or young fledged. Nests were not video-recorded on days when it was raining because rain may influence the provisioning behavior of adults.

The dates when young fledged were noted, as was the number of fledglings (which I assumed to be the same as the number of nestlings present when a nest was last checked). The typical interval between fledging of young from one nest and laying of the first egg of the next nest was expected to be about two weeks (Gowaty and Plissner

2015). As such, because the breeding territories of Eastern Bluebirds are typically about 2.1 ha in area (Gowaty and Plissner 2015), all nest boxes within a 100-m radius (the radius of a 2.1-ha circle is about 85 m) of the previously used nest-box (and including the previously used nest-box) were checked every other day beginning 10 days after young fledged to determine the date when the first egg of second nests was laid. Adults at second nests were observed and identified using the unique combinations of aluminum and color bands. Second nests (and third) were monitored and video-recorded using the same methods used for the first nests.

Video-recordings were subsequently viewed to quantify the provisioning behavior of male and female Eastern Bluebirds. Because placing camcorders in the plastic containers may influence adult behavior, only the behavior of adults following the initial thirty minutes of recording was quantified; the results of a previous study indicate that one-hour observation periods are sufficient to accurately quantify adult provisioning behavior (Murphy et al. 2015). Adult provisioning behavior was quantified as the number of food deliveries per hour per nestling, as well as by the size of prey (as an indicator of prey biomass) delivered. Prey size was estimated relative to the length of the bill of Eastern Bluebirds (mean = 12 mm) and using a semi-quantitative scale: half the length of a bluebird's bill (i.e., 0.5 = 6 mm, same length, or 1 = 12 mm, 1.5 = 18 mm, 2 = 24 mm, 2.5 = 30 mm, 3 = 36 mm, 3.5 = 42 mm, 4 = 48 mm, and so on). An estimate of total prey biomass delivered during an observation period by one adult was determined by multiplying the number of visits by the mean length of prey delivered.

To examine possible differences in clutch sizes, brood sizes, and number of young fledged among different broods, I used generalized linear models (GLM, Poisson distribution), with clutch size, brood size, and number of young fledged as response variables and brood number as the predictive factor. To examine possible variation in provisioning behavior (i.e., provisioning rates and prey size) with nestling age, brood number, and between the sexes, I used GLMs. Parental provisioning rates were measured as the number of times adults (males, females, and males and females combined) fed nestlings per hour per nestling. In my analysis of provisioning data, nestling age, brood number, adult sex, and the interaction between sex and nestling age were the main effects, and nest ID was a random effect to account for non-independence of provisioning by adults during the nestling period at the same nest. To examine possible factors that might influence the number of broods attempted by pairs of Eastern Bluebirds during a breeding season, first egg dates (ordinal dates), clutch and brood sizes of first broods, number of young fledged from first broods, provisioning rates (males, females, and males and females combined) for first broods, and the interaction between sex and provisioning rate were predictive factors, and number of broods attempted was the response variable. For pairs that successfully fledged young from second nests, the same analysis was conducted to determine if male provisioning behavior influenced the probability of females initiating a third nesting attempt. All analyses were conducted using the Statistical Analysis System (SAS Enterprise Guide 6.1, SAS Institute Inc., Cary, NC). Values are presented as means ± SE.

III. Results

During my study, I monitored the nests of 39 first broods, 34 second broods, and eight third broods. Mean clutch size varied with brood number ($F_{2,78} = 19.1$, $P < 0.0001$), with mean clutch sizes of 4.77 ± 0.10 eggs for first broods, 4.00 ± 0.10 eggs for second broods, and 3.75 ± 0.16 eggs for third broods. Post-hoc analysis revealed that first brood clutches were larger than those of second and third broods (Tukey's test, $P < 0.05$). However, mean brood size ($F_{2,77} = 1.9$, $P = 0.15$) and mean number of young fledged per nest ($F_{2,78} = 0.1$, $P = 0.99$) did not differ among different broods (Figure 1). Considering only successful nests (fledging at least one young), I found no difference among broods in the mean number of young that fledged per nest ($F_{2,58} = 0.7$, $P = 0.49$)

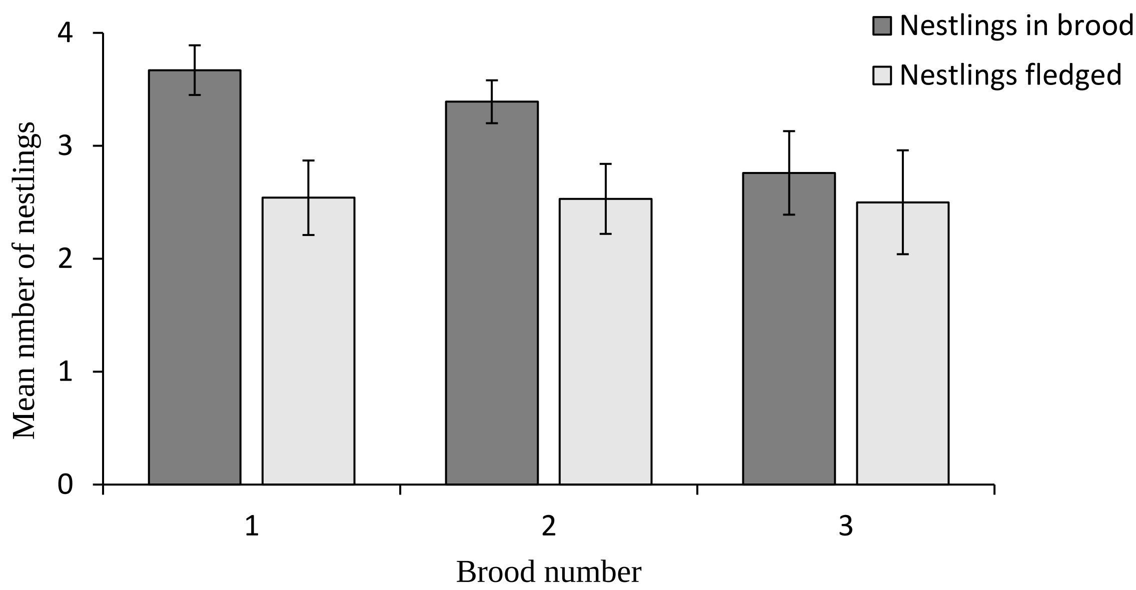

Figure 1. Mean brood size (± SE) and mean (± SE) number of young fledged per nest did not differ among different broods of Eastern Bluebirds.

Provisioning behavior of male and female Eastern Bluebirds

The provisioning rates (visits per hour per nestling) of adult Eastern Bluebirds (males and females combined) varied with nestling age for both first ($F_{8,133} = 2.7$, $P = 0.008$) and second ($F_{8,125} = 5.3$, $P < 0.0001$), with young fed at lower rates during the first four days post-hatching (Tukey's test, $P < 0.05$; Figure 2). Although based on small sizes ($N \leq 4$ pairs for different nestling ages), provisioning rates of adults did not vary with nestling age for third broods ($F_{8,13} = 0.6$, $P = 0.75$).

The provisioning rates of male and female Eastern Bluebirds were similar for first broods ($F_{1,32} = 0.3$, $P = 0.097$), second broods ($F_{1,9} = 0.1$, $P = 0.97$), and third broods ($F_{1,9} = 3.3$, $P = 0.17$) (Table 1). However, for first broods ($F_{1,9} = 5.8$, $P < 0.0001$) and second broods ($F_{1,9} = 3.9$, $P = 0.0004$), I found a significant interaction between sex and the age of young, with males feeding nestlings at higher rates than females during days 1 - 6 post-hatching (Figures 3 and 4). For third broods, the interaction between sex and nestling age was not significant ($F_{1,9} = 1.1$, $P = 0.46$).

Provisioning rates of adults (males and females combined) did not vary with brood size (range = 3 – 6) for either first broods ($F_{3,2} = 1.7$, $P = 0.39$) or second broods ($F_{3,1} = 2.2$, $P = 0.43$). Sample sizes for third broods were too small for analysis.

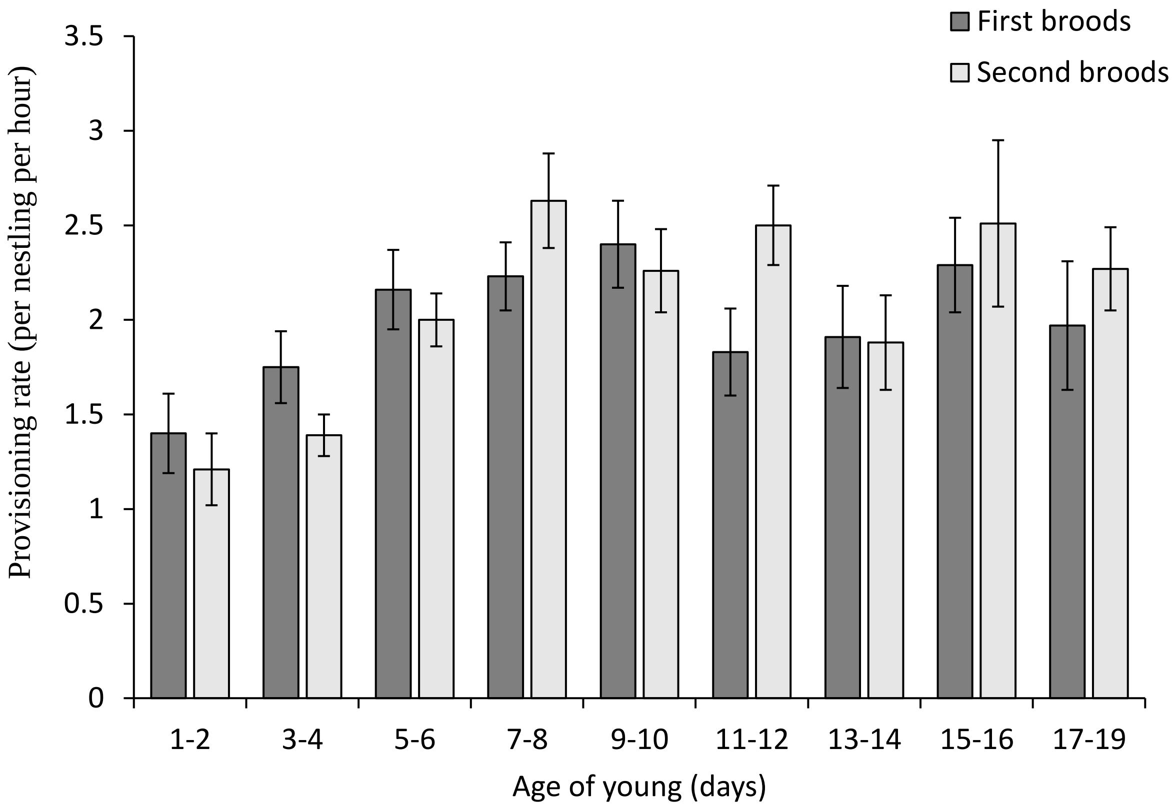

Figure 2. The mean (± SE) combined provisioning rates of adult male and female Eastern Bluebirds varied with nestling age for both first and second broods. Young were fed at lower rates (± SE) during the first four days post-hatching.

Table 1. The mean (± SE) provisioning rates of male and females Eastern Bluebirds (in terms of feeding trips/nestling/hour) were similar for first, second, and third broods.

		Brood one			Brood two			Brood three	
Nestling age	**N**	**Male provisioning**	**Female provisioning**	**N**	**Male provisioning**	**Female provisioning**	**N**	**Male provisioning**	**Female provisioning**
1-2	15	1.05 ± 0.18	0.36 ± 0.07	18	0.82 ± 0.15	0.39 ± 0.11	3	0.89 ± 0.73	0.89 ± 0.89
3-4	22	1.20 ± 0.17	0.55 ± 0.07	22	0.78 ± 0.09	0.60 ± 0.11	3	0.86 ± 0.32	0.25 ± 0.25
5-6	25	1.26 ± 0.13	0.90 ± 0.14	19	1.27 ± 0.14	0.74 ± 0.07	2	0.50 ± 0.50	0.29 ± 0.04
7-8	20	1.24 ± 0.13	0.99 ± 0.13	17	1.28 ± 0.15	1.36 ± 0.19	1	-	-
9-10	24	1.45 ± 0.16	0.94 ± 0.10	20	1.20 ± 0.16	1.07 ± 0.12	3	1.03 ± 0.61	0.22 ± 0.22
11-12	23	0.96 ± 0.16	0.87 ± 0.14	19	1.13 ± 0.15	1.37 ± 0.15	2	1.67 ± 0.33	0.38 ± 0.38
13-14	17	0.99 ± 0.18	0.92 ± 0.15	18	0.75 ± 0.16	1.12 ± 0.23	1	-	-
15-16	20	0.99 ± 0.11	1.41 ± 0.19	14	1.10 ± 0.31	1.40 ± 0.21	2	0.50 ± 0.50	0.79 ± 0.46
17-19	11	0.82 ± 0.15	1.31 ± 0.27	11	0.82 ± 0.15	1.45 ± 0.13	1	-	-

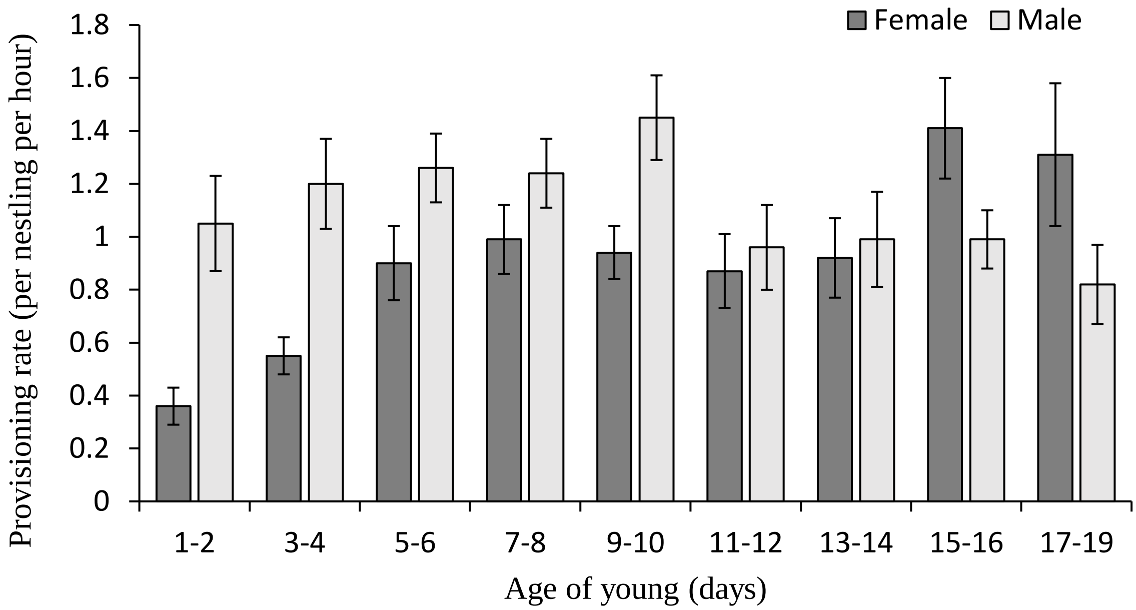

Figure 3. For first broods, mean (± SE) provisioning rates of male Eastern Bluebirds were higher than those of females during days 1 - 6 post-hatching.

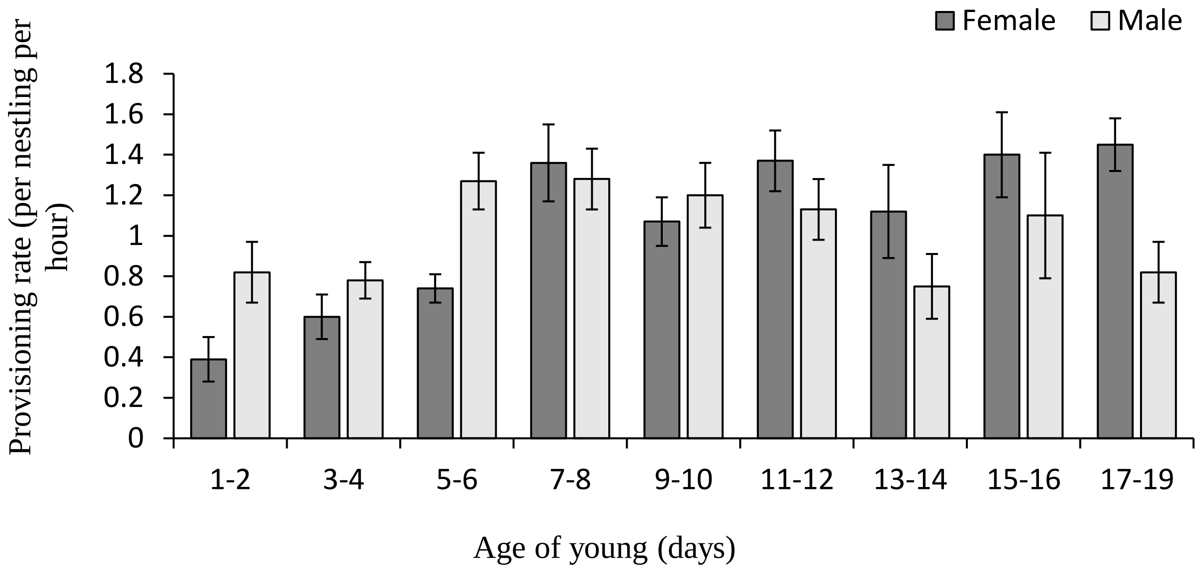

Figure 4. For second broods, mean (± SE) provisioning rates of male Eastern Bluebirds were higher than those of females during days 1 - 6 post-hatching.

Number of broods

Among pairs with different numbers of broods (range = 1 – 3), I found no difference in the dates on which first broods were initiated (i.e., first egg laid; $F_{2,25}$ = 0.5, P = 0.59). Similarly, for first nesting attempts, pairs with different number of broods during the breeding season did not differ in mean clutch size ($F_{2,25}$ = 0.1, P = 0.93), mean brood size ($F_{2,25}$ = 2.1, P = 0.14), or number of young fledged ($F_{2,25}$ = 1.0, P = 0.37).

Provisioning rates of adult Eastern Bluebirds (males and females combined) for first broods did not differ among pairs that differed in number of broods raised (1, 2, or 3) during the breeding season ($F_{2,19}$ = 0.6, P = 0.58). However, I found a significant interaction between sex and number of broods raised during the breeding season ($F_{2,3}$ = 5.4, P = 0.0055), with males in pairs that raised three broods during the breeding season provisioning nestlings in first broods at higher rates than males in pairs that raised just one or two broods and females that raised three broods during the breeding season provisioning at lower rates than females that raised just one or two broods (Figure 5). Similarly, provisioning rates for second broods did not differ among pairs that did or did not also raise third broods ($F_{2,30}$ = 1.0, P = 0.37), but the interaction between sex and number of broods was not significant ($F_{2,3}$ = 1.0, P = 0.36).

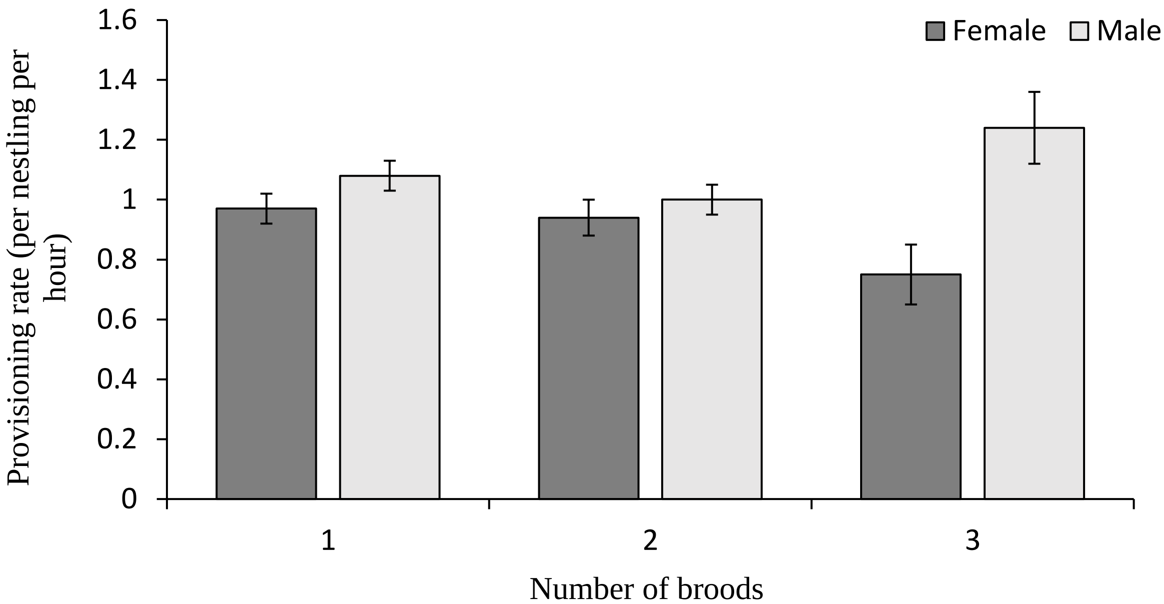

Figure 5. Males in pairs of Eastern Bluebirds that raised three broods during the breeding season provisioned nestlings in first broods at higher rates (± SE) than males in pairs that just raised one or two broods. Females that raised three broods during the breeding season provisioned nestlings at lower rates (± SE) than females that raised just one or two broods.

Prey size

The size (length) of prey items fed to nestlings by male (mean = 14.1 ± 0.5 mm, N = 349 prey items) and female (mean = 14.6 ± 0.5 mm, N = 379 prey items) Eastern Bluebirds ($F_{1,46} = 0.03$, $P = 0.85$) did not differ. However, the size of the prey delivered to nestlings by adults did vary with nestling age ($F_{8,62} = 5.2$, $P < 0.0001$), with nestlings fed smaller prey during days 1 – 4 post-hatching than during days 5 - 19 days post-hatching (Tukey's test, $P < 0.05$; Figure 6). The interaction between sex and nestling age was not significant ($F_{8,9} = 1.6$, $P = 0.12$). Although I found that the size of prey fed to young in different-sized broods differed ($F_{3,25} = 4.2$, $P=0.015$), no clear trend was apparent. Nestlings in broods of 3, 5, and 6 were provided with larger prey than nestlings in broods of 2 or 4 (Figure 7).

Among pairs of Eastern Bluebirds that raised different number of broods (1, 2, or 3) during the breeding season, the size of prey delivered to nestlings in first broods did not differ ($F_{2,19} = 1.1$, $P = 0.37$), with no interaction between sex and number of broods ($F_{2,3} = 0.5$, $P = 0.58$). Similarly, among pairs that raised two or three broods during the breeding season, I found no difference in the size of prey provided to nestlings in second broods ($F_{1,9} = 1.0$, $P = 0.35$), and no interaction between sex and number of broods ($F_{1,9} = 0.6$, $P = 0.47$).

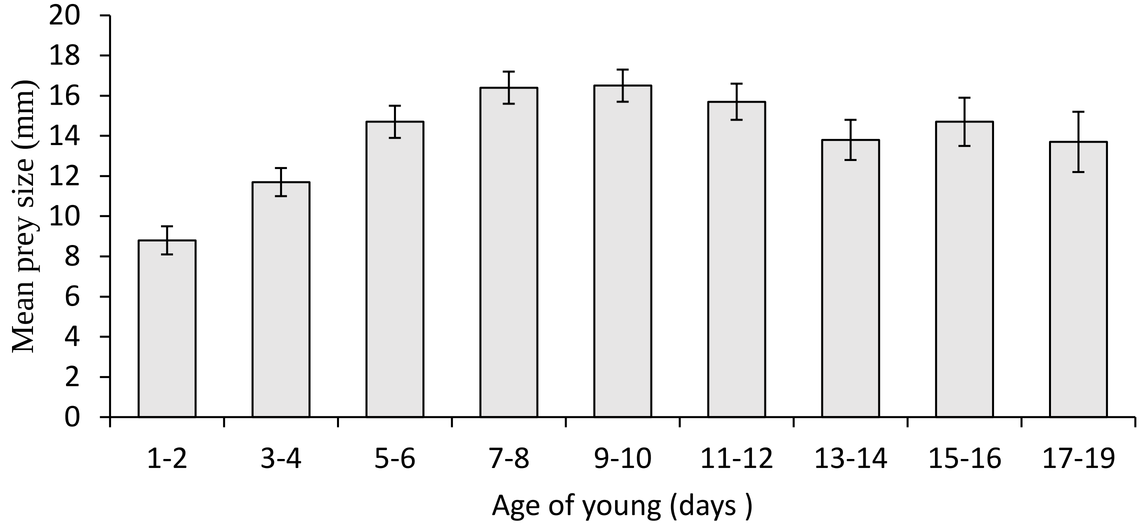

Figure 6. The size of prey (± SE) delivered to nestlings by adult Eastern Bluebirds varied with age. Nestlings were fed smaller prey during days 1-4 post-hatching than during days 5-19 post-hatching.

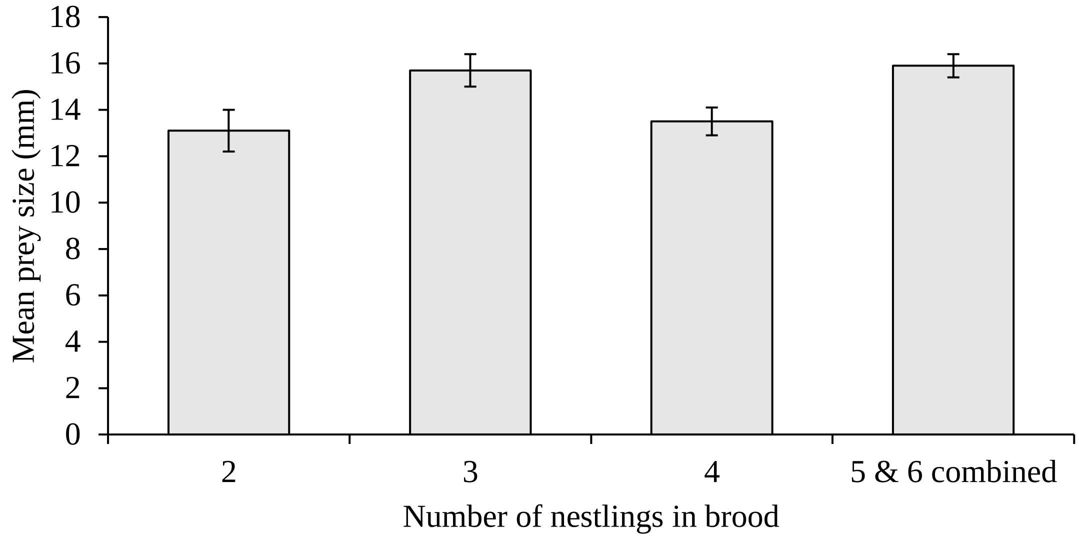

Figure 7. The size of prey (± SE) fed to nestlings by adult Eastern Bluebirds differed with brood size. Nestlings in broods with 3, 5, and 6 young were provided with larger prey than nestlings in broods of 2 or 4.

IV. Discussion

Provisioning rates

I found that the combined provisioning rates of male and female Eastern Bluebirds during the nestling period were similar across broods. However, because second and third broods were smaller than first broods, and rates were determined based on visits per nestling, it is apparent that overall visit rates by male and female Eastern Bluebirds declined with each successive brood. Similar results, with no change in provisioning rates per nestlings among different broods, have been reported for other species of songbirds, including Gray Catbirds (*Dumetella carolinensis*; Johnson and Best 1982), Song Sparrows (Nordlund and Barber 2005), Great Tits (Barba et al. 2009), and Eastern Phoebes (*Sayornis phoebe*; Horn and Ritchison 2017). In contrast, later broods were found to be fed at lower rates in other species, including Black-throated Blue Warblers (*Setophaga caerulescens*; Goodbred and Holmes 1996) and Yellow-breasted Chats (*Icteria virens*; Cooper and Ritchison 2005). Multiple factors can influence parental investment in different broods among multi-brooded species. For example, Goodbred and Holmes (1996) suggested that lower provisioning rates for later broods might be due to reduced food availability. Other investigators have suggested that the reproductive value of young declines later in the breeding season, e.g., due to a competitive disadvantage with young from earlier broods, so parents should reduce levels of investment for later broods (Curio 1983). Another possible reason for differences in provisioning rates among broods is that, later in the breeding season, parents must begin to allocate less energy to nestlings and more in self-maintenance, e.g., for molting or preparing for migration (Goodbred and Holmes 1996). Although multibrooded pairs of Eastern Bluebirds in my study provisioned nestlings in different broods at similar rates on a per nestling basis, they also had smaller broods later in the breeding season so provisioning rates on a per nest basis were lower for later broods. Reasons for this reduced investment in later broods by male and female Eastern Bluebirds remain unclear, but may be explained by any, or some combination, of the factors noted by previous investigators, e.g., reduced food availability later in the season, lower reproductive value of later fledged young, and the need to allocate more energy to adult self-maintenance.

Provisioning rates – effect of nestling age

For both first and second broods, male Eastern Bluebirds provisioned nestlings at higher rates than females during the first 5-6 days post-hatching, likely because female Eastern Bluebirds brood nestlings during this period (Gowaty and Plissner 2015). Young songbirds are unable to thermoregulate and require brooding to maintain their body temperatures (Pinkowski 1978, Konarzewksi 1995). Nestling Eastern Bluebirds are able to fully thermoregulate when 5-7 days old, which is when the provisioning rates of females become similar to or surpass that of males, as observed by Gowaty and Plissner (2015), as well as this study. With increasing age, nestling songbirds become better able to regulate their body temperatures and require less brooding (Johnson and Best 1982). Adult females then have additional time to provision nestlings (Johnson and Best 1982). In other species of songbirds, females have also been found to provision young at lower rates than males during the brooding period (Royama 1966, Johnson and Best 1982, Johnson et al. 2007, Ritchison et al. 2019).

Although based on a small sample size, male Eastern Bluebirds did not provision young at higher rates than females during the first eight days post-hatching for third broods. One possible explanation for this is that young that fledge later in the breeding season are less likely to survive than young that fledge earlier in the breeding season (Verboven and Visser 1998, Wheelwright et al. 2003, Müller et al. 2005, Grüebler and Naef-Daenzer 2008, Tarof et al. 2011). As such, males may be less willing to invest time and energy in caring for third broods (Patterson et al. 1980.) Another possible explanation is that the energy expended in caring for the first two broods may have had a negative impact on the condition of males (Houston et al. 2005). As a result, further investment for third broods at the same level as earlier broods could reduce the likelihood of male survival and the probability of future reproduction (Houston et al. 2005). By reducing their level of parental care for third broods, males may increase their chances of future reproduction (Conrad and Robertson 1993).

The combined provisioning rates of male and female Eastern Bluebirds for the first two broods was lower during the first four days post-hatching than for older nestlings. Variation of provisioning rates with nestling age has been reported in several other species of songbirds. For example, male and female Grasshopper Sparrows (*Ammodramus savannarum*) provisioned 1-4 day old nestlings at lower rates than nestlings 5-10 days old (Adler and Ritchison 2011). Similar results, with younger nestlings provisioned at lower rates than older nestlings have been reported in several other species of songbirds, including Great Tits (Barba et al. 2009), Long-tailed Tits (*Aegithalos caudatus*, Maccoll and Hatchwell 2003), Northern Cardinals (*Cardinalis cardinalis*, Filliater and Breitwisch 1997), Snow Buntings (*Plectrophenax nivalis*, Falconer et al. 2007), and Song Sparrows (Nordlund and Barber 2005). The likely explanation for the lower provisioning rates of younger nestlings is that they require less energy than larger, older nestlings (Goodbred and Holmes 1996, Nordlund and Barber 2005, Barba et al. 2009).

From days 1-4 post-hatching, nestlings in my study were fed at increasing rates, but provisioning rates were highest and remained similar from days 5-6 to days 17-19 post-hatching. Pinkowski (1975) found that nestling Eastern Bluebirds grow at the highest rates from about day 5 to day 10 post-hatching. During this time period, nestlings are receiving their maximum food intake to facilitate this rate of growth. Similar correspondence between provisioning and growth rates has been reported for Savannah Sparrows (*Passerculus sandwichensis*, Bédard and Meunier 1983). Species where adults continue to provision nestlings at similar rates until fledging typically have longer nestling periods and growth rates of nestlings plateau during the late nestling period rather than continuing to increase (Murphy 1981, Horn and Ritchison 2017). Among species with shorter nestling periods, and where nestlings continue to grow throughout the nestling period, such as Black-throated Blue Warblers, adults continue to increase provisioning rates until young fledge (Goodbred and Holmes 1996, Remes and Martin, 2002).

Provisioning rates – effect of brood size

I found that the number of young in broods did not affect the provisioning rates of male and female Eastern Bluebirds (in terms of feeding visits per nestling), with nestlings fed at similar rates regardless of the number of nestlings in a brood. Stauss et al. (2005) also found that adult Blue Tits (*Cyanistes caeruleus*) adjusted their provisioning rates so that nestlings were fed at similar rates as brood size increased, as long as food resources were not limited. Similar results have been reported for other songbirds, including Great Tits and Water Pipits (*Anthus spinoletta*, Gibb 1950, Rauter et al. 2000). Other investigators, however, have found that provisioning rates per nestling declines with increasing brood size (Royama 1966, MacColl and Hatchwell 2003, Falconer et al. 2008). One possible explanation for such results is that young in larger broods may require less food because they are better able to thermoregulate (Konarzewksi 1995, Falconer et al. 2008). When huddled together, nestlings in large broods have, collectively, less exposed surface area than nestlings in smaller broods and, therefore, lose less heat and require less energy for thermoregulation (Dunn 1976). This effect of brood size on energy savings, however, may be more important for species of birds that are open-cup nesters than species that nest in cavities like Eastern Bluebirds. Martin et al. (2017) found that nestlings in open-cup nests need more constant brooding than nestlings in enclosed nests because open-cup nests have less thermally stable microclimates than cavity nests.

Number of broods

I found that the likelihood of pairs having second and third broods was not influenced by nest initiation date (laying of the first egg), clutch size, and brood size of first broods. Initiation dates of first clutches have also been found to have no effect on the likelihood of females attempting to raise additional broods in other species, including Black-throated Blue Warblers (Nagy and Holmes 2005) and European

Starlings (*Sturnus vulgaris*; Cornell and Williams 2016). However, Ogden and Stutchbury (1996) found that female Hooded Warblers (*Setophaga citrina*) that were double-brooded initiated their first nesting attempts significantly earlier than females that attempted only a single brood. Similar results have been reported for other species of songbirds (Weggler 2006, Carro et al. 2014). Early initiation dates in some species may influence the likelihood of being multibrooded if initiation dates are correlated with the time of arrival on territories and early arrival is positively related with territory quality (Ogden and Stutchbury 1996, Bulluk et al. 2013).

Cornell and Williams (2016) found that the propensity of female European Starlings to be double-brooded was independent of laying date, and suggested that higher quality parents (e.g., genetic or physiological traits) were more likely to be double-brooded that those that raised single broods. Male Eastern Bluebirds with larger chestnut patches on their breasts and brighter blue-ultraviolet plumage on the head, back, and wings have been found to provision nestlings at higher rates than those with smaller breast patches and duller blue-ultraviolet plumage (Siefferman and Hill 2003), providing evidence of variation in male quality. Similarly, Grindstaff et al. (2012) found that female Eastern Bluebirds with brighter tail feathers were in better condition that those with duller tail feathers. Differences in individual quality among male and female Eastern Bluebirds in my study may help explain, as suggested by Cornell and Williams (2016) for European Starlings, differences among pairs in number of broods they attempted to raise. In support of this hypothesis, O'Brien and Dawson (2013) found that, for congeneric Mountain Bluebirds (*Sialia currucoides*), high-quality females were more likely to double-brood than lower-quality females.

The likelihood of pairs of Eastern Bluebirds having multiple broods in my study was not affected by the clutch and brood size of first broods. Stouffer (1991) reported similar results in European Starlings. However, Ogden and Stutchbury (1996) found that pairs of Hooded Warblers (*Setophaga citrina*) with larger clutches and broods in first nesting attempts were more likely to be double-brooded than those with smaller clutches. Conversely, large clutches and broods in first nests were found to reduce the likelihood of double-brooding in Black-throated Blue Warblers (Tinbergen and Verhulst 2000, Nagy and Holmes 2005). Similarly, Siefferman and Hill (2007) manipulated the size of first broods of Eastern Bluebirds and found that pairs with enlarged first broods were either less likely to be double-brooded or took longer to initiate second broods that pairs where the size of first broods had been reduced. Such results suggest that the size of first broods could potentially influence the likelihood of pairs of Eastern Bluebirds being multibrooded. However, differences in the clutch and brood sizes of first nests among pairs of Eastern Bluebirds that differed in number of broods attempted in my study were not significant. As such, factors other than clutch and brood sizes of first broods, possibly differences in individual quality as noted above, better explain differences among pairs of Eastern Bluebirds in my study of being multi-brooded.

Although based on a small sample size, males that helped raise three broods provisioned at higher rates during their first brood than males that only raised one or two broods. Conversely, females that raised three broods provisioned nestlings during the first brood at lower rates than those that only raised one or two broods. Stodola et al. (2009) found a similar tradeoff of provisioning energy in male and female Black-throated Blue Warblers. The male's increased provisioning behavior during the first brood could possibly allow for the female to sequester more energy to be used for expected future broods. The Arabian Babbler (*Turdoides squamiceps*) has been shown to compensate for decreased provisioning of the other parent so that total provisioning remains constant (Wright and Dingemanse 1999). This behavior supports the enhanced fecundity hypothesis (Tallamy 2000) or load-lightening hypothesis (West and Capellini 2016), in that males will increase their net reproductive output by increasing their parental care to allow the female to conserve energy for future reproduction. In Eastern Bluebirds, this tradeoff between increased male provisioning and decreased female provisioning during first broods could be the factor that allows for pairs to progress to a third brood during the breeding season.

Prey size

I found that the size of prey provided to nestlings in first broods did not differ among pairs of Eastern Bluebirds that differed in number of broods attempted. Similarly, the size of prey provided to nestlings by adults did not differ with brood size. One likely explanation for this is that the size of prey items that can be captured and eaten by Eastern Bluebirds and their nestlings is limited by their size, i.e., bill size and size of prey that can be swallowed. For example, Goldman (1975) found that ~75% of prey items captured by Eastern Bluebirds ranged in size from 0.25 to 1 bill lengths or, given a mean bill length of 1 cm (Lamb 2012), 0.25 to 1 cm in length. Another ~11% of prey items captured were about 2 cm long and only ~14% were 3 to 4 cm long (Goldman 1975). The gape size constraint hypothesis posits that predator diets generally consist of a subset of available prey and that predators may preferentially select prey of a size near that of the size of their gape (Zaret 1980). Thus, Eastern Bluebirds may exhibit a preference for either prey close to or somewhat smaller than their gape as, as a result, tend to consistently capture and provision nestlings with prey items within that relatively narrow range.

During the first four days post-hatching, nestling Eastern Bluebirds in my study were fed smaller prey than older nestlings. Pinkowski (1978) reported similar results in a study of Eastern Bluebirds conducted in Michigan. Younger nestlings are often fed smaller, more easily digested prey, like spiders, whereas older nestlings are fed larger, less digestible prey such as grasshoppers (Plinkowski 1974, Kieffer 2011). As the body size of nestlings increases, their energy requirements increase, as does their gape size, and providing them with larger prey makes it easier for provisioning adults to meet those demands (Wiebe and Slagsvold 2014). In addition, the intestinal and pancreatic enzyme activity of nestling digestive systems increase with age, improving digestive efficiency and allowing digestion of larger prey (Caviedes-Vidal and Karasov 2001).

In conclusion, the number of young in broods did not affect the provisioning rates of parent Eastern Bluebirds (in terms of feeding visits per nestling) and that the combined provisioning rates of both parents were similar for first, second, and third broods. Higher, early male provisioning during first and second broods was likely due to females actively incubating nestlings. Similarly, the lack of this higher provisioning during third broods is likely due to a lack of investment in the nestlings from the male. For broods one and two, the combined provisioning rates of males and females were lower during the first four days post-hatching than for older nestlings, likely because the lower energy requirements of young during the first few days post-hatching. Finally, the initiation date, clutch size, and brood size of first broods did not influence the likelihood of parents being multibrooded. Males that went on to raise three broods provisioned young at higher rates during their first brood than males that only had one or two broods during the breeding season. Conversely, females that went on to raise three broods provisioned young at lower rates during their first brood than females that only had one or two broods during the breeding season. This increase in early, male provisioning supports the load-lightening hypothesis and may explain some of a pair's tendency to be multibrooded. As such, other factors, possibly differences in the quality of individuals, better explain differences among pairs of Eastern Bluebirds in my study of being multi-brooded.

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