January 2011

Effect of nestling sex ratio on the provisioning behavior of adult Eastern Bluebirds (Sialia sialis)

Barbara Ellen Kieffer
Eastern Kentucky University

Recommended Citation

Kieffer, Barbara Ellen, "Effect of nestling sex ratio on the provisioning behavior of adult Eastern Bluebirds (Sialia sialis)" (2011). *Online Theses and Dissertations*. 37.
https://encompass.eku.edu/etd/37

Effect of nestling sex ratio on the provisioning behavior of adult Eastern Bluebirds (*Sialia sialis*)

By

Barbara Ellen Kieffer

Thesis Approved:

Chair, Advisory Committee

Member, Advisory Committee

Robert B.

Member, Advisory Committee

Dean, Graduate School

STATEMENT OF PERMISSION TO USE

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

Signature Barbara E. Kieffer

Date 7/15/11

Effect of nestling sex ratio on the provisioning behavior of adult Eastern Bluebirds (*Sialia sialis*)

By

Barbara Ellen Kieffer
Master of Science
Eastern Kentucky University
Richmond, Kentucky
2011

Submitted to the Faculty of the Graduate School of
Eastern Kentucky University
in partial fulfillment of the requirements
for the degree of
MASTER OF SCIENCE
August, 2011

ACKNOWLEDGMENTS

I would like to thank my faculty advisor, Dr. Gary Ritchison, for his guidance and wisdom. I would also like to thank my other committee members, Dr. Robert Frederick and Dr. Charles Elliott, for their assistance over the past years. I would like to express my thanks to my fiance, Bryan, for his understanding and patience during all those hours of research and writing. I would also like to thank the Kayde Gilbert and Jacqueline Bennett for helping me with all my research and keeping me sane while repeatedly checking over a hundred bluebird boxes every few days.

ABSTRACT

To maximize reproductive success, parents may, in some cases, differentially invest in sons and daughters, i.e., sex-biased parental investment. Preferential provisioning behavior has been reported in one population of Eastern Bluebirds (*Sialia sialis*) and attributed to local resource competition. To better understand this behavior, I studied the provisioning behavior of Eastern Bluebirds in Madison County, Kentucky, in 2004. I experimentally manipulated brood sex ratios in 24 bluebird nests, creating female-biased (N = 8), male-biased (N = 5), and control (N = 11) nests. Following manipulation, nests were video-taped to record adult provisioning behavior. Among experimental broods, the provisioning rates of male and female Eastern Bluebirds were not affected by brood sex ratio (P = 0.58). Similarly, for broods that naturally differed in the number of male and female nestlings (N = 9), I found no effect of brood sex ratio on provisioning rates (P = 0.34).

Female bluebirds provisioned nestlings at higher rates than males (P = 0.0046) and the provisioning rates of adult bluebirds varied with brood size (P = 0.017); with broods of 5 fed at lower rates than broods of either 3 or 4. Because surface area exposure per nestling is reduced in larger broods, nestlings in larger broods may expend energy at lower rates and require less food from adults.

Male and female bluebirds delivered a total of 2363 prey items to nestlings, with males delivering 821 prey items and females 1542 prey items. Of prey items I was able to identify, grasshoppers (Orthoptera) were the most common prey delivered to nestlings by both male and female bluebirds. Other common prey items included

Lepidopteran larvae, beetles (Coleoptera), crickets (Orthoptera), worms (*Oligochaeta* spp.), spiders (Araneae), and cicadas (Hemiptera). Overall, male and female bluebirds delivered similar types of prey to nestlings.

TABLE OF CONTENTS

CHAPTER I

INTRODUCTION

To maximize their reproductive success, parents are expected to invest in the offspring that will maximize their reproductive success. In some cases, this might involve differentially investing in sons and daughters, i.e., sex-biased parental investment (Leonard et al. 1994, Ligon and Hill 2009). For example, when resources are limited, parents may differentially invest in the sex with lower variance in reproductive success (i.e., females); but, when resources are not limited, they should invest more in the sex with higher variance in reproductive success (i.e., males). Differential investment can potentially be achieved in a variety of ways, including manipulating offspring sex ratios prior to birth (i.e., primary, or birth, sex ratio) or differentially investing in offspring after birth (Leonard et al. 1994 and Hasselquist and Kempanaers 2002).

Post-birth or post-hatching sex-biased parental investment has been studied in a variety of species. For example, sex-biased parental investment has been reported in several sexually dimorphic species of mammals, including Grey Seals (*Halichoerus grypus*), with female investment in offspring influenced by the size of the mother and the time in the breeding season when females give birth (Anderson and Fedak 1987). Larger female grey seals gave birth earlier, tended to give birth to males, and invested more in male offspring by providing more milk (as indicated by a greater loss of weight) because young males require more milk than females. Preferential provisioning has also been reported in California sea lions (*Zalophus californianus*) and northern fur seals (*Callorhinus ursinus*; Kretzmann et al. 1993).

Among birds, sex-biased parental investment can potentially occur via sex-biased provisioning of nestlings and might be expected if male and female young differ in their energetic needs. For example, in sexually size-dimorphic species, males are typically larger than females and, in such species, male offspring with greater energetic needs may be fed at higher rates than females (e.g., Green 2002, Magrath et al. 2007). However, even in size-dimorphic species, parents may provision male and female offspring at similar rates (e.g., Fiala 1981, Laaksonen et al. 2004).

Among species of birds with little or no sexual size dimorphism, differential provisioning might occur if the sexes differ in competitive abilities or physiological requirements (e.g., Boncoraglio et al. 2008). In addition, parents might differentially provision different-sexed young if male and female offspring differentially affect the reproductive success of parents after independence (Michler et al. 2010). For example, because male birds tend to be more philopatric than females (Greenwood 1980), males might differentially provision female nestlings because, after fledging, philopatric male offspring might represent potential competitors for important resources (Harper 1985, Stamps 1990). Alternatively, parents might differentially provision female offspring because females tend to disperse greater distances and extra food during development might improve their chances of survival during and after dispersal (Stamps 1990).

Most studies, to-date, have reported little evidence of sex-biased provisioning in species of birds with little or no sexual size dimorphism. For example, Michler et al. (2010) found that broods of Great Tits (*Parus major*) received similar amounts of food regardless of brood sex ratio. Similar results have been reported for Vinous-throated

Parrotbills (*Paradoxornis webbianus*; Lee et al. 2010) and Western Bluebirds (*Sialia mexicana*; Leonard et al. 1994). However, Droge et al. (1991) reported sex-biased provisioning by Eastern Bluebirds (*Sialia sialis*) in a study population in South Carolina, with males provisioning female-biased broods at higher rates than male-biased broods and selectively provisioning females within broods. Differences between the sexes in their energetic needs do not explain this behavior because the metabolic rates of young male and female bluebirds are similar (Droge et al. 1991). Rather, Gowaty and Droge (1991) suggested that male Eastern Bluebirds fed female nestlings more frequently than male nestlings because males are more philopatric and, therefore, more likely to compete with the same-sexed parent for resources such as mates, territories, or food resources (i.e., local resource competition).

Because sex-biased provisioning has been reported in so few species and there is little evidence for local resource competition between adult birds and their offspring (Weatherhead and Montgomerie 1995), additional study is needed to determine if birds exhibit sex-biased provisioning. The objective of this study was to determine if the provisioning behavior of male and female Eastern Bluebirds in Kentucky is influenced by brood sex ratio.

CHAPTER II

METHODS

I studied Eastern Bluebirds at the Blue Grass Army Depot (BGAD), located southeast of Richmond, Madison County, Kentucky, from 10 May to 11 August 2004. The BGAD encompasses 5,865 ha and consists of grasslands, open fields, pastures, and scattered woodlots.

Eastern Bluebirds are secondary cavity nesters that readily use artificial nest boxes (Gowaty and Plissner 1998). Thus, prior to the breeding season, nest boxes (N = 144) were placed throughout the BGAD to encourage nesting by bluebirds. Beginning in May 2004, nest boxes were checked every 7 to 10 days to determine if boxes were being used by bluebirds. When nests showed signs of nesting, they were then checked every three to six days to determine laying dates, hatching dates, and the age of nestlings.

Adult bluebirds at each nest box were captured and uniquely banded with a numbered USFWS aluminum bands plus a unique combination of three colored plastic leg bands. Adults were captured in mist nets, either by luring adults into nets by playback of bluebird songs or nestling distress calls or, passively, by simply placing nets in front of nest-box entrances.

Nestlings were banded with uniquely numbered USFWS aluminum bands 10 to 13 days after hatching when they could be reliably sexed. The sex of nestling bluebirds can be determined by plumage coloration (Pinkowski 1974, Gowaty and Plissner 1998). Emerging primary and tail feathers of male nestlings are bright blue, whereas those of females are dull, gray-black with a faint blue hue. The primary and tail feathers emerge at about 10 days post-hatching and, by 12-13 days post-hatching, are sufficiently emerged (about 6 mm) from sheaths to allow accurate sex determination (Pyle 1987, Leonard et al. 1994, Gowaty and Plissner 1998).

I performed manipulations at 24 bluebird nests, with nests placed in one of three categories: control, female-biased, and male-biased (Leonard et al. 1994). Manipulation involved changing the sex-ratios of nests from the original ratio to either male- or female-biased (Lessells et al. 1998). Control nests were subjected to the same procedure as manipulated nests, but nestlings were switched between boxes without changing sex ratios.

Manipulations occurred when nestlings were old enough to be sexed (10-12 days post-hatching; Pyle 1987, Gowaty and Plissner 1998), but sufficiently young so they would not fledge prematurely due to handling (Droge et al. 1991). Exchanges of nestlings were made between nests with similar brood sizes (± 1 nestling) and nestlings of similar age (± 1 day). For example, if nest box A had three female and two male nestlings and nest box B had two female and two male nestlings similar in age, then two males from box A would be moved to box B and two females from B would be moved to box A. This would create one female-biased box (box A) and one male-biased (box B). Control boxes were subjected to the same procedure, but equal numbers of nestlings of the same sex were exchanged. For example, if box C had four male nestlings and one female and box D had three male nestlings and one female, one male and one female from each box were exchanged without changing the sex ratio of either nest.

Nests were video-taped to record adult provisioning behavior. A plastic container (64 cm x 36 cm x 34 cm high; hereafter referred to as the camcorder box) was attached to the back of nest boxes at least one day before video-taping began to acclimate the birds to its presence. A black cardboard box, comparable in size to the camcorder, was placed in camera boxes to simulate the presence of a camcorder. The backs of nest boxes were removed when camcorder boxes were attached and were replaced with wire mesh to prevent adults and nestlings from entering camcorder boxes.

When video-taping, camcorders were placed in the camcorder boxes and focused on the inside of nest boxes. I video-taped nests beginning the day after brood manipulation (except in days with rain) and continued taping daily until nestlings fledged (18-20 days post-hatching). Nests were video-taped for two to four hours daily, with all taping occurring during the period from sunrise to 12:00 EDT. Procedures related to bluebird capture, handling, and video-taping were reviewed and approved by Eastern Kentucky University's Institutional Animal Care and Use Committee.

I subsequently reviewed all video-tapes using a video player that allowed frame-by-frame analysis. For each visit to a nest box by an adult bluebird, I noted the visiting bird's sex and, if possible, identified prey items to the lowest taxonomic category possible. For each nest, I determined the total number of visits by each adult and the total amount of time each nest was video-taped. I used multivariate analysis of variance (MANOVA) to examine the possible effects of nestling age, brood size, and brood sex ratio on the provisioning rates (nest visits/hour/nestling) of male and female Eastern

Bluebirds. All statistical analyses were performed using the Statistical Analysis System (SAS Institute 2004). Values are presented as means ± SE.

CHAPTER III

RESULTS

I conducted experiments with 24 pairs of bluebirds, including 11 controls, eight female-biased broods, and five male-biased broods. The mean brood size was 4.0 ± 0.1 (range = 3 – 5) and the mean age of nestlings when I videotaped nests was 14.2 ± 0.3 days post-hatching (range = 12 – 17 days). Nests were taped for an average of 6.8 ± 0.5 hrs (range = 2 – 12 hours). Provisioning rates of adult bluebirds did not vary with nestling age ($F_{6, 17} = 1.5$, $P = 0.21$).

Among experimentally skewed broods (i.e., all male or all female), the provisioning behavior of male and female Eastern Bluebirds was not affected by brood sex ratio ($F_{2, 21} = 0.6$, $P = 0.58$); with female-biased (1.3 ± 0.2 visits/nestling/hr), male-biased (1.2 ± 0.2 visits/nestling/hr), and control broods (1.1 ± 0.1 visits/nestling/hr) all fed at similar rates. Similarly, for control broods that naturally differed in the number of male and female nestlings (N = 9; 5 male-biased and 4 female-biased), I found no effect of brood sex ratio on provisioning rates (overall: $F_{1,16} = 1.0$, $P = 0.34$; adult males: $F_{1,7} = 0.1$, $P = 0.72$; adult females: $F_{1,7} = 1.2$, $P = 0.30$). Naturally male-biased and female-biased broods were fed at a rate of 1.3 ± 0.2 and 1.0 ± 0.2 visits/nestling/hr, respectively.

Female bluebirds provisioned nestlings at higher rates than males ($F_{1, 22} = 9.4$, $P = 0.0046$), with mean provisioning rates of 1.4 ± 0.1 visits/nestling/hr for females and 0.9 ± 0.1 visits/nestling/hr for males. Provisioning rates also varied with brood size ($F_{2, 21} = 4.7$, $P = 0.017$), with broods of 5 (0.8 ± 0.1 visits/nestling/hr) fed at lower rates than broods of either 3 (1.5 ± 0.2 visits/nestling/hr) or 4 (1.2 ± 0.1 visits/nestling/hr). I found no significant interactions between adult sex and either brood sex ratio ($F_{2, 46} = 0.1$, $P = 0.92$) or brood size ($F_{2, 46} = 0.1$, $P = 0.93$).

Male and female bluebirds delivered a total of 2363 prey items to nestlings, with males delivering 821 prey items and females 1542 prey items (Table 1[1]). Of prey items I was able to identify, grasshoppers (Orthoptera) were the most common prey delivered to nestlings by both male and female bluebirds. Other common prey items included Lepidopteran larvae, beetles (Coleoptera), crickets (Orthoptera), worms (*Oligochaeta* spp.), spiders (Araneae), and cicadas (Hemiptera; Table 1). Overall, male and female bluebirds delivered similar types of prey to nestlings. However, female bluebirds delivered more berries (N = 67; *Rhus* spp.) to nestlings than did male bluebirds (N = 2).

---

[1] See Appendix A for Tables.

CHAPTER IV

DISCUSSION

Provisioning – effect of brood sex ratios

I found that brood sex ratios did not affect the provisioning behavior of male and female Eastern Bluebirds. Similar results have been reported for Great Tits (Michler et al. 2010), Vinous-throated Parrotbills (Lee et al. 2010), and Western Bluebirds (Leonard et al. 1994). In contrast, Gowaty and Droge (1991) reported that male Eastern Bluebirds fed female-biased broods at higher rates than male-biased broods in a population in South Carolina. In general, young female birds disperse further than young males (Greenwood 1980) and, as a result, young females may be less likely to compete with their parents for resources (local resource competition). Young males tend to be more philopatric and, therefore, may be more likely to compete with fathers for food, nest sites, and other resources. If so, adult male birds might be expected to preferentially provision female nestlings, i.e., the non-competing sex (Koenig and Dickinson 1996). Gowaty and Droge (1991) suggested that, in their study population, preferential feeding of female nestlings by male Eastern Bluebirds could be explained by the possibility of local resource competition.

In agreement with most studies conducted to-date, I found no evidence of sex-biased provisioning in a species of bird with no sexual size dimorphism. Gowaty and Droge (1991) argued that adult male Eastern Bluebirds fed nestling males less than nestling females because sons were more likely to compete with them for resources. However, as noted by Leonard et al. (1994), it is not clear for any species of bird "why competition with kin should be any worse than competition with non-kin" and, in some situations, competition with kin would seem preferable to competition with non-kin. For example, losing a portion of a territory to a son that could then breed would be preferable, in terms of a parent's fitness, to losing a portion of a territory to an unrelated male (Leonard et al. 1994). In addition, such competition (i.e., local resource competition) seems unlikely because birds in general, including male birds, exhibit low rates of philopatry (Weatherhead and Montgomerie 1995) and mortality rates of first-year songbirds is relatively high (e.g., Sullivan 1989, Yackel Adams et al. 2001, Maxted 2001). For Eastern Bluebirds in South Carolina, Gowaty and Plissner (1998) reported that, of 3,798 banded and fledged young, only 0.6% bred at their natal boxes and only 1.7% bred in territories adjacent to natal territories. In addition, return rates to natal areas are even lower at higher latitudes (Gowaty and Plissner 1998). Available evidence, therefore, indicates that, for Eastern Bluebirds and other songbirds, local resource competition is unlikely to occur and unlikely to influence adult provisioning behavior.

Provisioning of nestlings by parents may be influenced more by nestling behavior than parental behavior, particularly in cavity-nesting birds where older young are fed at the cavity entrance. For example, Leonard et al. (1994) found nestlings most often fed by cavity-nesting adult Western Bluebirds were closer to entrance holes and started begging sooner than their siblings. Similarly, Hofstetter and Ritchison (1998) found that nestling Eastern Screech-Owls (*Megascops asio*) most often fed by adults arriving at cavity entrances started begging earlier and positioned their bills closer to adults. In these species, and perhaps other cavity-nesting birds including Eastern Bluebirds, the ability of parents to selectively feed particular offspring or offspring of a certain sex may be limited. This may be especially true later in the nestling period when parents may not enter cavities to feed young, and end up feeding the nestling closest to the cavity entrance or the individual who extends its head or bill out of the cavity entrance.

Empirical evidence for sex-biased provisioning by free-living birds is limited to a single study of Eastern Bluebirds (Gowaty and Droge 1991), and the reason(s) for differences between the results of other studies, including my results, and those of Gowaty and Droge (1991) is (are) unclear. Additional studies of the possible effect of brood sex ratios on the provisioning behavior of Eastern Bluebirds are needed to determine if factors such as brood number (i.e., bluebirds are multibrooded), latitude (e.g., variation in degree of natal philopatry), food availability, or availability of other resources (e.g., suitable cavities) might influence male behavior.

Provisioning rates – males vs. females

Female Eastern Bluebirds in my study provisioned nestlings at significantly higher rates than did males. Similarly, other investigators have also reported that female bluebirds provision nestlings at higher rates than males (Pinkowski 1978, Ligon and Hill 2010). In contrast, Gowaty and Plissner (1998) stated that male and female Eastern Bluebirds, on average, feed nestlings at similar rates.

Female Eastern Bluebirds are known to engage in extra-pair copulations (Gowaty and Plissner 1998, Ligon and Hill 2010) and, for species where extra-pair copulations are known to occur, it has been suggested that male birds may provision at lower rates because of uncertainty about the nestlings paternity (e.g., Møller 1988, Gowaty et al. 1989, Wright 1992). However, male provisioning behavior in some bird species has been reported to not be influenced by the paternity of offspring (e.g., Whittingham et al. 1993, García-Vigón et al. 2009). Dickinson (2003) found no evidence that paternity status affected the provisioning behavior of congeneric male Western Bluebirds.

Sex differences in provisioning rates suggest that males and females "may differ in either the cost of foraging and (or) the benefit of investing in young" (Ardia 2007). For Eastern Bluebirds, the costs of foraging by males and females are unknown. In some species that exhibit biparental care, males tend to forage further from nest sites than females because of their need to patrol territory boundaries (e.g., Morse 1968, Robins 1971) and longer foraging trips may mean lower provisioning rates. Pinkowski (1977a) found that the foraging ranges of different pairs of Eastern Bluebirds varied considerably during the nestling period and suggested that the distribution of perches may influence territory size. Males and females could potentially partition foraging areas and perches and, if so, males may tend to forage in areas further from nests, resulting in lower provisioning rates. Sex differences in foraging microhabitats could also contribute to differences in provisioning rates. For example, male Black Phoebes (*Sayornis nigricans*) forage in more open areas than females (Wolf 1997). Such differences in foraging habitat could contribute to differences in provisioning rates if distances from nest sites to the preferred foraging habitats of males and females differed. Further study of Eastern Bluebird foraging behavior is needed to determine if differences in foraging location due to differences in microhabitat use, or the need to defend territory boundaries, might contribute to differences in the provisioning rates of males and females.

Another possible explanation for differences in the provisioning rates of male and female Eastern Bluebirds observed in this study could be because males and females exhibit temporal differences in provisioning behavior. I monitored provisioning behavior during the period from sunrise to 12:00. Pinkowski (1978), in contrast, monitored the provisioning behavior of Eastern Bluebirds throughout the day and found that female bluebirds tended to provision at higher rates than males in the early morning (06:00 – 10:00), whereas males provisioned at higher rates than females during the afternoon (13:00 – 16:00) and early evening (16:00 – 20:00).

Provisioning - effects of brood size

I found that broods of five bluebirds were fed at lower rates than broods of three or four. Pinkowski (1978) also reported that adult Eastern Bluebirds fed broods of five at lower rates than broods of three or four. Similar results, with nestlings in larger broods fed at lower rates than those in smaller broods, have been reported in other species of songbirds (e.g., Nur 1984, Barba et al. 2009). Pinkowski (1978) suggested that lower feeding rates for larger broods may reflect a reduction in heat loss because larger broods have less surface area exposed. Studies of other cavity-nesting songbirds where birds nested in nest boxes indicate that nestlings in larger broods can thermoregulate earlier than nestlings in smaller broods (e.g., Clark 1985). For example, Dunn (1976) found that nestlings in broods of four House Wrens (*Troglodytes aedon*) can effectively thermoregulate when about five days old, whereas nestlings in broods of five or six can thermoregulate when about three or four days old. Surface exposure per nestling is reduced in larger broods, allowing young to thermoregulate at an earlier age (Dunn 1976). In addition to thermoregulating earlier, nestlings in larger broods expend energy at lower rates than those in smaller broods. For example, Sullivan and Weathers (1992) found that nestlings in broods of four Yellow-eyed Juncos (*Junco phaeonotus*) expended energy at lower rates than nestlings in broods of two or three. This reduction in energy expenditure in juncos, and perhaps in larger broods of other species such as Eastern Bluebirds, may explain why larger broods are fed at lower rates per nestling than smaller broods.

Another possible explanation for the reduction in provisioning rates per nestling for larger broods is that parents could potentially increase provisioning rates so that nestlings in larger broods are fed at rates similar to those in smaller broods, but doing so would be costly in terms of parental survival and future reproductive success (Nur 1984). Thus, reduced provisioning rates per nestling in larger broods may indicate that parents are attempting to maximize the difference between potential benefits (to offspring) and costs (survival and future reproduction). Minimizing costs may be particularly important for multibrooded species like Eastern Bluebirds, with pairs sometimes nesting up to four times in a breeding season (Gowaty and Plissner 1998). In support of this hypothesis, Pinkowski (1977b) found that, within a breeding season, female Eastern Bluebirds that had fledged young in a previous nest produced smaller clutches in subsequent nests than did females that had not yet nested, apparently because the energetic costs of breeding had a negative effect on female condition.

Prey delivered

Prey items delivered most frequently to nestlings by adult bluebirds in my study included grasshoppers (Orthoptera), Lepidopteran larvae, beetles (Coleoptera), crickets (Orthoptera), worms (Oligochaeta spp.), and spiders (Araneae, Table 1). Similarly, Pinkowski (1978) reported that the diet of nestling bluebirds in Michigan consisted primarily of Lepidopteran larvae, orthopterans (grasshoppers and crickets), spiders, beetles, and earthworms. Pitts (1978) noted that prey items fed to nestlings were primarily grasshoppers, crickets, spiders, and insect larvae. Nestling Western and Mountain (*Sialis currucoides*) bluebirds are also fed primarily orthopteran and coleopteran prey (Herlugson 1982). Bluebirds are primarily ground foragers and prey are generally taken and fed to nestlings based on availability (Pinkowski 1974). The relationship between availability and prey selection was apparent from the relative importance of periodical cicadas (*Magicicada* spp.) in the diet of nestling bluebirds in my study. Previous investigators have not reported cicadas in the diet of nestling bluebirds (Pinkowski 1974, Pitts 1978). During my study (conducted in 2004), large numbers of periodical cicadas (Brood X) emerged (Cooley et al. 2009) and comprised about 6% (108 out of 1886) of the identified prey items fed to nestlings.

I examined prey delivered to 12 to 20-day-old nestling bluebirds and, at that age, adults typically provided young with larger, more difficult to digest prey such as grasshoppers and crickets; younger nestlings are often fed smaller, more easily digested prey such as spiders (Pinkowski 1974). Male and female Eastern Bluebirds in my study generally provided nestlings with similar prey items. However, female bluebirds fed nestlings more blackberries than did males. Pinkowski (1974) reported that both male and female bluebirds sometimes fed fruit to nestling bluebirds, but only older nestlings that were homeothermic; such nestlings may benefit from the inclusion of more carbohydrates in their diet. In addition to their nutritive value, Pinkowski (1974) suggested that succulent fruits could also represent a source of water for nestlings.

LITERATURE CITED

Anderson, S. S., and M. A. Fedak. 1987. Grey seal, *Halichoerus grypus*, energetics: females invest more in male offspring. Journal of Zoology 211: 667–679.

Ardia, D. R. 2007. Site- and sex-level differences in adult feeding behaviour and its consequences to offspring quality in Tree Swallows (*Tachycineta bicolor*) following brood-size manipulation. Canadian Journal of Zoology 85:847-854.

Barba, E., F. Atiénzar, M. Marín, J. S. Monrós, and J. A. Gil-Delgado. 2009. Patterns of nestling provisioning by a single-prey loader bird, Great Tit *Parus major*. Bird Study 56: 187-197.

Boncoraglio, G., R. Martinelli, and N. Saino. 2008. Sex-related asymmetry in competitive ability of sexually monomorphic Barn Swallow nestlings. Behavioral Ecology and Sociobiology 62: 729-738.

Clark, L. 1985. Consequences of homeothermic capacity of nestlings on parental care in the European Starling. Oecologia 65: 387-393.

Cooley, J. R., G. Kritsky, M. J. Edwards, J. D. Zyla, D. C. Marshall, K. B. R. Hill, R. Kraus, and C. Simon. 2009. The distribution of periodical cicada Brood X in 2004. American Entomologist 55: 106-112.

Dickinson, J. L. 2003. Male share of provisioning is not influenced by actual or apparent loss of paternity in Western Bluebirds. Behavioral Ecology 14: 360-366.

Droge, D. L., P. A. Gowaty, and W. W. Weathers. 1991. Sex-biased provisioning: a test for differences in field metabolic rates of nestling Eastern Bluebirds. Condor 93: 793-798.

Dunn, E. H. 1976. The relationship between brood size and age of effective homeothermy in nestlings House Wrens. Wilson Bulletin 88: 478-482.

Fiala, K. L. 1981. Reproductive cost and the sex ratio in Red-winged Blackbirds. In: Natural selection and social behaviour: recent research and new theory (R. D. Alexander and D. W. Tinkle, eds.), pp. 198-214. Chiron Press, New York, NY.

García-Vigón, E., J. P. Veiga, and P. J. Cordero. 2009. Male feeding rate and extrapair paternity in the facultatively polygynous Spotless Starling. Animal Behaviour 78: 1335-1341.

Gowaty, P. A., and D. L. Droge. 1991. Sex ratio conflict and the evolution of sex-biased provisioning in birds. In: Proceedings of the 20th International Ornithology Congress (N. J. Adams and R. H. Slotow, eds.), pp. 932-945. BirdLife South Africa, Johannesburg, South Africa.

Gowaty, P. A., and J. H. Plissner. 1998. Eastern Bluebird (*Sialia sialis*). In: The Birds of North America Online (A. Poole, ed.). Cornell Lab of Ornithology, Ithaca, NY. Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu/bna/species/381

Gowaty, P. A., J. H. Plissner, and T. Williams. 1989. Behavioral correlates of uncertain parentage: mate guarding and nest guarding by Eastern Bluebirds, *Sialia sialis*. Animal Behaviour 38: 272-284.

Green, D. J. 2002. Pair bond duration influences paternal provisioning and the primary sex ratio of Brown Thornbill broods. Animal Behaviour 64: 791-800.

Greenwood, P. 1980. Mating systems, philopatry and dispersal in birds and mammals. Animal Behaviour 28: 1140-1162.

Harper, D. G. C. 1985. Brood division in robins. Animal Behaviour 33: 466-480.

Hasselquist, D. and B. Kempenaers. 2002. Parental care and adaptive brood sex ratio manipulation in birds. Pil. Trans. Royal Society of London 357:363-372.

Herlugson, C. J. 1982. Food of adult and nestling Western and Mountain bluebirds. Murrelet 63: 59-65.

Hofstetter, S. H., and G. Ritchison. 1998. The begging behavior of nestling Eastern Screech-Owls. Wilson Bulletin 110: 86-92.

Koenig, W. D., and J. L. Dickinson. 1996. Nestling sex-ratio variation in Western Bluebirds. Auk 113: 902-910.

Kretzmann, M. B., D. P. Costa, and B. J. Le Boeuf. 1993. Maternal energy investment in elephant seal pups: evidence for sexual equality. American Naturalist 141: 466-480.

Laaksonen, T., S. Lyytinen, and E. Korpimäki. 2004. Sex-specific recruitment and brood sex ratios of Eurasian Kestrels in a seasonally and annually fluctuating northern environment. Evolutionary Ecology 18: 215-230.

Lee, J.-W., H.-Y. Kim, and B. J. Hatchwell. 2010. Parental provisioning behaviour in a flock-living passerine, the Vinous-throated Parrotbill *Paradoxornis webbianus*. Journal of Ornithology 151: 483-490.

Leonard, M. L., K. L. Teather, A. G. Horn, W. D. Koenig, and J. L. Dickinson. 1994. Provisioning in Western Bluebirds is not related to offspring sex. Behavioral Ecology 5: 455-459.

Lessells, C. M., K. R. Oddiet, and A. C. Mateman. 1998. Parental behaviour is unrelated to experimentally manipulated Great Tit brood sex ratio. Animal Behaviour 56: 385-393.

Ligon, R. A., and G. E. Hill. 2010. Feeding decisions of Eastern Bluebirds are situationally influenced by fledgling plumage color. Behavioral Ecology 21: 456-464.

Ligon, R. A., and G. E. Hill. 2009. Sex-biased parental investment is correlated with mate ornamentation in Eastern Bluebirds. Animal Behaviour 79: 727-734.

Magrath, M. J. L., E. Van Lieshout, I. Pen, G. H. Visser, and J. Komdeur. 2007. Estimating expenditure on male and female offspring in a sexually size-dimorphic bird: a comparison of different methods. Journal of Animal Ecology 76: 1169-1180.

Maxted, A. M. 2001. Post-fledging survival, dispersal, and habitat use in two migratory shrubland bird species. M. S. thesis, Purdue University, Purdue, IN.

Michler, S. P. M., M. Bleeker, M. van der Velde, C. Both, J. Komdeur, and J. M. Tinbergen. 2010. Parental provisioning in relation to offspring sex and sex ratio in the Great Tit (*Parus major*). Behaviour 147: 1355-1378.

Møller, A. P. 1988. Paternity and parental care in the swallow, *Hirundo rustica*. Animal Behaviour 36: 996-1005.

Morse, D. H. 1968. A quantitative study of foraging of male and female spruce-woods warblers. Ecology 49:779-784.

Nur, N. 1984. Feeding frequencies of nestling Blue Tits *Parus caeruleus*: costs, benefits and a model of optimal feeding frequency. Oecologia 65: 125-137.

Pinkowski, B. C. 1974. A comparative study of the behavioral and breeding ecology of the Eastern Bluebird (*Sialia sialis*). Ph.D. dissertation, Wayne State University, Detroit, MI.

Pinkowski, B. C. 1977a. Foraging behavior of the Eastern Bluebird. Wilson Bulletin 89: 404-414.

Pinkowski, B. C. 1977b. Breeding adaptations of the Eastern Bluebird. Condor 79: 289-302.

Pinkowski, B. C. 1978. Feeding of nestling and fledgling Eastern Bluebirds. Wilson Bulletin 90: 84-98.

Pitts, T. D. 1978. Foods of Eastern Bluebird nestlings in northwest Tennessee. Journal of the Tennessee Academy of Science 53: 136-139.

Pyle, P. 1987. Identification guide to North American birds. Part 1. Slate Creek Press, Bolinas, CA.

Robins, J. D. 1971. Differential niche utilization in a grassland sparrow. Ecology 52: 1065-1070.

SAS Institute. 2004. SAS 9.1.2 user’s guide. SAS Institute Inc., Cary, NC.

Stamps, J. A. 1990. When should avian parents differentially provision sons and daughters? American Naturalist 135: 671-685.

Sullivan, K. A. 1989. Predation and starvation: age-specific mortality in juvenile juncos (*Junco phaenotus*). Journal of Animal Ecology 58: 275-286.

Sullivan, K. A., and W. W. Weathers. 1992. Brood size and thermal environment influence field metabolism of nestling Yellow-eyed Juncos. Auk 109: 112-118.

Weatherhead, P. J., and R. Montgomerie. 1995. Local resource competition and sex ratio variation in birds. Journal of Avian Biology 26: 168-171.

Whittingham, L. A., P. O. Dunn, and R. J. Robertson. 1993. Confidence of paternity and male parental care: an experimental study in Tree Swallows. Animal Behaviour 46: 139-147.

Wolf, B. O. 1997. Black Phoebe (*Sayornis nigricans*). In: The Birds of North America Online (A. Poole, ed.). Cornell Lab of Ornithology, Ithaca, NY. Retrieved from the Birds of North America Online <http://bna.birds.cornell.edu/bna/species/268>

Wright, J. 1992. Certainty of paternity and parental care. Animal Behaviour 44: 380-381.

Yackel Adams, A. A., S. K. Skagen, and R. D. Adams. 2001. Movements and survival of Lark Bunting fledglings. Condor 103: 643-647.

APPENDIX A:

Tables

Table 1. Prey items delivered to 12 to 20-day-old nestlings by male and female Eastern Bluebirds in central Kentucky, May-August 2004. N = 2363.

Item	Total %	Total N	Male %	Male N	Female %	Female N
Unidentified	20.2	477	18.3	150	21.2	327
Orthoptera (grasshoppers)	19.4	459	17.3	142	20.6	317
Lepidoptera (larvae)	11.2	265	13.3	109	10.1	156
Coleoptera (beetles)	9.1	216	10.6	87	8.3	129
Orthoptera (crickets)	8.5	200	10.8	89	7.2	111
Oligochaeta spp. (worms)	8.1	192	7.8	64	8.3	128
Araneae (spiders)	6.7	159	6.3	52	6.9	107
Hemiptera (cicadas)	4.6	108	5.5	45	4.1	63
Rhus spp. (berries)	2.9	69	0.2	2	4.4	67
Diptera (flies)	2.4	59	2.4	22	2.4	37
Hemiptera (leaf bugs)	1.7	41	2.2	18	1.5	23
Diptera (mosquitos)	1.2	29	1.6	13	1.0	16
Odonata (dragonflies)	1.1	27	1.5	12	1.0	15
Lepidoptera (moths)	1.0	24	0.6	5	1.2	19
Insect larvae (grubs/maggots)	0.7	16	0.5	4	0.8	12
Hymenoptera (ant)	0.5	11	0.4	3	0.5	8
Hymenoptera (wasps)	0.3	8	0.1	1	0.5	7
Hymenoptera (bee spp.)	0.2	2	0.5	2	0.0	0
Lepidoptera (butterflies)	<0.1	1	0.1	1	0.0	0