

## AN ABSTRACT OF THE THESIS OF

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Title: The effects of food supplements on Eastern Bluebird nestling growth and survival

Abstract approved: Elmer J. Finck

The number of young that avian parents attempt to raise during a breeding attempt is hypothetically constrained by the amount of food available in the environment. Costs of reproduction to parents, as is evident by declining physical condition of avian parents during nestling provision, are associated with insufficient procurement of food to maintain physical condition. Additionally, low body mass and decreased survival of underfed nestlings lends support to food limitation theories. However, equivocal results obtained in studies examining the effects of differential food availability on parents and nestlings provided the impetus for my study. The effects of increased food availability on Eastern Bluebird (*Sialia sialis*) nestling growth and survival were examined in east central Kansas during the 1996 and 1997 breeding seasons. Nestling growth and survival characteristics, including morphological measurements, nestling survival, fledging age of nestlings, and the number of nestlings to fledge were measured and compared between unsupplemented and food supplemented groups. No significant differences existed between any variables measured; thus, the Eastern Bluebird population in my study was not food limited. Other variables that might influence the degree of food limitation, such as weather and nest site competition, are discussed. Evidence suggests that food might be less limiting to

secondary cavity nesting species compared to open-cup and primary cavity nesting species because of competition for limited numbers of nest sites. Simultaneous investigation of breeding bird density and food limitation theory is needed to better understand the relative effect that food limitation has on regulating the number of young that adults can successfully raise per breeding attempt.

THE EFFECTS OF FOOD SUPPLEMENTS ON EASTERN BLUEBIRD  
NESTLING GROWTH AND SURVIVAL

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A Thesis

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Master of Science

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by

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## PREFACE

The study described herein was an alternate project designed to replace my original thesis project, which proposed to examine the evolutionary adaptiveness of mass loss in breeding adult Eastern Bluebirds. My original plan was dropped after the 1996 breeding season because too few adult Eastern Bluebirds were caught and measured. I changed my focus to birds that were more accessible, Eastern Bluebird nestlings, and for this reason, nestling Eastern Bluebird characteristics were monitored more extensively in 1997 than 1996.

Food limitation is only one of many factors that affect avian breeding life history traits, but it is thought to be the most important predictor of reproductive output. The present study examined how differential food availability affects Eastern Bluebird nestlings and adult productivity. My thesis is written in the format acceptable for publication in the avian biology journal, The Wilson Bulletin.

TABLE OF CONTENTS

	<u>Page</u>
ABSTRACT OF THESIS.....	i
ACKNOWLEDGMENTS.....	v
PREFACE.....	vi
LIST OF TABLES.....	viii
LIST OF FIGURES.....	x
LIST OF APPENDICES.....	xi

THE EFFECTS OF FOOD SUPPLEMENTS ON EASTERN BLUEBIRD  
NESTLING GROWTH AND SURVIVAL

ABSTRACT.....	1
INTRODUCTION.....	2
METHODS.....	6
RESULTS.....	15
DISCUSSION.....	34
LITERATURE CITED.....	47
APPENDIX I.....	55
APPENDIX II.....	57

LIST OF TABLES

	<u>Page</u>
TABLE 1. Results of ANOVA tests of Eastern Bluebird productivity in east central Kansas in 1996 and 1997. Treatments include the control (no food supplement) and experimental (food supplemented) groups. Measurements are the least-square mean $\pm$ standard error (SE).....	16
TABLE 2. Results of ANOVA tests of Eastern Bluebird nestling characteristics between control (no food supplement) and experimental (food supplemented) groups in east central Kansas in 1996 and 1997.....	21
TABLE 3. Results of ANOVA tests of pitfall trap and sweep net total sample mass. Insect samples were collected adjacent to Eastern Bluebird nest boxes in east central Kansas between 18 June and 1 August 1997. Measurements are reported as the least-square mean mass (g) $\pm$ standard error (SE). Treatments include the control (no food supplement) and experimental (food supplemented) groups.....	32
TABLE 4. Results of ANOVA tests of pitfall trap and sweep net sample order mass. All samples were collected adjacent to Eastern Bluebird nest boxes between 18 June and 1 August 1997. Treatments include the control (no food supplement) and experimental (food supplemented) groups.....	33



TABLE 5. Results of *t*-tests on weather data from 1986 to 1997 for Emporia, KS  
(38° 43' N, 96° 20' W). Only data between 1 March and 31 July were examined,  
as these dates approximate the Eastern Bluebird breeding period in east central  
Kansas. Measurements are reported as the mean ± standard error (SE). Weather  
data were obtained from the High Plains Climate Center, University of Nebraska,  
Lincoln, NE..... 38

LIST OF FIGURES

Page

FIG. 1. The percentage of Eastern Bluebird nests in each fate category based on data collected in east central Kansas during the 1996 and 1997 breeding seasons. Treatments include the control (no food supplement) and experimental (food supplemented) groups..... 20

FIG. 2. Least-square means  $\pm$  standard error (SE) of Eastern Bluebird nestling mass (g) in east central Kansas during the 1996 breeding season. Treatments include the control (no food supplement; ●) and experimental (food supplemented; ■) groups..... 23

FIG. 3. Least-square means  $\pm$  standard error (SE) of Eastern Bluebird nestling mass (g) in east central Kansas during the 1997 breeding season. Treatments include the control (no food supplement; ●) and experimental (food supplemented; ■) groups..... 25

FIG. 4. Least-square means  $\pm$  standard error (SE) of Eastern Bluebird nestling tarsus length (mm) in east central Kansas during the 1997 breeding season. Treatments include the control (no food supplement; ●) and experimental (food supplemented; ■) groups..... 28

FIG. 5. Least-square means  $\pm$  standard error (SE) of Eastern Bluebird nestling chord length (mm) in east central Kansas during the 1997 breeding season. Treatments include the control (no food supplement; ●) and experimental (food supplemented; ■) groups..... 30

LIST OF APPENDICES

Page

APPENDIX I. Summary of pitfall trap samples collected adjacent to Eastern Bluebird nest boxes in east central Kansas between 18 June and 1 August 1997. Treatments include the control (no food supplement) and experimental (food supplemented) groups. Order measurements are reported as least-square mean mass (g) ± standard error (SE), calculated as mean mass of an order captured over two trap-nights, divided by the total number of nest boxes where the order was caught (n). Also presented is the total number of individuals captured per order (# Ind), a proportion (%) based on the number of individuals per order divided by the total number of individuals captured per treatment, and, listed next to the treatment group name is the number of nest boxes where samples were collected..... 55

APPENDIX II. Summary of sweep net samples collected adjacent to Eastern Bluebird nest boxes in east central Kansas between 18 June and 1 August 1997. Treatments include the control (no food supplement) and experimental (food supplemented) groups. Order measurements are reported as least-square mean mass (g) ± standard error (SE), calculated by dividing the sum of an order’s mass from all samples by the number of nest boxes where the order was captured (n). Also reported is the total number of individuals captured per order (# Ind), a proportion (%) created by dividing the number of individuals captured in each order by the total number of individuals caught per treatment group, and the number of nest boxes sampled listed next to the treatment group name..... 57

# THE EFFECTS OF FOOD SUPPLEMENTS ON EASTERN BLUEBIRD NESTLING GROWTH AND SURVIVAL

ABSTRACT.-- Avian reproductive output is thought to be limited by several factors, the most important of which is food availability. I examined the effect of differential food availability on Eastern Bluebird (*Sialia sialis*) nestling growth and survival in east central Kansas during the 1996 and 1997 breeding seasons. Nestling mass, nor tarsus and chord lengths were not significantly between the unsupplemented and food supplemented treatment groups in either year. In both years, the proportion of young surviving after hatching was greater in unsupplemented than food supplemented nest boxes. However, fledging age and number of young fledged did not show consistent differences between the two treatment groups. Although food has been implicated as the primary factor limiting avian reproduction, Eastern Bluebirds did not appear food limited during my study. Further investigation of avian food limitation in conjunction with factors including depredation rates, and density-dependent interactions will lead to a better understanding of the proximate factors that affect avian lifetime reproductive success.

## INTRODUCTION

Life history traits of breeding birds have theoretically evolved to maximize lifetime reproductive output by successfully interpreting and responding to local environmental conditions. Consequently, Lack (1947) hypothesized that avian parents will raise, on average, the maximum number of young per breeding attempt according to limits imposed by food availability. Each breeding attempt potentially diminishes parental survival and future reproductive efforts, thus parents must hedge bets on how many young they can produce during the current breeding attempt while maintaining sufficient physical condition. Although Lack (1947) used the parsimonious reason that food availability limited clutch size, current evidence suggests that experience (Coulson 1966, DeSteven 1980), size of parents (Järvinen and Väisänen 1984), density of intraspecific (Arcese and Smith 1988) and interspecific breeders (Simons and Martin 1990), nest site availability (Bock and Fleck 1995), and the timing and abundance of food (Perrins 1965, Rodenhouse and Holmes 1992, Schoech 1996) can all affect nestling productivity.

Lack's hypothesis regarding food limitation in breeding birds has received much attention (Martin 1987, Boutin 1990), and food availability is generally accepted as the regulator of avian reproduction. Local food availability represents an energy source that will facilitate or hamper the costly activity of breeding, which can elevate daily energy expenditure to more than three times basal metabolic rates (Drent and Daan 1980, Moreno 1989a). Although indices of parental energy expenditure can be calculated through the injection and recovery of doubly labeled water (Lifson and McClintock 1966, Sanz and Tinbergen 1999), simple field techniques such as brood and food manipulation can give an

estimate of parental energy expenditure as measured by the characteristics and the fates of young. The underlying premise of these experimental procedures is that by increasing initial brood size or reducing current food availability (case 1), or decreasing initial brood size or increasing current food availability (case 2), parents should produce fewer, lighter, and less fit young in case 1 compared to case 2. Unfortunately, few methodologies have equivocally conceded food as the proximate factor regulating reproductive output. Orell and Koivula (1988) increased and decreased Willow Tit (*Parus montanus*) brood sizes by two nestlings and found that in poor breeding conditions (low temperatures, high rainfall) experimentally enlarged broods had smaller nestlings and fewer fledged young than control and reduced broods. However, no effect of brood manipulation could be discerned during a year with average temperature and rainfall. Arcese and Smith (1988) demonstrated that food supplements advanced laying date, increased nestling size, and increased number of young raised to independence in Song Sparrows (*Melospiza melodia*), but their experiment occurred when breeding densities were extremely high. Yom-Tov (1974) concluded that food supplements increased reproductive output of Carrion Crows (*Corvus corone*), but intraspecific nest predation rates were very high in the study area. Thus, Carrion Crow parents supplied with additional food devoted less time to foraging and more time to guarding their young compared to the control group, which had to locate food and defend young. These results imply food might not be the sole factor limiting avian reproduction, and call for examination of other bird species responses to differential food availability to confirm, dispute, or modify Lack's (1947) original hypothesis.

Pertinent to food manipulation studies is the determination of the focal species' local food availability to ensure that experimental food manipulations accurately reduce or supplement food available to breeding adults. Several food manipulation studies have estimated relative abundance of naturally occurring food through direct observation and knowledge of climate data (Simons and Martin 1990) and *post hoc* conclusions based on study results (Garcia et al. 1993), but few studies have collected local food abundance data (Rodenhouse and Holmes 1992). Theoretically, if food resources consumed by a study species are abundant, then food reduction experiments must encompass entire foraging territories to accurately determine parental response to low food availability in the context of their current breeding effort (Adams et al. 1994). Similarly, if experimental procedures are testing parental response to food supplementation, then relative food abundance should be estimated at supplemented and unsupplemented parental foraging grounds to determine whether experimental increases in food reflect true increases in food availability.

To better understand how food limitation affects avian breeding biology, my study was designed to assess the response of Eastern Bluebird (*Sialia sialis*) nestling morphological characteristics and survival to food supplements provisioned to adult Eastern Bluebirds. The Eastern Bluebird readily nests in artificial nest boxes placed along nest box 'trails'. The presence of these trails, the ease of access to nest boxes, and the steadfastness of Eastern Bluebird adults after human disturbance provide an excellent opportunity to study food limitation theory and breeding birds. To facilitate comparison with other food supplementation studies, the following characteristics of nestlings at

unsupplemented and supplemented nest boxes were examined: mass, tarsus and chord lengths, survival (number of young that fledged divided by the number of young that hatched), number of young fledged, and fledging age (age of nest-leaving). If food availability limits Eastern Bluebird reproductive output, then young in the food supplemented group should have greater daily mass, longer tarsus and chord lengths, greater survival rates, younger fledging ages, and a greater number of young should fledge (per nest) compared to young in the unsupplemented group. Relative food availability was measured adjacent to nest box territories of unsupplemented and food supplemented breeding parents to minimize environmental variability not accounted for in the study design. Differences in natural food availability might help explain any differences between supplemented and unsupplemented nestling or reproductive variables.



## METHODS

The Eastern Bluebird is a sexually dimorphic thrush (Family Turdidae) that nests in naturally occurring cavities, or those excavated by other organisms. Eastern Bluebirds readily nest in unnaturally occurring nest boxes in response to loss of natural secondary cavities due to management practices that eliminate snags and dead branches (Lee 1996, Gowaty and Plissner 1998). Eastern Bluebirds begin nesting in Kansas during late March or early April, and continue breeding through August (Henderson et al. 1990). Clutch size ranges from three to seven, with a mean of five (Bent 1949, Pinkowski 1977a). Females incubate the eggs and the incubation period lasts approximately 14 days (Kendeigh 1952, Gowaty and Plissner 1998). The female is the primary incubator, and the male assists with nest duties by feeding the female, and incubating the eggs while the female is foraging (Smith 1937). During the nestling period, both the male and female monitor the needs of the young (Pinkowski 1978, Meek and Robertson 1994). The young hatch synchronously and fledge when they are 15 to 22 days old (Smith 1937, Gowaty and Bridges 1991).

Data were collected from 28 March to 26 July 1996, and 21 March to 4 August 1997 in east central Kansas at locations with previously established Eastern Bluebird nest box trails. All nest box trails were located near the city of Emporia (38° 43' N, 96° 20' W), in Lyon County, Kansas. Eastern Bluebird nest box trails were previously established at the Flint Hills National Wildlife Refuge (38° 19' N, 95° 56' W)(FHNWR, n = 46), Melvern Lake State Wildlife Area (38° 32' N, 95° 58' W)(MLWA, n = 7), Lyon County State Fishing Lake (38° 33' N, 96° 4' W)(LCSL, n = 10), the Old Highway 50 nest box trail (HWY50, located 1 km east of Emporia, n = 13), and the Kanza Audubon nest box

trail (located between Emporia and Americus, Kansas (38° 30' N, 96° 16' W))(KAT, n = 34). A nest box trail was established at the F. B. and Reba Ross Natural History Reservation (38° 30' N, 96° 20' W)(RNHR, n = 9) in early March 1996, and several nest boxes were occupied by Eastern Bluebirds in 1996 (D. Robinson, pers. obs.). A total of 119 nest boxes were available for Eastern Bluebird nesting throughout the study. Nest boxes were all constructed of wood, but varied in the manner in which internal contents were accessed, and the type of opening (slit or hole) present on the nest box. All nest boxes were wired to metal or wood fence posts and positioned approximately 1.0 m to 1.5 m above the ground. All nest boxes in my study were approximately the same size, which prevented any differences in productivity due to nest box design and size (Radunzel et al. 1997). No anti-predator devices were placed on the nest boxes because depredation rates for each treatment group were of interest. In late February, all materials present in nest boxes was removed to minimize the effects of parasites on the present year's nestlings. Only non-avian nest structures were removed from nest boxes after birds began occupying nest boxes. I did not remove nesting material from nest boxes after the completion of breeding attempts because ectoparasites in Eastern Bluebird nests are not known to have detrimental effects on nestlings, except when there is a large number of parasites in a nest, weather conditions are poor, and food availability is low (Pinkowski 1977a, Wittmann and Beason 1992).

Nest box monitoring commenced in late March, and nest boxes were initially checked at 10-day intervals. Completed nests were checked at four-day intervals to determine date of clutch completion. Nests were closely monitored around the expected

day of hatching so that weighing and measuring of young and food supplementation could begin. All captured Eastern Bluebird adults and nestlings were banded with aluminum United States Fish and Wildlife Service bands (Federal Bird Marking and Salvage Permit # 07339 issued to Marvin J. Craft, Kansas Department of Wildlife and Parks, Emporia, Kansas) for permanent identification. Nestlings were banded after day age 10, and nestlings were only handled until day age 14 to prevent premature fledging (Pinkowski 1975, Meek and Robertson 1994). When possible, the sex of nestlings was determined based upon the methodology in Pinkowski (1974).

Nestling mass in 1996 and 1997, and nestling tarsus and chord lengths in 1997 only, were measured every other day. Mass was measured with a 50 g Pesola spring scale accurate to 0.5 g in 1996, and with an Acculab electronic balance (model no.V-333) accurate to 0.1 g in 1997. The change to the electronic balance in 1997 was due to methodological changes associated with a concurrent project analyzing adult Eastern Bluebird mass. Since year to year comparisons were not of interest, the change in balances between years is irrelevant. Tarsus length was considered the distance between the distal tip of the tibiotarsus bone and the distal tip of the tarsometatarsus bone. Chord length was considered the distance between the proximal tip of the ulna to the tip of the longest primary remige. Measurement of chord length took place after the shaft of the tenth primary had erupted from the skin, which occurred around nestling day age 8. Tarsus and chord lengths were measured to the nearest 0.5 mm with a stopped ruler. Only measurements recorded between 0500 and 1200 Central Standard Time (CST) were included in analyses to avoid morphological variation associated with time of day. Means

of morphological measurements for each brood represent the experimental unit in analyses. Survival characteristics for all broods were summarized by treatment group and year, and represent the experimental unit in analyses.

After a pair of Eastern Bluebird completed a nest and began laying eggs, it was assigned to one of two treatment groups: the control group, which did not receive a food supplement, or the experimental group, which received a food supplement. Beginning with the first and second completed nests, assignment to a treatment group was on an every-other nest box basis throughout the season to maintain equal sample size in the treatment groups. Random assignment to a group was not dependent upon a particular nest box trail, except on the KAT nest box trail in 1997, when all occupied nest boxes were assigned to the experimental group due to logistical constraints. Mealworms (larvae of the beetle *Tenebrio molitor*) were used as the food supplement. Although larvae of Family Coleoptera only constitute approximately 10% of nestling and 29% of adult Eastern Bluebird diet (Bent 1949, Pinkowski 1978), mealworm larvae were chosen as the food supplement because of their successful use in other avian food supplementation studies (Moreno 1989b, Simons and Martin 1990, Garcia et al. 1993)(M. Liles, pers. comm.). All experimental group nest boxes received 50 g (approximately 300 mealworms) of food per provisioning. Adult Eastern Bluebird daily energy expenditure during the nestling period is approximately 72 kJ/day (Buser 1980). Since parental daily energy expenditure can increase from two to four times basal metabolic rate (Drent and Daan 1980), Eastern Bluebird nestling energy expenditure is probably at least half that of foraging parents. The energy content of live mealworms is 11.59 kJ/g (calculated from

Bell 1990), and birds assimilate approximately 65% of the energy available in mealworms (Kacelnik 1984). Thus, a 50 g mealworm supplement provides 377 kJ of energy to an Eastern Bluebird family, which represents a generous proportion of daily energy requirements for parents and nestlings, depending upon how it is allocated. Food supplements were placed in a 9 cm x 3 cm plastic dish on top of the nest box or on a post adjacent to the nest box (Garcia et al. 1993). One food supplement per Eastern Bluebird pair was provided every other day between the hours of 0500 and 1200 CST, immediately following hatching of the first egg. Most food supplements were entirely consumed, and few dishes had any mealworms remaining in the dish. Any mealworms remaining in the plastic dish on the following visit were removed and a new supplement was provisioned. Short observation periods followed the food provisioning to determine parental usage of the food supplement and to ensure other bird species were not eating the food supplement. Only one other bird, an American Goldfinch (*Carduelis tristis*), was seen eating the food supplement (R. Thompson, pers. comm.). However, the resident pair of Eastern Bluebirds quickly chased the American Goldfinch from the area. Both parents were seen consuming the food supplement and carrying the mealworms into the nest box to presumably feed the nestlings (D. A. Robinson Jr., and R. Thompson, pers. obs.).

In 1997, the relative biomass of invertebrate and small vertebrate animals, such as small frogs (Pinkowski 1978), considered to be Eastern Bluebird prey was quantified around active nest boxes of both treatment groups. During the breeding season, Eastern Bluebird capture terrestrial-dwelling prey by dropping from a perch onto the prey item, and vegetation-dwelling prey by hovering above the prey item and then plucking it from

the substrate (Pinkowski 1977b). Pitfall trap and sweep net sampling are the most efficient means by which prey items assumed to be available to Eastern Bluebird adults during the nestling period could be sampled (Southwood 1966). Pitfall traps were used to sample terrestrial-dwelling prey, and sweep nets were used to sample vegetation-dwelling prey items. Pitfall and sweep net samples were only collected when a nest box had nestlings. All sampling took place between 18 June and 1 August 1997. Nestling day age when sampling began was randomly chosen, and only one pitfall trap and sweep net sample was collected adjacent to an active nest box. Pitfall trap and sweep net samples were not always collected on the same days due to methodological constraints (see below).

Pitfall traps were installed along a 50 m transect centered on the nest box. Ten pitfall traps were placed along the transect at 5 m intervals. Each pitfall trap consisted of two plastic cups (15 x 10 cm each), one inside the other, placed into the ground such that the top of the innermost cup was parallel to the ground's surface. A small amount of isopropyl alcohol topped with a thin layer of glycerol was placed in each pitfall trap to kill and preserve any items that fell into the trap (Schmidt and Lockwood 1992). Pitfall traps were installed after a nest box's contents were examined, and captured contents were collected after the nest box was monitored two days later. All contents were placed in alcohol-filled plastic bags and frozen until future examination. The average total sample mass was calculated by summing the mass of all pitfall trap contents, and dividing the sum by two (number of nights the pitfall traps were active). Similarly, an average mass for each order captured was calculated.

Prey items occurring in vegetation were sampled with the sweep net technique. A sweep net transect was centered on an active nest box, and 50 sweeps with a 40 cm diameter cloth net were done on opposite sides of the nest box. One sweep was completed by swinging the sweep net 0.5-1 m above ground at an arc of 180° parallel to the ground in front of the researcher. One sweep was completed as an assistant walked away from a nest box, thus 50 steps equals 50 sweeps. Sweeping began at the nest box and terminated after 50 sweeps were performed. Netted contents were placed in alcohol-filled plastic bags and frozen until further analyses could be performed. Sweep net samples were collected only between the hours of 0900 and 1500 CST, when cloud cover was  $\leq 50\%$ , wind speed was  $< 20 \text{ kmh}^{-1}$ , and temperature was between 16-50°C (O'Leske et al. 1997). All materials from pitfall and sweep net samples were thawed, and dried in a drying oven at 40° C for 48 h before sample masses were measured. All collected animals were identified to order, and orders were weighed to the nearest 0.1 mg.

All data were statistically analyzed with the SAS computer program (SAS 1990). Brood size, percent survival (number of young to fledge / number of young to hatch), number of young to fledge, and fledging age were analyzed with one way analysis of variance (ANOVA) with treatment group as the effect. Percent survival data were not arcsine transformed because neither the transformed nor the untransformed data were normally distributed. Brood size was tested as a potential covariate on all measurements of nesting success because brood size can potentially alter the amount of food provisioned per nestling, resulting in brood size-dependent nestling growth and development. Brood size was only included in the ANOVA model when all analysis of covariance (ANCOVA)

assumptions were met (Steel and Torrie 1960). The yearly number of nests succumbing to a particular fate during the nestling period (abandoned, depredated, or fledged) between treatment groups were compared with Fisher's Exact Test. Clutch size nor hatching rates were analyzed because effects of food limitation or other factors affecting clutch size or hatching were of interest. Least-square means were calculated for all nestling mass, tarsus and chord lengths and analyzed with a two way ANOVA, with treatment group and nestling day age as the effects. Means of daily nestling characteristics between the treatment groups were then analyzed with linear contrasts. Linear contrast analysis calculates sums of squares for each researcher-defined comparison based on the original ANOVA model sums of squares. This permits the examination of specific comparisons in the context of the original ANOVA model (Sokal and Rohlf 1995). Each comparison has the potential to indicate significant differences between treatment group morphological characteristics within nestling day ages that was not discernable with the two way ANOVA results. Comparisons of daily nestling measurements with linear contrasts were considered significantly different when the probability that the results were due to chance was less than  $0.05 / \# \text{ nestling day ages compared}$ . The corrected probability value reduces the experimental Type I error associated with simultaneous inference tests (Rice 1989).

Prey data were analyzed according to sampling technique because of order collection biases associated with each technique (Southwood 1966, Norment 1987). Treatment group average total mass per day for pitfall trap samples, and average total mass for sweep net samples was compared with a one way ANOVA. The effects of



treatment group and prey order were analyzed with a two way ANOVA. Treatment group mean order mass was compared with linear contrast analysis. Differences between order mass were considered significant when  $P$  was less than the corrected alpha level, or  $0.05 / \#$  insect orders compared (Rice 1989). All probability values are presented for the reader's inspection, but differences were considered significant only when  $P < 0.05$ , unless otherwise indicated.

## RESULTS

All comparisons included data collected throughout the 1996 and 1997 breeding seasons. I did not separate data according into time periods such as early, middle, and late breeding season because too few nests occurred in the early and late periods, which prevented any meaningful analyses. Forty seven and 58 Eastern Bluebird nests were monitored during the 1996 and 1997 breeding seasons, respectively. Two nests from 1996 were removed from analyses because one nest was abandoned and the other depredated, before hatching. Nineteen nests were removed from the 1997 analyses due to abandonment and depredation before hatching ( $n = 4$  and  $n = 7$ , respectively), incomplete monitoring of early nesting activity (before 20 May 1997,  $n = 4$ ), brood parasitism by Brown-headed Cowbirds ( $n = 3$ ), and incomplete food supplementation ( $n = 1$ ). The earliest known egg-laying dates occurred on 5 April 1996 and 29 March 1997, and breeding activity continued after data recording ceased on 26 July 1996 and 4 August 1997.

Of the 45 and 39 active nests monitored in 1996 and 1997, 34 and 23 nests were in the control group, and 11 and 16 nests were in the experimental group, respectively. Mean brood size of the treatment groups was not significantly different in either year; in 1996, the experimental group's mean brood size was larger than the control group's, but in 1997, the control group's mean brood size was larger than the experimental group's (Table 1).

The fates of 28 (62%) and 35 (90%) nests were known in 1996 and 1997, respectively. In 1996, the proportion of nests fledging at least one young was

TABLE 1. Results of ANOVA tests of Eastern Bluebird productivity in east central Kansas in 1996 and 1997. Nest boxes were assigned to the unsupplemented or food supplemented group. Measurements are the least-square mean  $\pm$  standard error (SE)

Variable	Year	Group	Mean ± SE	Group			Brood Sizea		
				F	df	P	F	df	P
Brood Size	1996	Unsupplemented	4.05 ± 0.20	0.99	1,43	0.3256			
		Food supplemented	4.45 ± 0.35						
	1997	Unsupplemented	4.22 ± 0.26	1.98	1,38	0.1162			
		Food supplemented	3.56 ± 0.31						
% Survival	1996	Unsupplemented	100.00 ± 0.02	3.18	1,13	0.0980			
		Food supplemented	91.67 ± 0.04						
	1997	Unsupplemented	97.92 ± 0.02	0.02	1,18	0.9000			
		Food supplemented	97.50 ± 0.03						

# Fledged	1996	Unsupplemented	3.91 ± 0.29	2.31	1,13	0.1523			
		Food supplemented	4.75 ± 0.47						
	1997	Unsupplemented	3.94 ± 0.10	0.46	1,18	0.5085	124.34	1,18	0.0001
		Food supplemented	3.84 ± 0.12						
Fledging Age	1996	Unsupplemented	17.55 ± 0.50	3.98	1,11	0.0715			
		Food supplemented	15.75 ± 0.75						
	1997	Unsupplemented	16.71 ± 0.51	1.73	1,13	0.2115			
		Food supplemented	17.63 ± 0.47						

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a Covariate effect.

approximately the same for both treatment groups (Fig. 1). In 1997, the same proportion of control and experimental nests fledged young (Fig. 1). Experimental nests in 1996 were abandoned slightly more than control nests, but succumbed to less depredation than control nests (Fig. 1). The percent of nests abandoned during the nestling period in 1997 was higher for experimental nests than control nests, but these percentages only represented one nest in each treatment group (Fig. 1). Control nests experienced greater nest depredation compared to experimental nests in 1996 and 1997 (Fig. 1). The number of nests in a fate category did not vary significantly between treatment groups in either year (1996, Fisher's Exact Test,  $P = 0.841$ ; 1997, Fisher's Exact Test,  $P = 1.000$ ).

Nestling characteristics were very similar between the treatment groups in 1996 and 1997. Analysis of least-squares means of daily nestling mass indicated significant differences in mass between days in 1996 and 1997, but average treatment group mass did not differ significantly in either year, nor were there any significant differences when the effects of treatment group and nestling day age were combined (Table 2). Linear contrast analysis did not indicate any significant differences in average brood mass on any nestling day age in 1996 or 1997. In 1996, control group nestling mass was heavier than experimental group mass on eight of the 15 nestling day ages (Fig. 2). In 1997, control group mass was heavier on 10 of 15 days (Fig. 3).

Analysis of tarsus and chord lengths measurements from 1997 yielded results similar to mass analyses. Mean tarsus length differed significantly on a day to day basis, but did not differ between the treatment groups for the entire nestling period, nor when the effects of nestling day age and treatment were combined (Table 2). Linear contrasts

FIG. 1. The percentage of Eastern Bluebird nests in each fate category based on data collected in east central Kansas during the 1996 and 1997 breeding seasons. Treatments include the control (no food supplement) and experimental (food supplemented) groups.

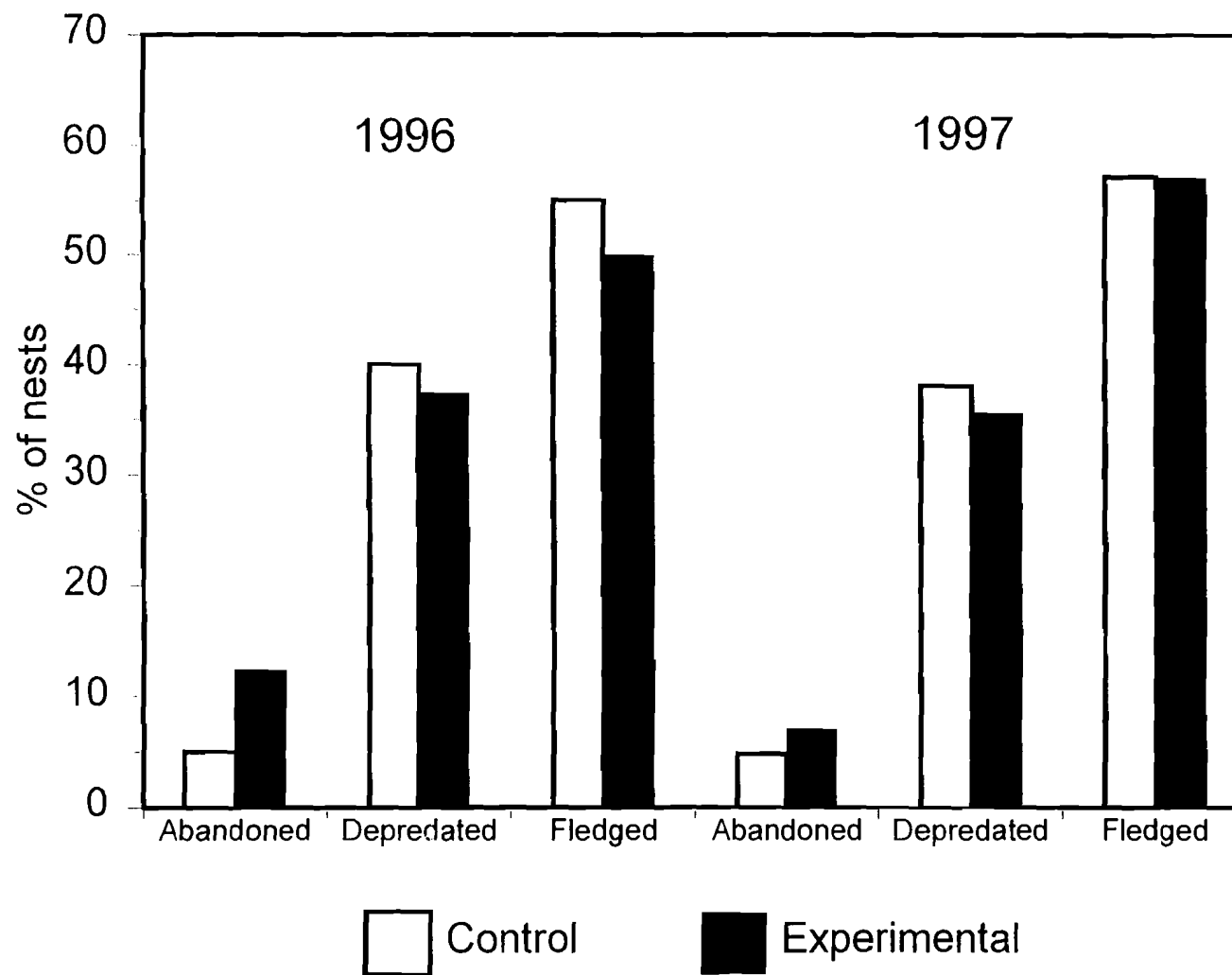


TABLE 2. Results of ANOVA tests of Eastern Bluebird nestling characteristics between control (no food supplement) and experimental (food supplemented) groups in east central Kansas in 1996 and 1997.

Variable	Year	Treatment			Day Age			Treatment * Day Age		
		F	df	P	F	df	P	F	df	P
Brood Mass	1996	0.09	1,159	0.7604	127.26	14,146	0.0001	1.38	14,146	0.1694
	1997	1.99	1,153	0.1502	226.81	14,130	0.0001	0.59	14,130	0.8689
Tarsus Length	1997	1.33	1,84	0.2537	108.28	14,71	0.0001	0.84	13,74	0.6179
Chord Length	1997	0.00	1,29	0.9964	14.80	7,23	0.0001	1.24	5,25	0.3323



FIG. 2. Least-square means  $\pm$  standard error (SE) of Eastern Bluebird nestling mass (g) in east central Kansas during the 1996 breeding season. Treatments include the control (no food supplement; ●) and experimental (food supplemented; ■) groups.

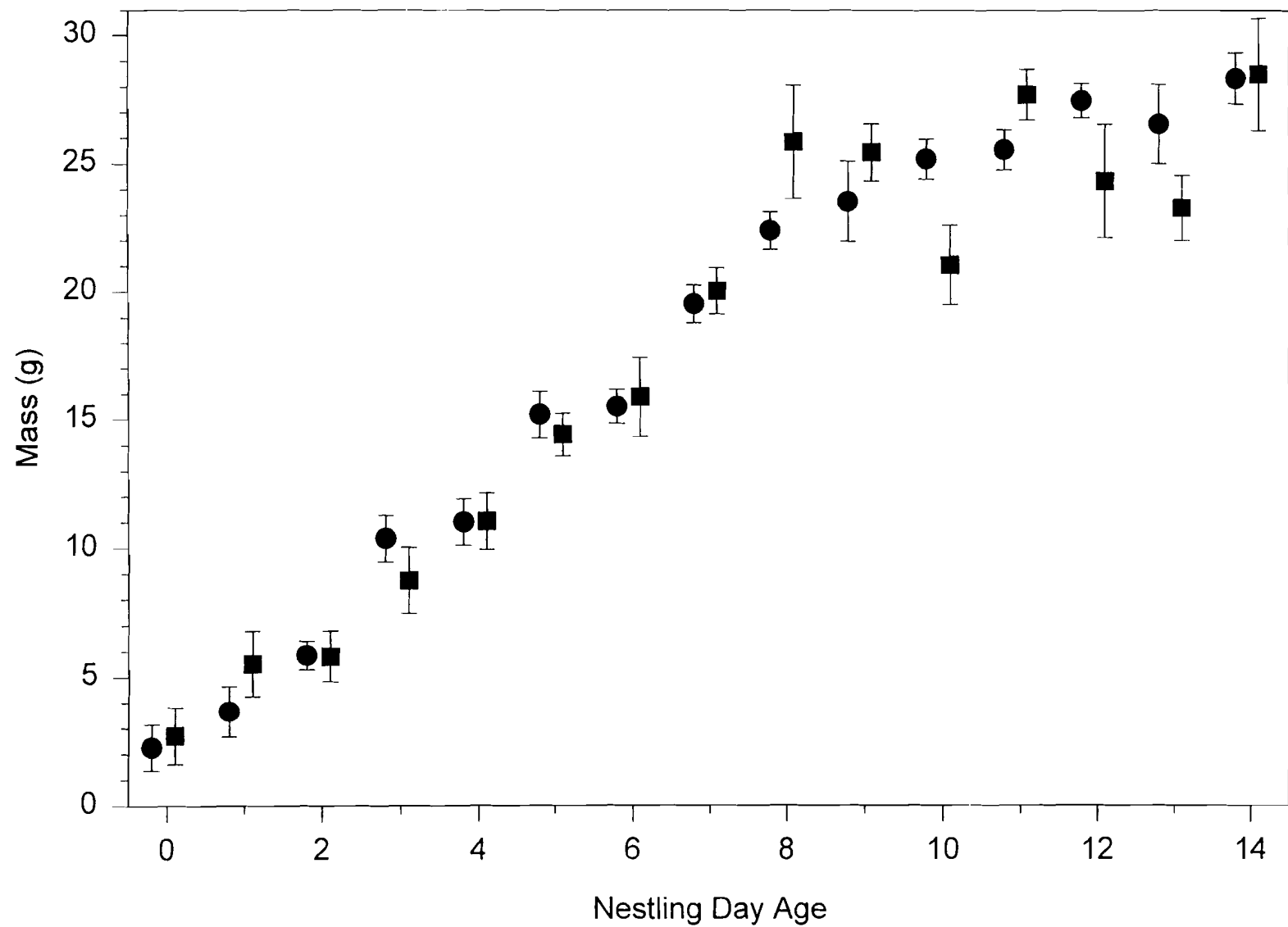
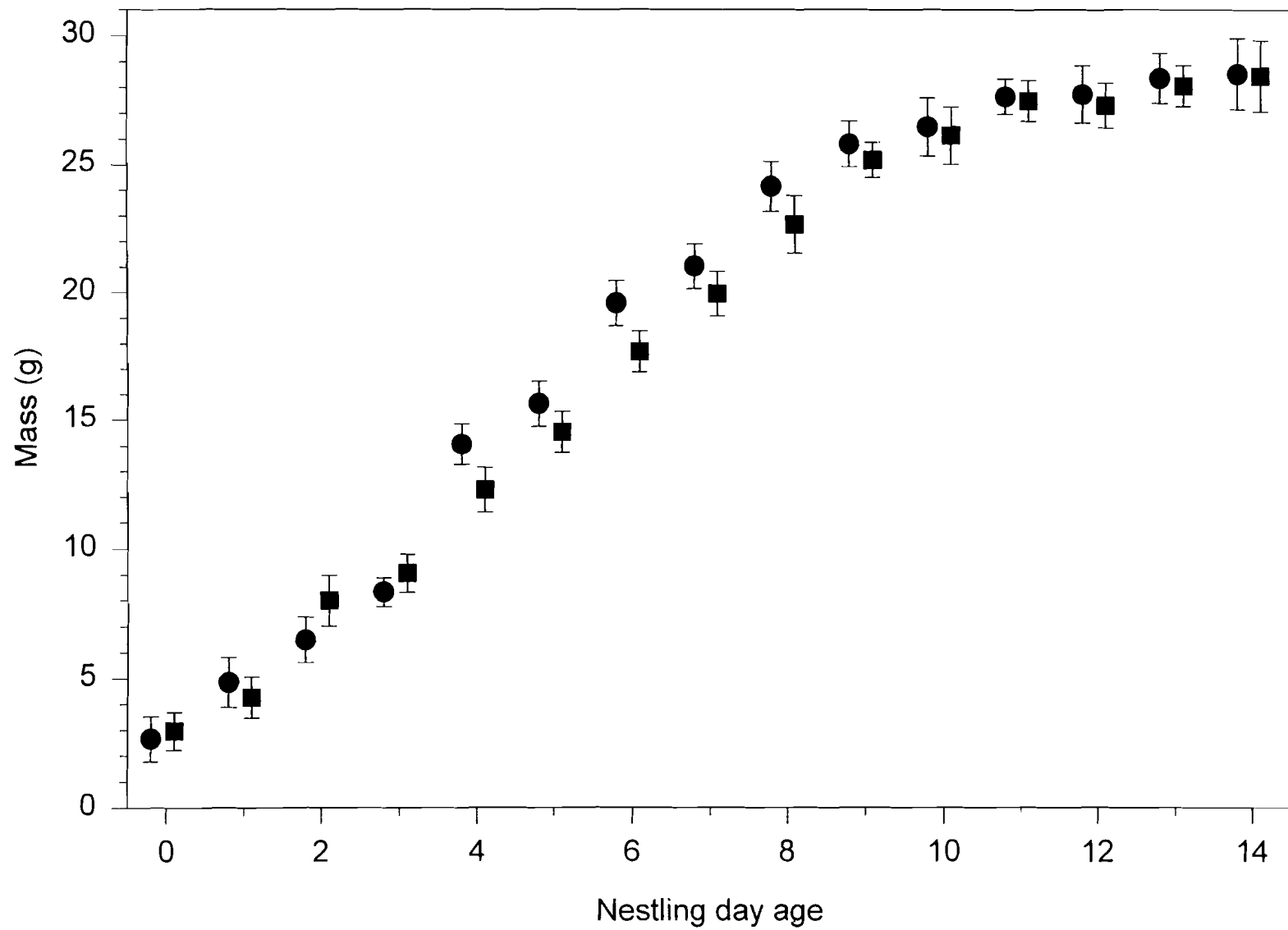


FIG. 3. Least-square means  $\pm$  standard error (SE) of Eastern Bluebird nestling mass (g) in east central Kansas during the 1997 breeding season. Treatments include the control (no food supplement; ●) and experimental (food supplemented; ■) groups.



did not indicate any significant differences between treatment group average tarsus lengths on any nestling day age. Control group tarsus length was longer on 11 of the 14 nestling day ages (Fig. 4).

Daily chord length varied significantly, but there was no significant difference between treatment groups, or in the interaction term of nestling day age and treatment (Table 2). Linear contrasts did not indicate any significant differences between treatment group average chord lengths on any nestling day age (Fig. 5). The control group had longer average chord lengths on 2 of the 5 nestling day ages that were examined.

Little variation in percent survival, number of young fledged, and mean fledging age existed between the control and experimental groups. Percent survival in both treatment groups was relatively high in both years, and averaged above 90%. Control nests had higher survival rates than the experimental nests in both years, and in 1996, no young that hatched died in nests where nest fate was known (Table 1). The relatively high survival rates did not differ significantly between treatment groups (Table 1).

Number of young fledged was not significantly different between treatment groups, but did vary between years and treatments (Table 1). Number of young fledged was greater in the experimental group in 1996, but was greater in the control group in 1997 (Table 1).

Age at fledging between the treatment groups varied, but ages did not differ significantly between treatment groups in either year (Table 1). There was a tendency for food supplemented young to leave the nest at a younger age than control group young in 1996, but the reverse was true in 1997 (Table 1).

FIG. 4. Least-square means  $\pm$  standard error (SE) of Eastern Bluebird nestling tarsus length (mm) in east central Kansas during the 1997 breeding season. Treatments include the control (no food supplement; ●) and experimental (food supplemented; ■) groups.

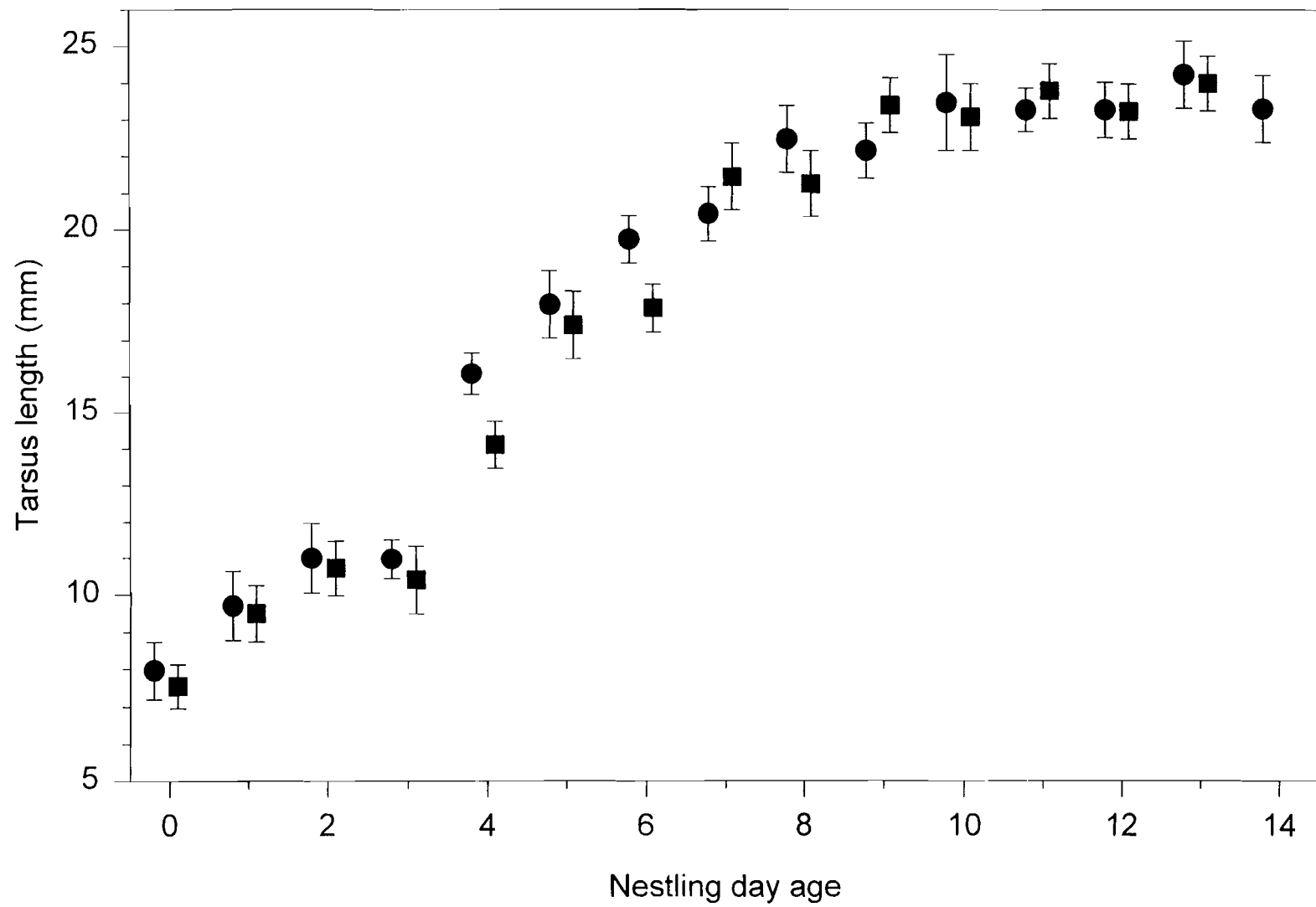
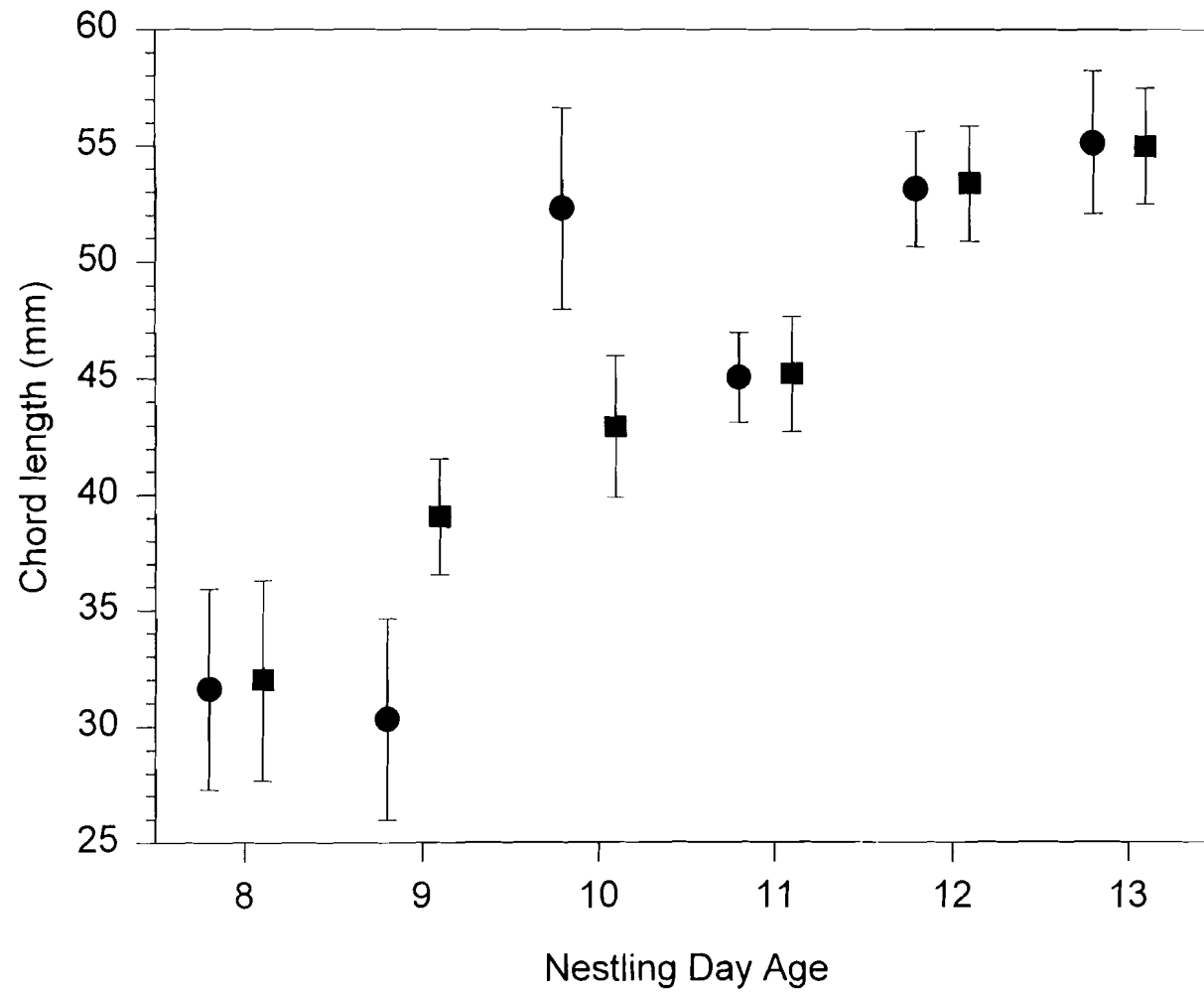


FIG. 5. Least-square means  $\pm$  standard error (SE) of Eastern Bluebird nestling chord length (mm) in east central Kansas during the 1997 breeding season. Treatments include the control (no food supplement; ●) and experimental (food supplemented; ■) groups.





Comparison of total sample mass and individual prey order mass did not differ between treatment groups for pitfall trap or sweep net samples (Table 3). Average sample mass for pitfall traps was heavier in the control group compared to the experimental group, but this difference was not significant (Table 3, Appendix 1). Experimental nest box total sample mass for sweep net samples was heavier than the control group's, but this difference was not significant (Table 3, Appendix 2). Mean prey order masses were not significantly different between the treatment groups, but there was a significant difference among individual prey order masses between treatment groups in pitfall trap and sweep net samples (Table 4). Analysis of pitfall trap and sweep net data indicate no significant interaction between treatment group and order mass, thus prey availability was relatively similar at experimental and control nest boxes. Only pairwise comparisons of orders were made in each sampling technique because differences in mass of an order between the treatment groups could affect results of the food supplementation. Linear contrasts did not indicate any significant differences in order mass between treatment groups for either sampling technique.

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TABLE 3. Results of ANOVA tests of pitfall trap and sweep net total sample mass. Insect samples were collected adjacent to Eastern Bluebird nest boxes in east central Kansas between 18 June and 1 August 1997. Measurements are reported as the least-square mean mass (g)  $\pm$  standard error (SE). Treatments include the control (no food supplement) and experimental (food supplemented) groups.

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Technique	Treatment	Mean $\pm$ SE	Treatment		
			F	df	P
Pitfall trap	Control	2.90 $\pm$ 0.77	1.51	1,12	0.2405
	Experimental	2.01 $\pm$ 0.34			
Sweep net	Control	0.87 $\pm$ 0.27	0.00	1,10	0.9609
	Experimental	0.90 $\pm$ 0.37			

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TABLE 4. Results of ANOVA tests of pitfall trap and sweep net sample order mass. All samples were collected adjacent to Eastern Bluebird nest boxes between 18 June and 1 August 1997. Treatments include the control (no food supplement) and experimental (food supplemented) groups.

Technique	Treatment	Order			Treatment			Order * Treatment		
		F	df	P	F	df	P	F	df	P
Pitfall trap	Control	4.60	19,79	0.0001	0.60	1,97	0.4415	0.35	12,86	0.9760
	Experimental									
Sweep net	Control	2.46	12,68	0.0117	0.00	1,79	0.9444	0.06	10,70	1.0000
	Experimental									

## DISCUSSION

Empirically, my results do not support the hypothesis food availability limits avian reproduction (Lack 1947). However, the lack of response in any of the measured variables might be a result of environmental conditions preventing a detectable difference between the unsupplemented and food supplemented nestlings, i.e., Lack's hypothesis (1947) might have been supported. I present evidence that both refutes and supports the hypothesis that food limits avian reproduction.

Nest fate is one response susceptible to the effects of increased food availability. In my study, the number of nests per fate category did not differ significantly between treatment groups in either year (Fig.1). Nest success rates in my study were similar to Pinkowski's Michigan population ( $\bar{x} = 55.5$ ; 1977a), and within the range of results reported by Gowaty and Plissner (1998). Abandonment rates for the control nests was similar to results reported by Kruger (1985). Predation rates in my study were relatively high compared to studies in South Carolina ( $\bar{x} = 2\%$ , Gowaty and Plissner 1998), and Wisconsin ( $\bar{x} = 9\%$ , Kruger 1985), but my results might be due to the small number of known nest fates (see RESULTS). Studies have demonstrated that food supplements elevate parental vigilance time around nests, and decrease the probability of their nest being depredated (Yom-Tov 1974, Richner 1992). If increased food availability around nest boxes allowed parents to spend more time around their nest box, then it could be predicted that predation rates would be lower for the experimental group. Both treatment groups had predation rates equal to approximately 35%, which were high compared to other Eastern Bluebird studies (Fig. 1; see Gowaty and Plissner 1998 for summary). Nest

box location and or conspicuousness might have contributed to the probability of being depredated. For example, nest box numbers 7.13 and 8.2 at FHNWR were each depredated twice in as many nesting attempts in 1997, one of which was located along a fenceline (7.13), the other in the middle of a pasture. Although these nest boxes might have been fixated upon by a particular predator, their relative location was similar to the placement of other nest boxes throughout the study area. Random assignment of nest boxes to a treatment group might explain similar depredation rates between treatment groups, but it does not explain why they were similar. Depredation events might have occurred at night, when nest defense by parents was likely to be low. If nest boxes were attacked at night, then any advantage food supplements offered to parents in the way of increased time in a territory, or increased vigilance time, would be insignificant.

Investigative protocol designed to directly examine the interaction between unsupplemented and food supplemented nest boxes and time of depredation event would better elucidate my nest fate results. At the ultimate level, Eastern Bluebird and other secondary cavity nesting species might be adapted to relatively high depredation rates (Ekman and Askemo 1986, Martin 1995) by increasing the average number of broods attempted per season. For example, evidence exists of some Eastern Bluebird parents attempting three and four broods in a season (Peakall 1970, Tucker 1990). The number of multi-brooded parents for the east central Kansas population is unknown, but at least four females attempted second broods (D. A. Robinson Jr., unpubl. banding data). If the Eastern Bluebird is adapted to high predation rates, then clutch size might be adjusted to minimize immediate losses, while maximizing output by increasing the number of broods

raised in a season. Testing this prediction would require long term evaluation of an Eastern Bluebird population exposed to artificially high and low depredation rates while monitoring all breeding attempts by parents. Parents with low predation rates would be expected to raise fewer, larger clutches than those parents exposed to high predation rates (Martin 1995).

Differences in nestling morphological characteristics between the treatment groups were expected to be the most prominent evidence of food limitation. Average nestling brood mass was not significantly different between the control and experimental treatments in either year, and contrary to predictions, control group nestlings were heavier than experimental group nestlings on a majority of the nestling day ages (Figs. 2 and 3). Additionally, nestling tarsus and chord lengths were not significantly different between the treatment groups in 1997; again, control group nestlings were larger than the experimental group nestlings in most comparisons (Table 2, Figs. 4 and 5). My results suggest one of four possibilities: first, Eastern Bluebird nestlings do not benefit from increased food availability; second, the food supplement was not qualitatively sufficient to elicit a response; third, the quantity of the food supplement was not sufficient to elicit detectable differences between the treatment groups; or fourth, parents did not provision a significant amount of food to nestlings. Calculations of mealworm larvae macromolecule components (e.g., fat and protein) given by Bell (1990) indicate that the food supplement should have provided adequate nutrition for Eastern Bluebird nestlings. Relative to the quantity of the food supplement, 50g of mealworms was sufficient to feed at least one parent and all the young for the two day interval between food provisioning, or feed both

parents and a few of the nestlings for two days. Examination of adult masses during the nestling period does not suggest that parents are allocating a significant proportion of the food to themselves because females and males both lost weight at this time (D. A. Robinson Jr., unpubl. data). The finding that control group nestlings had heavier masses, and larger tarsus and chord lengths suggests that experimental group nestlings might not have received all the required nutrients for growth. Experimental group nestlings might have been receiving a sufficient amount and a nutritionally adequate food stuff, but if the food supplement replaced natural food stuffs, then growth could have been stunted. Documentation of the exact food types brought to control and experimental group nest boxes would permit a better understanding of what advantages food supplements provided for breeding Eastern Bluebird.

Additionally, the lack of response to food supplements by Eastern Bluebird nestlings might have been due to favorable weather conditions during the study period. Other studies have documented improved growth rates of nestlings when provisioned with supplemental food, especially when breeding season weather conditions were poor (Simons and Martin 1990, Garcia et al. 1993). If environmental conditions were harsh, responses to food supplements similar to the above studies would have been expected. Thus, to better understand the relative influence of climate on Eastern Bluebird breeding conditions, average precipitation, and average minimum and maximum temperatures from Emporia, Kansas for the breeding period of 1 March to 31 July of 1996 and 1997 were analyzed with *t*-tests. No weather measurements were significantly different between breeding seasons, nor between 10-year averages (Table 5). Little climatological variation



TABLE 5. Results of *t*-tests on weather data from 1986 to 1997 for Emporia, KS (38° 43' N, 96° 20' W). Only data between 1 March to 31 June were examined, as these dates approximate the Eastern Bluebird breeding period in east central Kansas. Measurements are reported as the mean  $\pm$  standard error (SE). Weather data were obtained from the High Plains Climate Center, University of Nebraska, Lincoln, NE.

Variable	#	Year(s)	Mean $\pm$ SE	Comparison	t	P
Precipitation (cm)	1	1996	0.290 $\pm$ 0.078	1 and 2	0.2208	0.8254
	2	1997	0.312 $\pm$ 0.065			
	3	1986-1995	0.346 $\pm$ 0.025	1 and 3	0.6928	0.4891
	4	1987-1996	0.341 $\pm$ 0.023	2 and 4	0.3606	0.7187
Minimum	5	1996	9.895 $\pm$ 0.829	5 and 7	0.0062	0.9950
Temperature (°C)	6	1997	9.888 $\pm$ 0.688			
	7	1986-1995	11.102 $\pm$ 0.221			
Maximum	8	1987-1996	10.992 $\pm$ 0.211	6 and 8	1.4300	0.1306
	9	1996	22.705 $\pm$ 0.764	9 and 10	0.1342	0.8934
	10	1997	22.571 $\pm$ 0.647			
	11	1986-1995	23.366 $\pm$ 0.220	9 and 11	0.9055	0.3649
	12	1987-1996	23.306 $\pm$ 0.208	10 and 12	1.0198	0.3088

between the 1996 and 1997 breeding seasons supports the consistent responses of nestling mass, and tarsus and chord lengths between treatment groups in the two year study. If the climatological data differed significantly between years, or from 10-year averages, then dissimilar results between the two years might have resulted. The precipitation and temperature levels during 1996 and 1997 appear to be appropriate for raising Eastern Bluebird, and, therefore, reproductive output was probably maximized. Extremely cold or wet weather is known to delay laying (Bryant 1979), and when freezing temperatures occurred early in the 1997 breeding season, all active Eastern Bluebird nests were abandoned. Because severe weather conditions did not occur at any other time during the main part of the breeding season, thermal stress might not have created conditions capable of affecting breeding. Because Eastern Bluebird feed on a diversity of food items (Pinkowski 1978), if food shortage did occur, they might be able to subsist on food items not affected by the inclement weather. Conversely, aerial insectivores, such as species in Family Hirundinidae, are severely affected by weather conditions (Bryant 1979, Jones 1987, McCarty and Winkler 1999). My study suggests that weather conditions did not impose restrictions on Eastern Bluebird reproduction. If weather conditions were poor, food limitation consequences might have been evident.

Martin's (1987) examination of food limitation studies found Lack's hypothesis to be true in most investigations of food theory studies. Reproductive success in terms of size of young, growth rates of young, and number of young raised to fledging all appear to increase when greater amounts food are available within study sites, nesting territories, and at sites where food is artificially increased (see review in Martin 1987). Recent

studies both confirm (Simons and Martin 1990, Garcia et al. 1993), and refute (Cavitt and Thompson 1997) the benefits of increased food availability. In Alberta, Garcia et al. (1993) demonstrated that young of Mountain Bluebird (*Sialia currocoides*) parents that received a food supplement equal to approximately 18% of one parent's daily energetic needs was sufficient to improve nestling growth rates and mass at fledging compared to young in unsupplemented nests. In Arizona, Simons and Martin (1990) demonstrated a similar response to food supplements by Cactus Wrens (*Campylorhynchus brunneicapillus*) in one of two years of study. Conversely, Cavitt and Thompson (1997) could not elicit increased nestling size variables in a food supplementation study on Illinois House Wrens. Cavitt and Thompson (1997) suggested that some responses to food supplementation might be a consequence of latitudinal gradient. For example, Mountain Bluebirds breeding in Alberta were probably more stressed by a lower average temperature than House Wrens breeding in Illinois, thus, the Mountain Bluebirds responded favorably to the food supplement but the House Wrens did not. Intraspecific comparison of results from food supplementation studies at different latitudes would best answer questions relative to regional climate.

In my study, nestling survival rates in both treatment groups were very high compared to other studies (see Gowaty and Plissner 1998), and, thus, nestling mortality rates were very low. My results refute predictions based on Lack's food limitation hypothesis because there were no significant differences between the control and treatment group survival rates. However, high nestling survival rates in the unsupplemented and food supplemented nestlings reflects an almost certain lack of food limitation. Thus, food

supplementation effects might be masked because survival rates are already very high, i.e., survival rates can not be greater than 100%, as they were for the control group in 1996 (Table 1).

Fledging age varies with period of breeding season (Pinkowski 1975, Gowaty and Plissner 1998), but overall seasonal average fledging age for Michigan broods is 18.8 days (Pinkowski 1975), 17.6 days for Georgia broods (Gowaty and Plissner 1998), and 17.6 days for South Carolina broods (Gowaty and Plissner 1998). Broods in my study fledged at a younger age than their continental counterparts, however, food supplements did not consistently decrease average fledging age (Table 1). Inconsistent differences in the number of young fledged and age at fledging between treatment groups in my study lends little support to the hypothesis that food limits Eastern Bluebird reproduction (Table 1). If greater food availability is beneficial to breeding birds, then responses should include an increase in the number of young fledged per nest (Högstedt 1981), as well as younger ages at fledging because nestlings could theoretically attain the appropriate pre-fledging mass (~90% of adult mass) earlier than nestlings in unsupplemented nests, and thus leave the nest in better condition (Richner 1992). Nestling survival and probability of breeding increases with greater morphological measurements at the time of fledging (Simons and Martin 1990, Richner 1992), but if any benefits of food supplements were conferred to young in my study, it is not apparent from nestling morphological or survival measurements.

Although not tested, brood size, number of fledglings, and fledging age appear to vary consistently among the treatment groups. The largest brood size fledged the most

young at the youngest age, while the smallest brood size fledged the fewest young at the oldest age (Table 1). The overall mean brood size was  $4.06 \pm 0.13$  (standard error), and upon examination of Table 1, young belonging to broods below the overall mean fledged at an older age than young belonging to broods larger than the overall mean. These results suggests that a larger than average brood size is better than a below average brood size, perhaps because the balance between energy allocation and thermoregulatory processes is correct (Mertens 1969, Crossner 1977, Westerterp et al. 1982). Young in nests with brood sizes equal to or above the 'optimal' brood size might be attaining mass and balancing thermoregulatory processes such that increased food provisioning will not improve their condition from its current state. Additional concurrent studies of the effects of brood and food manipulations on breeding birds (e.g., Crossner 1977) might better explain nestling energy dynamics occurring between below average, average, and above average brood sizes.

Variation in natural food availability is known to influence the date at which avian parents will begin laying eggs (Bryant 1975), and when peak numbers of birds will be begin breeding (Lack 1968). Quantifying natural food availability facilitates explanation of differential productivity or nestling growth relative to food supplementation effects. Simons and Martin (1990) were able to discern the impact of food supplements on Cactus Wren nestlings and parent productivity by examining the size of prey types brought to nestlings. Observations of prey types brought to the nest offer one means of determining diet, as does collection of food provisioned to nestlings through the use of throat collars (Pinkowski 1978). Such information is indeed important, however, it was not the

intention of the prey sampling regime in my study. Relative estimates of food availability around nest boxes was done simply to ensure food supplements provisioned to experimental group nest boxes represented an increase in food availability. With the exception of Lepidopteran larvae, prey sampling in my study adequately sampled insect orders that were most often fed to nestlings in a southeastern Michigan study (e.g., orders Orthoptera, Araneae, and Coleoptera; Pinkowski 1978). Despite the difference between my study's prey samples and Pinkowski's (1978) prey sampling summary, my sampling effort collected adequate data to compare relative food abundance adjacent to control and experimental group nest boxes .

The lumping of favorable or negative responses to food supplements across all avian taxa potentially fails to address the more pertinent issue of how species at different nesting sites (excavator, nonexcavator, or open nesting) respond to environmental variation associated with food availability, nest depredation, and density-dependent processes. Martin (1995) addressed several issues that affect clutch size in altricial birds, including adult mortality, number of broods attempted, predation, and food availability. Clutch size and number of broods attempted per season was strongly negatively related to nesting site from fewest attempts (excavator species, e.g., Downy Woodpecker (*Picoides pubescens*)) to intermediate (secondary cavity nesting species, e.g., Eastern Bluebird), to greatest number of attempts (non-cavity nesting species, e.g., Savannah Sparrow (*Passerculus sandwichensis*)). Relative to this was the strong correlation between nesting site and predation rates, such that secondary cavity nesting species and non-cavity nesting species had similar predation rates, and excavator species had low predation rates. Most

importantly, nestling growth rates increased from excavator species to secondary cavity nesting species to non-cavity nesting species. The combination of these factors potentially reduces the susceptibility of all cavity nesting species to food availability, in the form of reduced nestling growth rates and decreased nestling demands for food. The limiting factor to secondary cavity nesters, then, is the number of nest sites available and the amount of energy parents must expend competing for a nest site (Nice 1957, von Haartman 1957, Newton 1980, Martin 1995). Secondary cavity nesters often take immediate advantage of cavities when they become available (Perrins 1965, Bock and Fleck 1995), and hypothetically maximize each breeding attempt. Different densities of breeders potentially can affect the degree of food limitation by Eastern Bluebirds, as well as other secondary cavity nesters. In an experimental manipulation of nest box density, Gowaty and Bridges (1991) demonstrated that as the density of nest boxes in an area increased, parental infidelity, measured as the percentage of nestlings that were not completely related to both parents found at a nest box, increased. Furthermore, when nest boxes were removed from a portion of the study site partially through the breeding season, the number of intraspecific parasitism events increased. Gowaty and Bridges (1991) explicitly tested several hypotheses relative to adaptive reproductive mechanisms when nesting sites are limited, and their results lend support to the prediction that limited numbers of nesting sites available to secondary cavity nesters alters reproductive decisions. As the density of secondary cavity nest breeders increased, the average clutch size would increase due to extra pair copulations or nest parasitism, and thus, greater effort would be necessitated on behalf of the parents to successfully raise their young. As

reproductive effort increases, overall nestling survival would probably decrease, as has been demonstrated in brood manipulation studies (DeSteven 1980). In these situations reproductive output would be food limited. In my study, most nest boxes were located approximately 100 m apart, and thus were probably not likely to affect reproductive variables between neighboring Eastern Bluebirds. However, several nests were abandoned when adjacent nest boxes were simultaneously active (1996, HWY50 #8, KAT #23), and in one instance, neighboring pairs both abandoned their breeding attempt (1997, MLWA #s 1 and 7). Density-dependent interactions are known to affect reproductive strategies (Arcese and Smith 1988), but its effects on Eastern Bluebird nestling characteristics and reproductive output are not known. Nest box density manipulations (e.g., Gowaty and Bridges 1991) in conjunction with food availability manipulations would best test whether Eastern Bluebird reproduction is affected by density-dependent processes.

My results refute and, indirectly, support Lack's (1947, 1954) hypothesis that avian parents raise the maximum number of young per breeding attempt. Eastern Bluebird nestling growth and survival variables were not improved when food supplements were provided. However, high nestling survival rate in both treatment groups gives circumstantial evidence that clutch size was adjusted to current environmental conditions, and that no amount of additional food could elicit responses appropriate to refute the food limitation hypothesis. The lack of any significant differences between the control and experimental group does not necessarily mean that Eastern Bluebird nestling growth and survival indices are not affected by food limitation. Rather, environmental conditions in my study probably did not provide the opportunity to dismiss the food limitation



hypothesis. Further investigation of nest site limitation and Eastern Bluebird breeding biology is necessary before concluding that food limits Eastern Bluebird reproduction.

Literal interpretation of Lack's food limitation hypothesis (1947, 1954) can obscure understanding how food availability shapes avian life history traits. Few investigators would dismiss the role of energy in avian reproduction decisions (or any other behavior). However, further investigations of food's role relative to other environmental variables will best explain how food availability affects nestling growth and survival.

## LITERATURE CITED

- Adams, J. S., R. L. Knight, L. C. McEwen, and T. L. George. 1994. Survival and growth of nestling Vesper Sparrows exposed to experimental food reductions. *Condor* 96:739-748.
- Arcese, P., and J. N. M. Smith. 1988. Effects of population density and supplemental food on reproduction in Song Sparrows. *J. Anim. Ecol.* 57:119-136.
- Bell, G. P. 1990. Birds and mammals on an insect diet: a primer on diet composition analysis in relation to ecological energetics. *Stud. Avian Biol.* 13:416-422.
- Bent, A. C. 1949. Life histories of North American thrushes, kinglets, and their allies. United States National Museum Bulletin 196. Washington, D. C.
- Bock, C. E., and D. C. Fleck. 1995. Avian response to nest box addition in two forests of the Colorado front range. *J. Field. Ornithol.* 66:352-362.
- Boutin, S. 1990. Food supplementation experiments with terrestrial vertebrates: patterns, problems, and the future. *Can. J. Zool.* 68:203-220.
- Bryant, D. M. 1975. Breeding biology of House Martins *Delichon urbica* in relation to aerial insect abundance. *Ibis* 117:180-216.
- Bryant, D. M. 1979. Reproductive costs in the House Martin (*Delichon urbica*). *J. Anim. Ecol.* 48:655-675.
- Buser, C. S. 1980. A time and energy budget study of the Eastern Bluebird (*Sialia sialis*) during the breeding season. M.S. thesis, Rutgers Univ., New Brunswick, New Jersey.
- Cavitt, J. F., and C. F. Thompson. 1997. Mass loss in breeding house wrens: effects of food supplements. *Ecology* 78:2512-2523.

- Coulson, J. C. 1966. The influence of the pair-bond and age on the breeding biology of the Kittiwake Gull *Rissa tridactyla*. *J. Anim. Ecol.* 35:269-279.
- Crossner, K. A. 1977. Natural selection and clutch size in the European Starling. *Ecology* 58:885-892.
- Crowell, K. L., and S. I. Rothstein. 1981. Clutch sizes and breeding strategies among Bermudan and North American passerines. *Ibis* 123:42-50.
- DeSteven, D. 1980. Clutch size, breeding success, and parental survival in the Tree Swallow (*Iridoprocne bicolor*). *Evolution* 34:278-291.
- Drent, R. H., and S. Daan. 1980. The prudent parent: energetic adjustments in avian breeding. *Ardea* 68:225-252.
- Ekman, J., and C. Askemo. 1986. Reproductive cost, age-specific survival and comparison of the reproductive strategy in two European tits (Genus *Parus*). *Evolution* 40:159-168.
- Garcia, P. F. J., M. S. Merkle, and R. M. R. Barclay. 1993. Energy allocation to reproduction and maintenance in Mountain Bluebirds (*Sialia currucoides*): a food supplementation experiment. *Can. J. Zool.* 71:2352-2357.
- Gowaty, P. A., and W. C. Bridges. 1991. Nestbox availability affects extra-pair fertilizations and conspecific nest parasitism in Eastern Bluebirds, *Sialia sialis*. *Anim. Behav.* 41:661-675.
- Gowaty, P. A., and J. H. Plissner. 1998. Eastern Bluebird (*Sialia sialis*). In *The Birds of North America*, no. 381 (A. Poole and F. Gill, Eds.). The Academy of National Sciences, Philadelphia, Pennsylvania; The American Ornithologists' Union,

Washington, D.C.

Hartshorne, J. M. 1962. Behavior of the Eastern Bluebird at the nest. *Living Bird* 1:131-149.

Henderson, R. F., M. Schwilling, W. Seyler, O. H. Darrow, E. L. Fittell, and E. S. Bagley. 1990. Increasing Eastern Bluebirds in Kansas. Coop. Ext. Serv., Kansas State Univ., Manhattan, Kansas.

Högestedt, G. 1981. Effect of additional food on reproductive success in the magpie (*Pica pica*). *J. Anim. Ecol.* 50:219-229.

Järvinen, A., and R. A. Väisänen. 1984. Reproduction of Pied Flycatchers (*Ficedula hypoleuca*) in good and bad breeding seasons in a northern marginal area. *Auk* 101:439-450.

Jones, G. 1987. Parent-offspring resource allocation in swallows during nestling rearing: an experimental study. *Ardea* 75:145-168.

Kacelnik, A. 1984. Central place foraging in Starlings (*Sturnus vulgaris*). I. Patch residence time. *J. Anim. Ecol.* 53:283-299.

Kendeigh, S. C. 1952. Parental care and its evolution in birds. Ill. Biol. Monogr. 22:1-356.

Kruger, S. M. 1985. Productivity and nest-site selection of Eastern Bluebirds in Wisconsin. MS Thesis, Univ. of Wisconsin, Stevens Point.

Lack, D. 1947. The significance of clutch size. *Ibis* 89:302-352.

Lack, D. 1954. The natural regulation of animal numbers. Oxford Univ. Press, London, UK.

- Lack, D. 1968. Ecological adaptations for breeding in birds. Methuen, London, UK.
- Lee, L. R. 1996. Eastern Bluebirds: effects of environment on reproductive strategies. Ill. Nat. Hist. Surv. No. 340. 8 pp.
- Lifson, N., and R. McClintock. 1966. Theory of use of the turnover rates of body water for measuring energy and material balance. *J. Theor. Biol.* 12:46-74.
- Martin, T. E. 1987. Food as a limit on breeding birds: a life-history perspective. *Annu. Rev. Evol. Syst.* 18:453-487.
- Martin, T. E. 1995. Avian life history evolution in relation to nest sites, nest predation, and food. *Ecol. Monogr.* 65:101-127.
- McCarty, J. P., and D. W. Winkler. 1999. Relative importance of environmental variables in determining the growth of nestling Tree Swallows *Tachycineta bicolor*. *Ibis* 141:286-296.
- Meek, S. B., and R. J. Robertson. 1994. Effects of male removal on the behaviour and reproductive success of female Eastern Bluebirds *Sialia sialis*. *Ibis* 136:305-312.
- Mertens, J. A. L. 1969. The influence of brood size on the energy metabolism and water loss of nestling Great Tits *Parus major major*. *Ibis* 111:11-16.
- Moreno, J. 1989a. Variation in daily energy expenditure in nesting Northern Wheatears (*Oenanthe oenanthe*). *Auk* 106:18-25.
- Moreno, J. 1989b. Body-mass variation in breeding Northern Wheatears: a field experiment with supplementary food. *Condor* 91:178-186.
- Newton, I. 1980. The role of food in limiting bird numbers. *Ardea* 68: 11-30.
- Nice, M. M. 1957. Nesting success in altricial birds. *Auk* 74:305-321.

- Norment, C. J. 1987. A comparison of three methods for measuring arthropod abundance in tundra habitats and its implications in avian ecology. *Northwest Sci.* 61:191-198.
- O'Leske, D.L., R.J. Robel, and K.E. Kemp. 1997. Sweepnet-collected invertebrate biomass from high- and low-input agricultural fields in Kansas. *Wildl. Soc. Bull.* 25:133-138.
- Orell, M., and K. Koivula. 1988. Cost of reproduction: parental survival and production of recruits in the Willow Tit *Parus montanus*. *Oecologia* 77:423-432.
- Peakall, D. B. 1970. The Eastern Bluebird: its breeding season, clutch size, and nesting success. *Living Bird* 9:239-255.
- Perrins, C. M. 1965. Population fluctuations and clutch-size in the Great Tit, *Parus major* L. *J. Anim. Ecol.* 34:601-647.
- Pinkowski, B. C. 1974. Criteria for sexing Eastern Bluebirds in juvenile plumage. *Inland Bird Band. News* 46:88-91.
- Pinkowski, B. C. 1975. Growth and Development of Eastern Bluebirds. *Bird Banding* 46:273-289.
- Pinkowski, B. C. 1977a. Breeding adaptations in the Eastern Bluebird. *Condor* 79:289-302.
- Pinkowski, B. C. 1977b. Foraging behavior of Eastern Bluebird. *Wilson Bull.* 89:404-414.
- Pinkowski, B. C. 1978. Feeding of nestling and fledgling Eastern Bluebirds. *Wilson Bull.* 90:84-98.

- Radunzel, L. A., D. M. Muschitz, V. M. Bauldry, and P. Arcese. 1997. A long-term study of the breeding success of Eastern Bluebirds by year and cavity type. *J. Field Ornith.* 68:7-18.
- Rice, W. R. 1989. Analyzing tables of statistical tests. *Evolution* 43:223-225.
- Richner, H. 1992. The effect of extra food on fitness in breeding Carrion Crows. *Ecology* 73:330-335.
- Rodenhouse, N. L., and R. T. Holmes. 1992. Results of experimental and natural food reductions for breeding Black-throated Blue Warblers. *Ecology* 73:357-372.
- Sanz, J. J., and J. M. Tinbergen. 1999. Energy expenditure, nestling age, and brood size: an experimental study of parental behavior in the Great Tit *Parus major*. *Behav. Ecol.* 10:598-606.
- SAS Institute. 1990. SAS/STAT User's Guide, Vol. 2. Cary, North Carolina.
- Schmidt, P., and J. A. Lockwood. 1992. Subnivean arthropod fauna of southeastern Wyoming: habitat and seasonal effects of population density. *Am. Midl. Nat.* 127:66-76.
- Schoech, S. J. 1996. The effect of supplemental food on body condition and the timing of reproduction in a cooperative breeder, the Florida Scrub-Jay. *Condor* 98:234-244.
- Simons, L. S., and T. E. Martin. 1990. Food limitation of avian reproduction: an experiment with the Cactus Wren. *Ecology* 71:869-876.
- Smith, W. P. 1937. Some bluebird observations. *Bird Banding* 8:25-30.
- Sokal, R. R., and F. J. Rohlf. 1995. *Biometry*, 3<sup>rd</sup> ed. Freeman, New York.
- Southwood, T. R. E. 1966. *Ecological methods with particular reference to the study of*



insect populations. Methuen, London, UK.

Steel, R. G. D., and J. H. Torrie. 1960. Principles and procedures of statistics with special reference to the biological sciences. McGraw-Hill, New York.

Tucker, J. W., Jr. 1990. Male Eastern Bluebird rears four broods during one nesting season. *Wilson Bull.* 102:726-728.

von Haartman, L. 1957. Adaptation in hole-nesting birds. *Evolution* 11:339-347.

Westerterp, K., W. Gortmaker, and H. Wijngaarden. 1982. An energetic optimum in brood-raising in the Starling *Sturnus vulgaris*: an experimental study. *Ardea* 70:153-162.

Wittmann, K., and R. C. Beason. 1992. The effect of blowfly parasitism on nestling Eastern Bluebird development. *J. Field. Ornithol.* 63:286-293.

Yom-Tov, Y. 1974. The effect of food and predation on breeding density and success, clutch size and laying date of the crow (*Corvus corone* L.). *J. Anim. Ecol.* 43:479-498.

APPENDIX I. Summary of pitfall trap samples collected adjacent to Eastern Bluebird nest boxes in east central Kansas between 18 June and 1 August 1997. Treatments include the control (no food supplement) and experimental (food supplemented) groups. Order measurements are reported as least-square mean mass (g)  $\pm$  standard error (SE), calculated as mean mass of an order captured over two trap-nights, divided by the total number of nest boxes where the order was caught (n). Also presented is the total number of individuals captured per order (# Ind), a proportion (%) based on the number of individuals per per order divided by the total number of individuals captured per treatment, and, listed next to the treatment group name is the number of nest boxes where samples were collected.

Order	Control (5)				Experimental (9)			
	n	Mean $\pm$ SE	# Ind	%	n	Mean $\pm$ SE	# Ind	%
Gastropoda	1	0.0741 $\pm$ 0.0000	4	0.4	1	0.0445 $\pm$ 0.0000	3	0.3
Oligochaeta	1	0.0049 $\pm$ 0.0000	1	0.1				
Isopoda	3	0.8864 $\pm$ 0.7357	338	33.9	4	0.1802 $\pm$ 0.0724	122	13.5
Diplopoda	1	0.2248 $\pm$ 0.0000	2	0.2	1	0.0219 $\pm$ 0.0000	1	0.1
Chilopoda					1	0.1206 $\pm$ 0.0000	1	0.1
Thysanura					1	0.0176 $\pm$ 0.0000	14	1.6

Orthoptera	5	$0.5082 \pm 0.2384$	126	12.7	9	$0.4985 \pm 0.1462$	132	14.7
Dermaptera					2	$0.0101 \pm 0.0076$	2	0.2
Hemiptera	2	$0.0151 \pm 0.0112$	2	0.2	1	$0.0005 \pm 0.0000$	1	0.1
Homoptera	1	$0.0030 \pm 0.0000$	1	0.1	1	$0.0000 \pm 0.0000$	1	0.1
Neuroptera (Larvae)	1	$0.0014 \pm 0.0000$	1	0.1				
Coleoptera (Adult)	5	$1.4169 \pm 0.3640$	146	14.6	9	$1.2142 \pm 0.2459$	196	21.7
Lepidoptera (Adult)	1	$0.0447 \pm 0.0000$	1	0.1	2	$0.1566 \pm 0.1395$	4	0.4
Lepidoptera (Larvae)	2	$0.0042 \pm 0.0011$	3	0.3	4	$0.0345 \pm 0.0158$	7	0.8
Diptera	2	$0.0109 \pm 0.0104$	3	0.3	4	$0.0040 \pm 0.0022$	4	0.4
Hymenoptera (Wingless)	4	$0.0624 \pm 0.0412$	242	24.3	8	$0.0468 \pm 0.0169$	305	33.9
Hymenoptera (Winged)					1	$0.0078 \pm 0.0000$	1	0.1
Unknown Insect	3	$0.0118 \pm 0.0021$	9	0.9	3	$0.0219 \pm 0.0162$	14	1.6
Araneae	5	$0.2989 \pm 0.0619$	117	11.7	9	$0.0872 \pm 0.0212$	94	10.4
Anura	1	$0.0174 \pm 0.0000$	1	0.1				

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APPENDIX II. Summary of sweep net samples collected adjacent to Eastern Bluebird nest boxes in east central Kansas between 18 June and 1 August 1997. Treatments include the control (no food supplement) and experimental (food supplemented) groups. Order measurements are reported as least-square mean mass (g)  $\pm$  standard error (SE), calculated by dividing the sum of an order's mass from all samples by the number of nest boxes where the order was captured (n). Also reported is the total number of individuals captured per order (# Ind), a proportion (%) created by dividing the number individuals captured in each order by the total number of individuals caught per treatment group, and the number of nest boxes sampled listed next to the treatment group name.

Order	Control (4)				Experimental (8)			
	n	Mean $\pm$ SE	# Ind	%	n	Mean $\pm$ SE	# Ind	%
Ephemeroptera (Larvae)	1	0.0061 $\pm$ 0.0000	1	0.3				
Odonata	2	0.0047 $\pm$ 0.0007	3	0.8	2	0.0231 $\pm$ 0.0224	4	1.2
Orthoptera	4	0.5929 $\pm$ 0.2028	87	22.8	8	0.7654 $\pm$ 0.3513	178	53.6
Hemiptera	4	0.0389 $\pm$ 0.0208	17	4.5	5	0.0300 $\pm$ 0.0173	15	4.5
Homoptera	4	0.0206 $\pm$ 0.0084	35	9.1	4	0.0131 $\pm$ 0.0031	19	5.7
Neuroptera (Larvae)	1	0.0018 $\pm$ 0.0000	1	0.3				
Coleoptera (Adult)	3	0.0597 $\pm$ 0.0293	24	6.2	6	0.0774 $\pm$ 0.0377	19	5.7

Lepidoptera (Adult)	2	$0.0091 \pm 0.0061$	3	0.8	3	$0.0186 \pm 0.0116$	5	1.5
Lepidoptera (Larvae)	1	$0.0631 \pm 0.0000$	9	2.4	3	$0.0119 \pm 0.0063$	5	1.5
Diptera	4	$0.0213 \pm 0.0048$	37	9.7	4	$0.0245 \pm 0.0010$	20	6.0
Hymenoptera (Wingless)	4	$0.0344 \pm 0.0200$	83	21.7	4	$0.0058 \pm 0.0021$	16	4.8
Hymenoptera (Winged)	2	$0.0800 \pm 0.0004$	2	0.5	2	$0.0035 \pm 0.0005$	2	0.7
Araneae	4	$0.0933 \pm 0.0399$	80	20.9	4	$0.0422 \pm 0.0239$	49	14.8

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Douglas A. Robinson, Jr.

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3/16/00

Date

The effects of food supplements on Eastern Bluebird nestling growth and survival

Title of Thesis

Joey Cooper

Signature of Graduate Office Staff

May 11, 2000

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