Online Theses and Dissertations

Student Scholarship

January 2011

Ultraviolet reflectance of nestling plumage and the provisioning strategies of adult Eastern Phoebes (Sayornis phoebe)

Alyssa Rae Underwood
Eastern Kentucky University

Follow this and additional works at: https://encompass.eku.edu/etd

Part of the Biology Commons

ULTRAVIOLET REFLECTANCE OF NESTLING PLUMAGE AND THE

PROVISIONING STRATEGIES OF ADULT EASTERN PHOEBES (*SAYORNIS*

PHOEBE)

By

Alyssa Rae Underwood

Thesis Approved:

_____
Chair, Advisory Committee

_____
Member, Advisory Committee

_____
Member, Advisory Committee

_____
Dean, Graduate School

STATEMENT OF PERMISSION TO USE

In presenting this thesis in partial fulfillment of the requirements for a Master's 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 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 _____ *Alyssa M Ludwica* _____

Date _____ 6-1-11 _____

ULTRAVIOLET REFLECTANCE OF NESTLING PLUMAGE AND THE

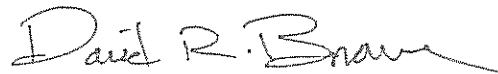PROVISIONING STRATEGIES OF ADULT EASTERN PHOEBES (*SAYORNIS*
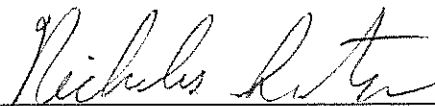
PHOEBE)

By

Alyssa Rae Underwood

Bachelor of Science
Youngstown State University
Youngstown, Ohio
2009

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

DEDICATION

This thesis is dedicated to my parents
Paula and Bill Geidner who have supported me throughout the years along with the rest
of my family.

ACKNOWLEDGMENTS

I would like to thank my advisor, Dr. Gary Ritchison, for all of his time and advice, both in the field and with help in preparing this thesis. I would also like to thank my committee members, Dr. Nick Santangelo, for his guidance with academic questions as well as his ability to inspire me to continue my education, and Dr. David Brown for all of his statistical support. In addition, I thank the friends I have met along the way. Without their encouragement, this may not have been possible.

ABSTRACT

Most songbirds are visually sensitive to ultraviolet (UV) wavelengths and, in some species, variation in the extent to which plumage reflects in the UV range provides information about individual quality that influences mate-choice decisions. Less is known about the possible importance of plumage UV reflectance in parent-offspring relationships. The lower breast and belly plumage of nestling Eastern Phoebes (*Sayornis phoebe*) reflects in the UV and adults may use variation in this reflectance to evaluate nestling quality and vary their provisioning behavior accordingly. To examine this possibility, I manipulated UV reflectance of nestling plumage by applying preen oil that either did or did not contain UV-blocker. After treatment, nestlings were placed in an experimental apparatus with individual chambers for each nestling and the provisioning behavior of adult phoebes was monitored over a two-day period by videorecording. I conducted experiments with 25 broods of Eastern Phoebes at the Blue Grass Army Depot in Madison County, Kentucky, in 2010, including 13 first broods and 12 second broods. Control and UV-blocked nestlings were fed at similar rates (P = 0.72) by male and female Eastern Phoebes, indicating that variation in UV reflectance of nestling lower breast and belly plumage does not influence adult provisioning behavior. The color of the yellow breast and belly feathers of nestling phoebes may be a selection neutral trait that is correlated with adult plumage characteristics that have other signaling functions. I found that first broods were fed at higher rates than second broods during both pre- (P = 0.001) and post-treatment time periods (P < 0.0001). Young in first broods may survive at higher rates than those in second broods. As such, adult phoebes may invest

more in those young that are most likely to contribute to their reproductive fitness. However, reduced provisioning rates for second broods may also result from decreased thermoregulatory demands of nestlings hatching later in the summer when ambient temperatures are higher. Finally, female Eastern Phoebes fed nestlings at higher rates than males during post-treatment time periods ($P = 0.001$). Differences between the sexes may be due to sex-specific differences in the costs and benefits of investing in young or to sex-specific differences in parental roles. For example, male phoebes may spend more time in other activities, such as territory defense, while females spend more time provisioning nestlings.

TABLE OF CONTENTS

LIST OF FIGURES

Chapter 1

INTRODUCTION

Individual variation in the degree to which plumage or skin reflects in the

ultraviolet (UV) range has been found to play a role in avian mate choice (Andersson and

Amundsen 1997, Bennett et al. 1997, Hunt et al. 1999, Siitari et al. 2002). However,

among some species of birds, juveniles also have plumage or skin that reflects UV

wavelengths. Little is known of the possible significance of UV reflectance in parent-

offspring interactions, but variation among nestlings in the extent of this reflectance

may provide parents with information about nestling quality that could affect food

allocation to their young (Galván et al. 2008).

Parents incur costs when caring for young (e.g., time and energy) and tradeoffs

between the costs and benefits (i.e., potential survival of offspring) should be

continuously evaluated during the breeding season, with parents allocating resources

(i.e., feeding effort) accordingly. Parent birds have been shown to assess many aspects

of nestling quality, such as plumage ornaments (Lyon et al. 1994), nestling begging

behavior (Ottoson et al. 1997), nestling size (Shiao et al. 2009), and mouth gape

coloration (Götmark and Ahlström 1997), when making decisions regarding provisioning

strategies. Life history theory predicts that parents will choose strategies that maximize

lifetime reproductive output (Williams 1966), and the evolution of mechanisms that

help evaluate nestling quality may help in making those decisions. If variation in UV

reflectance is correlated with variation in nestling quality (Andersson and Amundsen

1997), adult birds may use that variation to assess offspring condition and allocate food resources accordingly.

Several investigators have examined the possible relationship between variation in the UV reflectance of the plumage of nestling songbirds and adult provisioning rates (Bize 2006, Galvan 2008, Tanner and Richner 2008). For example, Galván et al. (2008) found that tarsi of nestling Great Tits (*Parus major*) whose plumage was treated to reduce UV reflectance subsequently grew more slowly than the tarsi of control nestlings because adults fed the treated nestlings at lower rates than their siblings. Similarly, Tanner and Richner (2008) manipulated UV reflectance of the plumage of fledgling Great Tits by treating breast and cheek feathers with a lotion that either did or did not contain UV blockers. They found that adult females fed fledglings whose plumage still reflected in the UV at higher rates than UV-blocked fledglings. Adult male Great Tits, however, fed UV-blocked and control fledglings at similar rates (Tanner and Richner 2008). Bize et al. (2006) found that adult European Starlings fed nestlings with plumage that reflected less in UV wavelengths at higher rates than control nestlings (higher UV reflectance) earlier in the breeding season, but then fed the same nestlings at lower rates than control nestlings in second broods, later in the season.

Although these studies suggest that adult songbirds in at least two species (Great Tits and European Starlings) may alter their provisioning behavior in response to manipulation in the extent to which the plumage of nestlings reflects UV wavelengths, there is clearly a need for additional studies of other species. In a study focusing on possible relationships between a number of morphological characteristics and the

provisioning behavior of male and female Eastern Phoebes (*Sayornis phoebe*), Horn (2009) found that the yellow breast and belly plumage of adult phoebes exhibits reflectance peaks in the yellow wavelengths (500-600 nm), but also in UV wavelengths (320-400 nm). The yellow plumage of nestling phoebes also reflects strongly in both the yellow and UV wavelengths (Underwood, pers. observ.; Figure 1A[1]). This yellow plumage first becomes apparent in nestling phoebes beginning about 6 or 7 days post-hatching and appears similar to that of adults as nestlings near fledgling age (i.e., 16 – 19 days post-hatching; Underwood, pers. observ.). As reported in studies of other species, differences among nestlings in the extent to which their plumage reflects UV wavelengths might provide adult phoebes with information about nestling quality that could affect their provisioning behavior. Thus, the main objective of my study was to examine the possible effect of manipulating the extent to which the plumage of nestling phoebes reflected UV wavelengths on the provisioning behavior of male and female Eastern Phoebes.

Additional objectives of my study will be to examine the possible effects of brood size and brood number on the provisioning strategies of male and female Eastern Phoebes. Clutch and brood sizes of Eastern Phoebes range from two to six, with most broods consist of three to five young (Ritchison, unpubl. data). Previous studies of songbirds have provided conflicting results concerning the effect of variation in brood size on adult provisioning behavior, with provisioning rates not changing in response to

---

[1] All figures are located within the appendix.

increases in brood size in some species (e.g., Schadd and Ritchison 1998) and increasing

with brood size in other species (e.g., Bédard and Meunier 1983, Barba et al. 2009).

Given such variation among species, additional studies are needed to better understand

the factors that contribute to variation in the responses of adults to variation in brood

size.

Eastern Phoebes are typically double-brooded (Weeks 2011), and previous

studies of other species of songbirds have revealed that, in temperate areas, young that

fledge from nests earlier in the breeding season have higher survival rates (e.g.,

Verboven and Visser 1998, Naef-Daenzer et al. 2001, Verhulst and Nilsson 2008). If

young in earlier nests are more valuable to parents in terms of lifetime fitness, then the

provisioning strategies of adult phoebes may differ for first and second broods.

Chapter 2

METHODS

Study species

Eastern Phoebes (*Sayornis phoebe*) are migratory songbirds that breed

throughout eastern North America (Weeks 2011). Phoebes are socially monogamous

and exhibit biparental care. Hatching of eggs is synchronous and young phoebes are

altricial. Both parents care for and feed nestlings until young fledge at 16 to 19 days

post-hatching (Conrad and Robertson 1992).

Study site and nest selection

My study was conducted at the Blue Grass Army Depot (BGAD) in Madison

County, Kentucky. The BGAD encompasses 5906 ha and consists primarily of pastures,

ungrazed grasslands, and scattered woodlots of various sizes. Phoebes on the BGAD

nest in small, concrete shelters (about 2.5 x 5 x 2.5 m; N = 55) that were constructed to

provide protection in case of emergencies; the shelters are no longer used by Army

personnel.

Beginning on 1 April 2010, adult phoebes were captured in mist-nets as they

attempted to enter or exit shelters. Captured phoebes were banded with a U.S.

Geological Survey numbered aluminum band plus a unique combination of three

colored leg bands to permit individual recognition. Phoebes were sexed by the presence

of either a brood patch on females or cloacal protuberance of males. Most pairs in my

study had two broods. I defined first broods as those that fledged prior to 31 May; second broods fledged in June or July. Previous success was not a factor in categorizing second broods.

Beginning in early April, I checked nests in shelters every 2-4 days to determine status. The date nestlings hatched was recorded as day one. When nests were checked after eggs had hatched, nestling age was determined by their size, whether their eyes had opened, and other morphological features (Murphy 1981). On day 16 post-hatching, nestlings were removed from nests and weighed (± 0.5 gm). In addition, I collected yellow breast and belly feathers (N = 6-8) from each nestling; feathers were placed in individual micro-centrifuge tubes for later spectrographic analysis. Nestlings were then placed in the experimental apparatus (see below) and videorecorded for four days, including two days prior to treatment and two days post-treatment.

Treatment and test apparatus

All nestlings in a brood were placed in the experimental apparatus on day 16 post-hatching following their measurements and treatment. The apparatus was made of cardboard and wire mesh, with a chamber (10 x 10 x 12 cm) for each nestling (Figure 2). The front and bottom of the apparatus were made of wire mesh to: 1) allow adult phoebes to see and feed nestlings, and 2) ensure droppings did not accumulate in test chambers. Three perches were constructed and attached to the experimental box. The first perch was located 20 cm from the front of the apparatus to provide a convenient perch when adults first approach the young. The two remaining perches, located 2 and

5 cm from the apparatus, were placed to give adults a choice as far as the best position for provisioning nestlings that projected their heads variable distances from the front of the apparatus as they attempt to obtain food from adults. The apparatus was placed in a corner of the shelter on a tripod near the nest. Individual test chambers were numbered and nestlings were randomly assigned to the test chambers.

After the two day pre-treatment period, nestlings were randomly assigned to experimental (UV-reduced) and control groups. One nestling in broods of three and four, and two nestlings in broods of five received the UV-reduction treatment. The UV-reduction solution consisted of the UV absorbing chemicals Eusolex 2292 and Eusolex 9020 (50/50 by weight) (Picon Chemicals, Inc., Homewood, IL) mixed with duck preen oil in a 40/60 ratio (by weight). Selected nestlings were treated by applying the UV-reduction solution with a small brush to the breast and belly. The remaining nestlings (controls) were treated only with preen oil. This method of UV reduction has been previously used (Andersson and Amundsen 1997, Limbourg et al. 2004, Tanner and Richner 2008) and the treatment is known to effectively block UV reflectance for at least four days (Korsten et al. 2006). Prior to the experiment, I confirmed the effectiveness of the treatment by conducting spectrographic analysis of phoebe feathers to ensure that reflectance in the UV wavelengths was reduced, but reflectance levels at other wavelengths were not affected (Figure 1B). After treatment with either the UV-reduction solution or preen oil, nestlings were weighed and returned to the same chambers of the test apparatus that they were previously located in and videorecorded

for two days. At the end of the experiment, young phoebes were removed from the

test chambers, weighed, and released.

Video recording and reviewing

Videos were recorded with digital or analog camcorders. In the shelters,

camcorders were placed on tripods about 1.5 to 2 m from test chambers. Recording

sessions were two to six hours long, with differences due to use of different batteries

and camcorders. On the first day of recording, the provisioning behavior of adult

phoebes during the first hour was not used in my analyses, providing time for them to

become familiar with the test apparatus.

Videos were subsequently reviewed using either a Sony VCR (analog tapes) or

with Windows Media Player Classic Home Cinema (digital videos), respectively. Four to

six hours of observation were reviewed for each pre- and post-treatment block per

shelter (N = 29) for a total of 330 hours. For each visit by an adult phoebe, I noted the

sex of the visiting adult (determined by the unique combinations of colored leg bands).

Feather reflectance

Collected feathers were mounted on non-glossy, black poster board for

scanning. I took five scans of each feather sample and averaged them for analysis with

Spectra Suite software (Ocean Optics). Feathers were scanned with a Jaz spectrometer

(Ocean Optics, Dunedin, FL), with a Jaz-PX module lamp used as a light source. A

bifurcated micron fiber-optic probe was placed approximately 5 mm (± 1 mm) from the

feathers in a black metal sheath to hold it in place. Reflectance curves were analyzed

using CLR 1.05 (Montgomerie 2008) and values were determined for mean brightness,

UV chroma, and carotenoid chroma. All colors were calculated within the visible color

spectrum for birds (320-700 nm; Cuthill et al. 2000).

Mean brightness is defined as the sum of $R_{\lambda320-\lambda700}$ / 381 (381 is the total number

of reflectance data points between $_\lambda320$ and $_\lambda700$). Carotenoid chroma was calculated

as $R_{\lambda700}-R_{\lambda450}/R_{\lambda700}$ (Andersson and Prager 2006), with 700 nm and 450 nm being the

minimum and maximum wavelengths reflected by carotenoids (Montgomerie 2006). UV

chroma is defined as the sum of $R_{\lambda320-\lambda400}$/ the sum of $R_{\lambda320-\lambda700}$ (Jacot and Kempenaers

2006).

Statistical analysis

I used t-tests to compare nestling body mass between broods and differences in

brood sizes between broods, and analysis of variance to test for differences in change in

mass from day 16 to day 18 and day 18 to day 20. Provisioning data was averaged to a

rate of feedings per nestling per hour. I used repeated measures analysis of variance to

examine possible relationships between UV chroma, carotenoid chroma, mean

brightness, brood size and brood number with adult provisioning rates prior to

treatment. Sex was treated as a within subjects factor because male and female

provisioning was measured separately at each nest. To test for post-treatment effects, I

used a similar repeated measures model, but with post-treatment provisioning as the

response and nestling status (UV-reduced or control) as an additional explanatory

factor. I also tested for interactions between brood number and sex and brood size and sex for pre- and post-treatment periods, as well as between status and sex, brood and status, and brood, sex and status for post-treatment time periods. All analyses were conducted with the PASW Statistics 18, Release Version 18.0.0 (SPSS 2009). All levels of significance are $P < 0.05$. Values are presented as means ± SE.

Chapter 3

RESULTS

I conducted experiments with 25 broods of Eastern Phoebes, including 13 first broods and 12 second broods. Of the 25 broods, eight were broods of three, 10 were broods of four, and seven were broods of five. Mean brood size did not differ between first (mean = 4.0) and second (mean = 3.9) broods (t_{23} = 0.26, P = 0.80).

Nestling mass

On day 16 post-hatching (when nestlings were transferred to the test apparatus), the mean mass of nestlings did not differ with either brood size ($F_{2, 94}$ = 1.0, P = 0.37) or between nestlings that, on day 18 post-hatching, would subsequently be assigned either UV-blocked or control status ($F_{1, 94}$ = 1.0, P = 0.33). However, the mean mass of nestlings in first broods (18.4 ± 0.20 gms; N = 37) was greater ($F_{1, 94}$ = 15.1, P < 0.001) than that of nestlings in second broods (17.6 ± 0.16 gms; N = 47). When weighed two days later, on day 18 post-hatching, young phoebes in both first (mean = -1.2 ± 0.2 gms; N = 44) and second (mean = -1.2 ± 0.1 gms; N = 47) broods had lost mass, with the decline in mass similar for both broods ($F_{1, 86}$ = 0.002, P = 0.96). On day 20 post-hatching, two days after treatment and when young were removed from the test apparatus, young phoebes in both first (mean = 0.7 ± 0.1 gms; N = 37) and second (mean = 0.6 ± 0.1 gms; N = 45) broods had gained mass since day 18, with the gain in mass similar for both broods ($F_{1, 77}$ = 0.2, P = 0.68).

Provisioning rates – effect of sex, brood number, and brood size

Male and female phoebes fed nestlings at similar rates during the pre-treatment period ($F_{1, 86}$ = 1.3, P = 0.26), but females fed nestlings at higher rates than males during the post-treatment period ($F_{1, 93}$ = 11.4, P = 0.001). During the pre-treatment period, nestlings were fed at mean rates of 3.38 ± 0.19 times/nestling/hour by females and 1.89 ± 0.16 times/nestling/hour by males. After treatment, nestlings were fed at mean rates of 3.57 ± 0.29 times/nestling/hour by females and 2.38 ± 0.19 times/nestling/hour by males.

Overall (males and females combined), nestlings in first broods were fed at higher rates than those in second broods during both pre- ($F_{1, 86}$ = 12.9, P = 0.001) and post-treatment ($F_{1, 93}$ =23.9, P < 0.001) periods (Figure 3). The interaction between brood number and sex was not significant for either the pre- ($F_{1, 86}$ = 1.3, P = 0.26) or post-treatment ($F_{1, 93}$ = 0.3, P = 0.57) periods, indicating that both males and females fed second broods at lower rates than first broods (Figure 4).

Provisioning rates of adult phoebes varied with brood size during the pre-treatment period ($F_{2, 86}$ = 6.2, P = 0.02), but not during the post-treatment period ($F_{2, 93}$ = 0.5, P = 0.95), with provisioning rates of 6.11 ± 0.44 (N = 21), 5.30 ± 0.36 (N = 44), and 4.66 ± 0.33 (N = 30) feedings/nestling/hour for broods of 3, 4, and 5, respectively, during the pre-treatment period and provisioning rates of 6.02 ± 0.83 (N = 24), 5.87 ± 0.39 (N = 40), and 6.01 ± 0.51 (N = 35) feedings/nestling/hour for broods of 3, 4, and 5 during the post-treatment period. In addition, the interaction between brood size and sex was not significant during either the pre- ($F_{1, 86}$ = 0.02, P = 0.89) or post-treatment ($F_{2, 93}$ = 0.5, P

= 0.61) periods, indicating that males and females provisioned different-sized broods in similar ways (Figure 5).

Provisioning rates - effect of UV reduction

Overall, control and UV-reduced nestlings were fed at similar rates ($F_{1, 93} = 0.1$, P = 0.72), with provisioning rates of 5.88 ± 0.36 (N = 67) and 6.11 ± 0.59 (N = 32) feedings/nestling/hour for control and UV-reduced nestlings, respectively. In addition, I found no significant interactions between sex and status (i.e., control vs. UV-reduced; $F_{1, 93} = 1.6$, P = 0.20), brood and status ($F_{1, 93} = 0.02$, P = 0.90; Figure 6), and brood, sex, and status ($F_{1, 93} = 1.5$, P = 0.23).

Nestling plumage – pre-treatment

Reflectance curves for feathers from the belly regions of nestling Eastern Phoebes exhibited a bimodal pattern, with peaks in both the UV (320-400 nm) and yellow (550-600 nm) wavelengths (Figure 1A). Mean color values for phoebe nestlings were 0.314 ± 0.012 for brightness, 0.160 ± 0.004 for UV chroma, and 0.427 ± 0.012 for carotenoid chroma. I found no relationship between provisioning rates and any of the measured variables, including UV chroma ($F_{1, 86} = 2.3$, P = 0.13), carotenoid chroma ($F_{1, 86} = 0.2$, P = 0.66), and brightness ($F_{1, 86} = 0.1$, P = 0.78).

Chapter 4

DISCUSSION

Brood size

I found that brood sizes did not differ between first and second broods of

Eastern Phoebes. In another study conducted at the BGAD, Horn (2009) also found no

significant difference in the size of first and second broods of phoebes. However, Horn

(2009) also reported a significant difference in clutch size between first and second

nests, with means of 4.89 eggs/clutch for first nests and 4.50 eggs/clutch for second

nests. Beheler (2001) also reported that clutch sizes were larger for first nests than

second nests in a population of Eastern Phoebes in Indiana, and first nests also had

greater hatching and fledging success. In addition, Hill and Gates (1988) found that

fledging success was generally greater for early nests than late nests, and Murphy

(1994) reported that spring nests fledged more young than summer nests. Although I

did not record clutch sizes, most studies, including one also conducted at the BGAD

(Horn 2009), indicate that first nests of Eastern Phoebes typically have larger clutches

than second nests. However, I found that the number of nestlings in first and second

nests did not differ, and Horn (2009) reported similar results. This suggests that hatching

success, survival of nestlings prior to day 16 post-hatching (when I removed nestlings

from nests and placed them in the test apparatus), or both are lower for first nests than

second nests. One possible explanation for this is that Eastern Phoebes are one of the

earliest migrants to initiate nests in the United States and Canada (Weeks 2011). As a

result, eggs and young in first nests are more likely to be exposed to cold temperatures

14

that can cause mortality of embryos (Weeks 2011) and nestlings (G. Ritchison, pers.

commun.).

Nestling phoebes in broods of three, four, and five in my study were provisioned

at similar rates during the post-treatment period (18-19 days post-hatching), but not

during the pre-treatment period (16-17 days post-hatching). Reasons for this difference

in provisioning behavior between treatments are unclear. However, these results

indicate that, just prior to typical fledging age, adult phoebes with larger broods must

provision at higher rates than phoebes with smaller broods. Similar results have been

reported for other species of songbirds, including Tree Swallows (*Tachycineta bicolor*;

Leffelaar and Robertson 1986) and Blue Tits (*Cyanistes caeruleus*; Stauss et al. 2005),

with adults increasing their feeding rates with increasing brood size so per nestling rates

were similar. Perhaps because adult phoebes compensate for larger broods by

increasing provisioning rates, I found that the mass of nestlings in different-sized broods

did not differ significantly. This suggests that full compensation for increases in brood

size by adult Eastern Phoebes may enhance their reproductive success because mass at

fledging is an important predictor of survival for young birds (Magrath 1991, Ringsby et

al. 1998, Schwagmeyer and Mock 2008).

Nestling mass

I found that the mean mass of nestling phoebes in first broods was greater than

that of nestlings in second broods on days 16 and 20 post-hatching. Other investigators

have also reported seasonal declines in the mass of nestling songbirds (e.g., Wardrop

and Ydenberg 2003, Smith and Moore 2005). I also found that adult phoebes

provisioned nestlings in second broods at significantly lower rates than those in first

broods (see Discussion below). The lower mass of nestling phoebes in second broods is

likely due to this reduction in provisioning rates. Among single-brooded species,

seasonal declines in adult provisioning rates and nestling mass may be explained by

variation in parental quality, i.e., seasonal variation in reproductive performance is due

to differences in phenotype (e.g., age, condition, or provisioning ability; de Neve et al.

2004) or territory quality (Alatalo et al. 1986) between early and later breeders.

Phenotypic differences, however, clearly cannot explain seasonal differences in

provisioning rates or nestling mass in double-brooded species like Eastern Phoebes.

Territory quality could potentially decline later in the season if, for example, food

availability declined. However, Murphy (1994) found that egg mass was significantly

greater in second nests than first nests of Eastern Phoebes in Kansas, and suggested

that increased food availability later in the season likely contributed to this difference.

Although I did not examine the availability of insect prey in my study, other investigators

have found that arthropod abundance is either higher during the summer than during

the spring (e.g., Greenberg and Forrest 2003) or is relatively constant (e.g., Moorman et

al. 2007) in temperate areas. As discussed in more detail below, more plausible

explanations for the decline in both provisioning rates of Eastern Phoebes and nestling

mass for second broods is that it either represents a trade-off between current and

future reproduction (i.e., young that fledge later in the breeding season are less likely

survive and, as a result, natural selection has favored reduced investment by parents in

later broods) or higher temperatures later in the breeding season in temperate areas lower the energy requirements of nestlings.

After two days in the experimental apparatus, I found that both control and UV-reduced phoebes lost mass. One possible explanation for this loss in mass is that the young phoebes expended more energy as they struggled to escape from the test apparatus. However, I observed little or no such struggling when viewing video-recordings. Alternatively, the loss in mass was caused by a decline in adult provisioning rates after young phoebes were placed in the test apparatus. One possible explanation for such a decline is that adult phoebes were 'apparatus-shy' and, therefore, fed their young less than they would have if young had still been in the nest or had fledged. However, Horn (2009) found that provisioning rates of adult Eastern Phoebes peaked when nestlings were 7 to 8 days old and declined for nestlings 9 to 17 days old. In addition, Murphy (1981) reported that the weight of nestling Eastern Phoebes reached an asymptote about 14 days after hatching. It is possible, therefore, that the mass of nestling Eastern Phoebes normally declines as they approach fledging age. Reduced provisioning rates for nestlings approaching fledging age may in fact be adaptive because a reduction in weight may enhance the flying ability of fledglings (Martins 1997, Mauck and Ricklefs 2005, Wright et al. 2006).

Provisioning rates

I found that female Eastern Phoebes fed nestlings at higher rates than males during the post-treatment period, but provisioning rates of males and females did not differ significantly during the pre-treatment period. The difference in nestling age during the two treatment periods (16-17 days for pre-treatment, and 18-19 days for post-treatment) is one possible explanation for this difference, with provisioning strategies of male and female phoebes differing with changes in nestling age. Other investigators have reported that female Eastern Phoebes typically provision nestlings at higher rates throughout the nestling period (Conrad and Robertson 1993, Horn 2009) and similar results, with females provisioning at higher rates than males, have also been reported in other species of songbirds (Lombardo 1991, Keyser and Hill 1999, Ardia 2007). In other species of songbirds, however, males and females provision at similar rates (Goodbred and Holmes 1996, Wright et al. 1998, Wiebe and Elchuk 2003). Differences between male and female reproductive effort, including provisioning behavior, may result from differences in the sex-specific costs and benefits of investing in young (Sanz et al. 2000, Ardia 2007).

Costs associated with parental investment could include energy expenditure, predation risk, or tradeoffs with investment in self maintenance (Howe 1979, Reznick 1985, Wright et al. 1998). The benefit of current and future reproduction can be linked to the specific value each adult associates with the young and this value may be affected by parental relatedness to the offspring. Females are certain of the paternity of the offspring, whereas male certainty is reduced (Møller 1988) and, therefore, selection

18

may favor reduced paternal effort. Reduced paternal effort in response to reduced parental relatedness has been recorded in several species (Lifjeld et al. 1998, Chuang-Dobbs et al. 2001, Neff 2003). Eastern Phoebes are known to engage in extra-pair copulations (EPC's; Beheler 2001), and Beheler and Rhodes (2003) reported that 9.2% of young phoebes in a population in Indiana were the result of extrapair fertilizations. Thus, uncertainty of paternity could be one factor contributing to differences in provisioning rates of male and female Eastern Phoebes. When uncertain of paternity, males in other species of birds (but not all, e.g., Whittingham and Lifjeld 1995, Yezerinac et al. 1996) have also been found to provide less parental care, including lower provisioning rates (Møller and Birkhead 1993, Whittingham and Dunn 1998).

Differences in the provisioning rates of males and females may also be due to the different sex-specific roles in species with biparental care (Wesolowski 1994). In many species of birds with biparental care, females are the primary caretakers of young, participating more in incubation and feeding, whereas males play a greater role in territory defense (Clutton-Brock 1991, Lombardo 1991). Although both male and female Eastern Phoebes participate in incubating eggs and feeding young, each sex differentially allocated time spent engaged in such behaviors. Males may, for example, spend less time feeding young to provide more time to defend the territory against conspecifics, resulting in females having higher provisioning rates than males.

Horn (2009) suggested that differences in the costs of foraging might also contribute to differences in the provisioning rates of male and female Eastern Phoebes, with males possibly foraging further from nest sites than females because of their need

to patrol territory boundaries. Differences in the provisioning rates of male and female

Eastern Phoebes could also results from differences in preferred foraging microhabitats

(Horn 2009). Although little is known about the foraging behavior of Eastern Phoebes,

male Black Phoebes (*Sayornis nigricans*) forage in more open areas than females (Wolf

1997). Such differences in use of foraging habitats could contribute to differences in

provisioning rates if distances from nest sites to preferred foraging habitats of males

and females consistently differed. As noted by Horn (2009), further study 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 provisioning

rates of male and female Eastern Phoebes.

Provisioning rates and brood number

As noted previously, I found that second broods of Eastern Phoebes were fed at

significantly lower rates than first broods. Similar results have been reported for other

species of songbirds, including Blue Tits (*Cyanistes caeruleus*; García-Navas and Sanz

2011) and Black-throated Blue Warblers (*Dendroica caerulescens*; Goodbred and Holmes

1996). In many species, young in later broods exhibit decreased survival (Wiggins et al.

1994, Naef-Daenzer et al. 2001) and recruitment rates (Hochachka and Smith 1991,

Brinkhof et al. 1997). Young that fledge earlier in the breeding season have longer to

learn general skills needed to survive (Grüebler and Naef-Daenzer 2008), such as how to

forage and evade predators, and also have more time to build up fat reserves for winter.

Adult phoebes may provision first broods at higher rates because of their increased

likelihood of surviving. Provisioning second broods at lower rates may represent a trade-off between current and future reproduction, with adult phoebes focusing less and provisioning nestlings that are less likely to survive and more on self-maintenance. In support of this hypothesis, Hauber (2002) reported evidence that parental care is costly for Eastern Phoebes and that, as a result, phoebes do make trade-offs between current and future reproduction.

Seasonal reductions in provisioning rates may also be influenced by ambient temperatures and thermoregulatory costs, with lower temperatures early in the breeding season resulting in a higher demand of food by nestlings (Rauter et al. 2000). Eastern Phoebes have one of the earliest arrival dates of migratory songbirds (Weeks 1994) and may begin nesting during inclement weather (e.g., cool temperatures). Adult phoebes may provision first broods at higher rates because cooler temperatures may increase thermoregulatory costs of the nestlings. Because temperatures are typically higher later in the breeding season in temperate areas, nestlings in second broods may have lower energy requirements and require less food (Goodbred and Holmes 1996).

Provisioning rates and nestling plumage

Prior to treatment, provisioning rates of adult Eastern Phoebes in my study were not correlated with any of the color variables examined (i.e., UV chroma, carotenoid chroma, or brightness). In addition, I found that control and UV-reduced nestlings were fed by adult phoebes at similar rates by male and female Eastern Phoebes. Other investigators have reported similar results with other species. For example, Ligon and

Hill (2010) found that provisioning rates of adult Eastern Bluebirds (*Sialia sialis*) were not influenced by the brightness of nestling plumage, and Tschirren et al. (2005) found that carotenoid levels in the yellow breast feathers of nestling Great Tits (*Parus major*) did not influence the provisioning rates of adults. In other species, evidence suggests that the provisioning behavior of adults is influenced by variation in the plumage or skin color of their nestlings (e.g., Griggio et al. 2009, Parejo et al. 2010). In addition, experiments demonstrated that the provisioning behavior of Great Tits (Galván et al. 2008, Tanner and Richner 2008) and European Starlings (Bize et al. 2006) was influenced by variation in the UV reflectance of the plumage of nestlings.

My results indicate that variation in UV reflectance of the breast and belly plumage of nestling Eastern Phoebes does not influence the provisioning strategies of adults. One explanation for my results is that the plumage on the lower breast and belly of nestling Eastern Phoebes has no signal function. Because phoebes have cup-shaped nests (Harrison 1975) and nestlings sit within the cup and typically huddle close together (Underwood, pers. observ.), plumage on the lower body of nestling Eastern Phoebes may generally not be visible to provisioning adults during the nestling period. In contrast, the UV-reflecting plumage of nestling Great Tits and skin of nestling European Starlings is located on the head and upper body and is clearly visible to provisioning adults. Although the belly plumage of phoebes may serve a signal function in adults (Horn 2009), natural selection would likely not favor the use of difficult-to-observe belly plumage as a signal of nestling quality. If nestling phoebes do provide adults with honest signals correlated with quality, mouth coloration may serve as the cue rather than belly

plumage. Mouth coloration has been found to signal nestling quality in other species of birds, including Barn Swallows (*Hirundo rustica*; de Ayala et al. 2007, Thorogood et al. 2008) and House Sparrows (*Passer domesticus*; Dugas 2009).

Because I tested nestlings that were near fledging age, my results also suggest that the lower breast and belly plumage of young Eastern Phoebes likely does not serve a signal function for adults even when it would be clearly visible after fledging. Because available evidence suggests that plumage colors are costly to produce or maintain (e.g., Cotton et al. 2004, Hill 2006), it seems likely that the lower breast and belly plumage of Eastern Phoebes does serve some function(s) (Horn 2009). However, the plumage of nestlings may simply develop as a correlated response, i.e., natural selection favors certain plumage characteristics in adults and, for nestlings, the trait is selection neutral (Fitze and Tschirren 2006). Alternatively, Delhey et al. (2010) suggested that carotenoid deposition in bird plumage may serve a background-matching function and help make birds more cryptic. For Eastern Phoebes, such a function seems unlikely because their yellow plumage also reflects UV wavelengths that might be visible to predators and, in addition, the persistent tail wagging of phoebes (Carder and Ritchison 2009, Weeks 2011) that may serve a predator-deterrent function (Carder and Ritchison 2009) would likely counterbalance any gain in crypticity provided by their plumage.

In sum, my results indicate that the lower breast and belly plumage of nestling phoebes has no influence on the provisioning behavior of adult Eastern Phoebes. Additional study is needed to determine if this plumage might serve other functions for young phoebes, e.g., as a signal of individual quality in interactions with conspecifics

after fledging, or simply occurs as a correlated response, serving a signaling function for

adult phoebes, but being a selection neutral trait in nestlings.

LITERATURE CITED

Alatalo, R. V., A. Lundberg, and C. Glynn. 1986. Female pied flycatchers choose territory quality and not male characteristics. Nature 323: 152-153.

Andersson, S., and T. Amundsen. 1997. Ultraviolet colour vision and ornamentation in Bluethroats. Proc. R. Soc. Lond. B 264:1587-1591.

Andersson, S., and M. Prager. 2006. Quantifying colors. In: Bird coloration. V. 1: Perception and measurements (G. E. Hill and K. J. McGraw, eds.), pp. 41-89. Harvard University Press, Cambridge, MA.

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. Can. J. Zool. 85: 847-854.

Barba, E., F. Atienzar, M. Marin, J. S. Monros, 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.

Bédard, J., and M. Meunier. 1983. Parental care in the Savannah Sparrow. Canadian Journal of Zoology 61:2836-2843.

Beheler, A. S. 2001. Characterization of dispersal and reproductive strategies in the Eastern Phoebe (*Sayornis phoebe*). Ph.D. dissertation, Purdue University, West Lafayette, IN.

Beheler, A. S., and O. E. Rhodes. 2003. Within-season prevalence of extra-pair young in

broods of double-brooded and mate-faithful Eastern Phoebes (*Sayornis phoebe)*

in Indiana. Auk 120: 1054-1061.

Bennett, A. T., I. C. Cuthill, J. C. Partridge, and K. Lunau. 1997. Ultraviolet plumage colors

predict mate preferences in starlings. Proc. Natl. Acad. Sci. USA 94:8618-8621.

Bize, P., R. Piault, B. Moureau, and P. Heeb. 2006. A UV signal of offspring condition

mediated context-dependent parental favoritism. Proc R. Soc. Lond. B 273: 2063-

2068.

Brinkhof, M. W. G., A. J. Cave, and A. C. Perdeck. 1997. The seasonal decline in the first-

year survival of juvenile coots: an experimental approach. J. Anim. Ecol. 66: 73–

82.

Carder, M. L. and G. Ritchison. 2009. Tail pumping by Eastern Phoebes: an honest,

persistent predator-deterrent signal? J. Field Ornithol. 80: 163-170.

Chuang-Dobbs, H. C., M. S. Webster, and R. T. Holmes. 2001. Paternity and parental care

in the Black-throated Blue Warbler *Dendroica caerulescens*. Anim. Behav. 62: 83-

92.

Clutton-Brock, T. H. 1991. Parental care in birds and mammals. In: The evolution of

parental care (T. H. Clutton-Brock, ed.), pp. 130-152. Princeton Univ. Press,

Princeton, NJ.

Conrad, K. F., and R. J. Robertson. 1992. Intraseasonal effects of clutch manipulation on

parental provisioning and residual reproductive value of Eastern Phoebes

(*Sayornis phoebe).* Oecologia 89: 356-364.

Conrad, K. F., and R. J. Robertson. 1993. Patterns of parental provisioning by Eastern

Phoebes. Condor 95: 57-62.

Cotton, S., K. Fowler, and A. Pomiankowsi. 2004. Do sexual ornaments show heightened

condition-dependent expression as predicted by the handicap hypothesis? Proc.

R. Soc. Lond. B 271: 771-783.

Cuthill, I. C., J. C. Partridge, A. T. D. Bennett, S. C. Church, N. S. Hart, and S. Hunt. 2000.

Ultraviolet vision in birds. In: Advances in the study of behavior (P. J. B. Slater, J.

S. Rosenblatt, C. T. Snowdon, and T. J. Roper, eds.), pp.159-214. Academic Press,

San Diego, CA.

De Ayala, R. M., N. Saino, A. P. Møller, and C. Anselmi. 2007. Mouth coloration of

nestlings covaries with offspring quality and influences parental feeding

behavior. Behavioral Ecology 18: 526-534.

Delhey, K., M. L. Roberts, and A. Peters. 2010. The carotenoid-continuum: carotenoid-

based plumage ranges from conspicuous to cryptic and back again. BMC Ecology

10: 13.

De Neve L., J. J. Soler, M. Soler, and T.Perez-Contreras. 2004. Differential maternal

investment counteracts for late breeding in magpies *Pica pica*: an experimental

study. J. Avian Biol. 35:237–245.

Dugas, M. B. 2009. House Sparrow, *Passer domesticus*, parents preferentially feed

nestlings with mouth colours that appear carotenoid-rich. Animal Behaviour 78:

767-772.

Fitze, P. S., and B. Tschirren. 2006. No evidence for survival selection on carotenoid-

   based nestling coloration in Great Tits (*Parus major*). J. Evol. Biol. 19: 616-624.

Galván, I., L. Amo, and J. Sanz. 2008. Ultraviolet-blue reflectance of some nestling

   plumage patches mediates parental favouritism in Great Tits *Parus major*. J.

   Avian Biol. 39: 277-282.

García-Navas, V., and J. J. Sanz. 2011. Seasonal decline in provisioning effort and nestling

   mass of Blue Tits *Cyanistes caeruleus*: experimental support for the parent

   quality hypothesis. Ibis 153: 59-69.

Goodbred, C. O., and R. T. Holmes. 1996. Factors affecting food provisioning of nestling

   Black-throated Blue Warblers. Wilson Bull. 108: 467-479.

Götmark, F., and M. Ahlström. 1997. Parental preference for red mouth of chicks in a

   songbird. Proc. R. Soc. Lond. B 264: 959–962.

Greenberg, C. H., and T. G. Forrest. 2003. Seasonal abundance of ground-occurring

   macroarthropods in forest and canopy gaps in the southern Appalachians.

   Southeast. Nat. 2: 591-608.

Griggio, M., C. Morosinotto, and A. Pilastro. 2009. Nestlings' carotenoid feather

   ornament affects parental allocation strategy and reduces maternal survival. J.

   Evol. Biol. 22: 2077-2085.

Grüebler, M., and B. Naef-Daenzer. 2008. Fitness consequences of pre- and post-

   fledgling timing decisions in a double-brooded passerine. Ecology 89: 2736-2745.

Harrison, H. H. 1975. A field guide to birds' nests. Houghton-Mifflin Co., Boston, MA.

Hauber, M. E. 2002. Is reduced clutch size a cost of parental care in Eastern Phoebes (*Sayornis phoebe*)? Behav. Ecol. Sociobiol. 51: 503-509.

Hill, G. E. 2006. Environmental regulation of ornamental coloration. In: Bird coloration: mechanisms and measurements, vol. 1 (G. E. Hill and K. J. McGraw, eds.), pp. 507-560. Harvard Univ. Press, Cambridge, MA.

Hill, S. R., and E. Gates. 1988. Nesting ecology and microhabitat of the Eastern Phoebe in the central Appalachians. Amer. Midl. Nat. 120: 313-324.

Hochachka, W., and J. N. M. Smith. 1991. Determinants and consequences of nestling condition in Song Sparrows. J. Anim. Ecol. 60: 995-1008.

Horn, R. I. 2009. Individual quality and provisioning behavior of male and female Eastern Phoebes, *Sayornis phoebe*. M. S. thesis, Eastern Kentucky University, Richmond, KY.

Howe, H.F. 1979. Evolutionary aspects of parental care in the Common Grackle, *Quiscalus quiscula.* Evolution 33: 41-51.

Hunt, S., I. C. Cuthill, A. T. D. Bennett, and R. Griffiths. 1999. Preferences for ultraviolet partners on the Blue Tit. Anim. Behav. 58: 809-815.

Jacot, A., and B. Kempenaers. 2006. Effects of nestling condition on UV plumage traits in Blue Tits: an experimental approach. Behav. Ecol. 29: 34-40.

Keyser, A.J., and G. E. Hill. 1999. Structurally based plumage coloration is an honest signal of quality in male Blue Grosbeaks. Behav. Ecol. 11: 202-209.

Korsten, P., T. Limbourg, C. M. Lessells, and J. Komdeur. 2006. Effectiveness of a

commonly used technique for experimentally reducing plumage UV reflectance.

J. Avian Biol. 38: 399-403.

Kose, M., and A. P. Møller. 1999. Sexual selection, feather breakage and parasites: the

importance of white spots in the tail of the Barn Swallow. Behav. Ecol. Sociobiol.

45: 430–436.

Leffelaar D., R. J. Robertson. 1986. Equality of feeding roles and the maintenance of

monogamy in tree swallows. Behav. Ecol. Sociobiol. 18: 199-206.

Lifjeld, J. T., T. Slagsvold, and H. Ellegren. 1998. Experimentally reduced paternity affects

paternal effort and reproductive success in Pied Flycatchers. Anim. Behav. 55:

319-329.

Ligon, R. A., and G. E. Hill. 2010. Feeding decisions of Eastern Bluebirds are situationally

influenced by fledgling plumage color. Behav. Ecol. 21: 456-464.

Limbourg, T., A. Mateman, S. Andersson, and C. M. Lessells. 2004. Female Blue Tits

adjust parental effort to manipulated male UV attractiveness. Proc. R. Soc. Lond.

B 271: 1903-1908.

Lombardo, M. P. 1991. Sexual differences in parental effort during the nestling period in

Tree Swallows (*Tachycineta bicolor*). Auk 108: 393-404.

Lyon, B., J. Eadie, and L. Hamilton. 1994. Parental choice selects for ornamental plumage

in American Coot chicks. Nature 371: 240-243.

Magrath, R. 1991. Nestling weight and juvenile survival in the blackbird (*Turdus merula*).

J. Anim. Ecol. 60: 335-351.

Martins, T. L. F. 1997. Fledging in the Common Swift, *Apus apus*: weight-watching with a

      difference. Anim. Behav. 54:99-108.

Mauck, R. A., and R. E. Ricklefs. 2005. Control of fledging age in Leach's Storm-Petrel,

      Oceanodroma leucorhoa: chick development and prefledging mass loss. Funct.

      Ecol. 19:73-80.

Møller, A. P. 1988. Paternity and paternal care in the swallow, *Hirundo rustica*. Anim.

      Behav. 36: 996-1005.

Møller, A. P., and T. R. Birkhead. 1993. Certainty of paternity covaries with paternal care

      in birds. Behav. Ecol. Sociobiol. 33:261-268.

Montgomerie, R. 2006. Analyzing colors. In: Bird coloration, vol. 1: perception and

      measurements (G. E. Hill and K. J. McGraw, eds.), pp. 41-89. Harvard University

      Press, Cambridge, MA.

Montgomerie, R. 2008. CLR, version 1.05. Queen's University, Kingston, Canada.

      <http://post.queensu.ca/~mont/color/analyze.html>

Moorman, C. E., L. T. Bowen, J. C. Kilgo, C. E. Sorenson, J. L. Hanula, S. Horn, and M. D.

      Ulyshen. 2007. Seasonal diets of insectivorous birds using canopy gaps in a

      bottomland forest. J. Field Ornithol. 78: 11-20.

Murphy, M. T. 1981. Growth and aging of nestling Eastern Kingbirds and Eastern

      Phoebes. J. Field Ornithol. 52: 309-316.

Murphy, M. T. 1994. Breeding patterns of Eastern Phoebes in Kansas: adaptive

      strategies or physiological constraint? Auk 111: 617-633.

Naef-Daenzer, B. F. 2001. Differential post-fledging survival of the Great and Coal tits in

relation to their condition and fledgling date. J. Anim. Ecol. 70: 730-738.

Naef-Daenzer, B., F. Widmer, and M. Nuber. 2001. Differential post-fledging survival of

Great and Coal tits in relation to their condition and fledging date. Journal of

Animal Ecology 70: 730-738.

Neff, B. D. 2003. Decisions about parental care in response to perceived paternity.

Nature 422: 716-719.

Ottoson, U., J. Bäckman, and H. G. Smith. 1997. Begging affects parental effort in the

Pied Flycatcher, *Ficedula hypoleuca*. Behav. Ecol. Sociobiol. 41: 381-384.

Parejo, D., J. M. Aviles, and J. Rodriguez. 2010. Visual cues and parental favouritism in a

nocturnal bird. Biol. Letters 6: 171-173.

Rauter, C. M., P. A. Brodmann, and H. U. Reyer. 2000. Provisioning behaviour in relation

to food availability and nestling food demand in the Water Pipit *Anthus

spinoletta*. Ardea 88: 81–90.

Ringsby, T. H., B.-E. Sæther, and E. J. Solberg. 1998. Factors affecting juvenile survival in

House Sparrow *Passer domesticus*. J. Avian Biol. 29: 241-249.

Reznick, D. N. 1985. The cost of reproduction: evaluation of the empirical evidence.

Oikos 44: 257-267.

Sanz, J. J., S. Kranenbarg, and J. M. Tinbergen. 2000. Differential response by males and

females to manipulation of partner contribution in the Great Tit. J. Anim. Ecol.

69: 74-84.

Schwagmeyer, P. L., and D. W. Mock. 2008. Parental provisioning and offspring fitness: size matters. Anim. Behav. 75: 291-298.

Shiao, M. T., M. C. Chuang, and Y. Wang. 2009. Differential food distribution by male and female Green-backed Tits (*Parus monticolus*) in relation to nestling size. Auk 126: 906-914.

Siitari, H., J. Honkavaara, E. Huhta, and J. Viitala. 2002. Ultraviolet reflection and female mate choice in the Pied Flycatcher, *Ficedula hypoleuca*. Anim. Behav. 63: 97-102.

Smith R. J., and F. R. Moore. 2005. Arrival timing and seasonal reproductive performance in a long-distance migratory landbird. Behav. Ecol. Sociobiol. 57: 231–239.

Stauss, M. J., J. F. Burkhardt, and J. Tomiuk. 2005. Foraging flight distances as a measure of parental effort in Blue Tits *Parus caeruleus* differ with environmental conditions. J. Avian Biol. 36: 47 – 56.

Tanner, M., and H. Richner. 2007. Differential food allocation by male and female Great Tit, *Parus major,* parents: are parents or offspring in control? Anim. Behav. 75: 1563-1569.

Tanner, M., and H. Richner. 2008. Ultraviolet reflectance of plumage for parent-offspring communication in the Great Tit (*Parus major).* Behav. Ecol. 19: 369-373.

Thorogood, R., R. M. Kilner, F. Karadas, and J. G. Ewen. 2008. Spectral mouth colour of nestlings changes with carotenoid availability. Funct. Ecol. 22: 1044-1051.

Tschirren, B., P. S. Fitze, and H. Richner. 2005.Carotenoid-based nestling condition and

    parental favouritism in the Great Tit. Oecologia 143: 477-482.

Verboven, N., and M. E. Visser. 1998. Seasonal variation in local recruitment of Great

    Tits: the importance of being early. Oikos 81: 511-524.

Verhulst, S., and J.-Å. Nilsson. 2008. The timing of birds' breeding seasons: a review of

    experiments that manipulated timing of breeding. Philosophical Transactions of

    the Royal Society B 363: 399-410.

Wardrop, S. L., and R. C. Ydenberg. 2003. Date and parental quality effects in the

    seasonal decline in reproductive performance of the Tree Swallow *Tachycineta*

    bicolor: interpreting results in light of potential experimental bias. Ibis 145: 439-

    447.

Weeks, H. P. 2011. Eastern Phoebe (*Sayornis phoebe*). In: 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/094>

Wesolowski, T. 1994. On the origin of parental care and the early evolution of male and

    female parental roles in birds. Am. Nat. 143: 39–58.

Whittingham, L. A., and P. O. Dunn. 1998. Male parental effort and paternity in a

    variable mating system. Anim. Behav. 55:629-640.

Whittingham, L. A., and J. T. Lifjeld. 1995. High paternal investment in unrelated young:

    extra-pair paternity and male parental care in house martins. Behav. Ecol.

    Sociobiol. 37: 103-108.

Wiebe, K. L., and C. L. Elchuk. 2003. Correlates of parental care in Northern Flickers
Colaptes auratus: do the sexes contribute equally when provisioning young?
Ardea 91: 91-101.

Wiggins, D. A., T. Pärt, and L. Gustafsson. 1994. Seasonal decline in Collared Flycatcher
Fidecula albicollis reproductive success: an experimental approach. Oikos 70:
359-364.

Williams, G. C. 1966. Natural selection, the costs of reproduction, and a refinement of
Lack's principle. Am. Nat. 100: 687–690.

Wolf, B. O. 1997. Black Phoebe (Sayornis nigricans). In The birds of North America, No.
268 (A. Poole and F. Gill, eds.). The Birds of North America, Inc., Philadelphia, PA.

Wright, J., C. Both, P. A. Cotton, and D. Bryant. 1998. Quality vs. quantity: energetic and
nutritional trade-offs in parental provisioning strategies. J. Anim. Ecol. 67: 620-
634.

Wright, J., S. Markman, and S. M. Denney. 2006. Facultative adjustment of pre-fledging
mass loss by nestling swifts preparing for flight. Proc. R. Soc. Lond. B 273: 1895-
1900.

Yezerinac, S. M., P. J. Weatherhead, and P. Boag. 1996. Cuckoldry and lack of parentage-
dependent paternal care in yellow warblers: a cost-benefit approach. Anim.
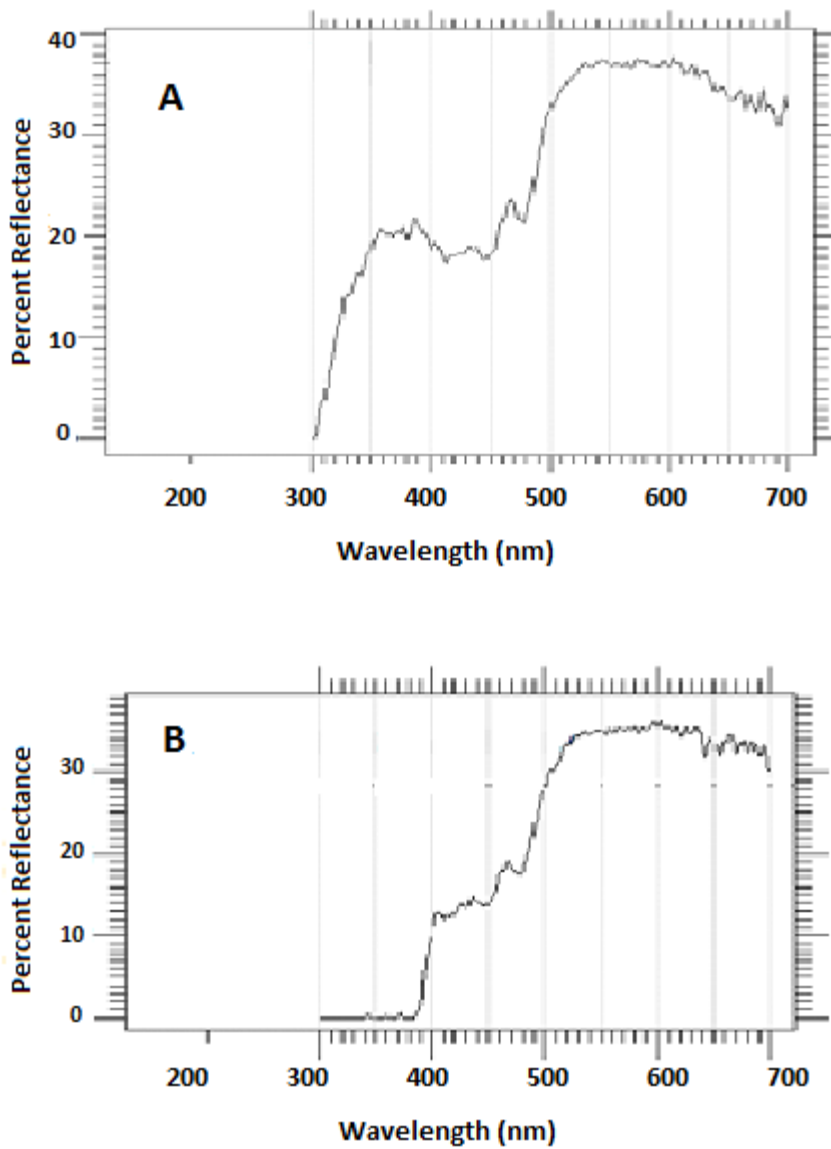Behav. 52: 821-832.

APPENDIX A:

FIGURES

Figure 1. Reflectance spectrum of feathers from the lower breast and belly of a

nestling Eastern Phoebe (A) before treatment and (B) after treatment with UV-blocking

chemicals.

Figure 2. Experimental apparatus used to examine the possible effect of UV

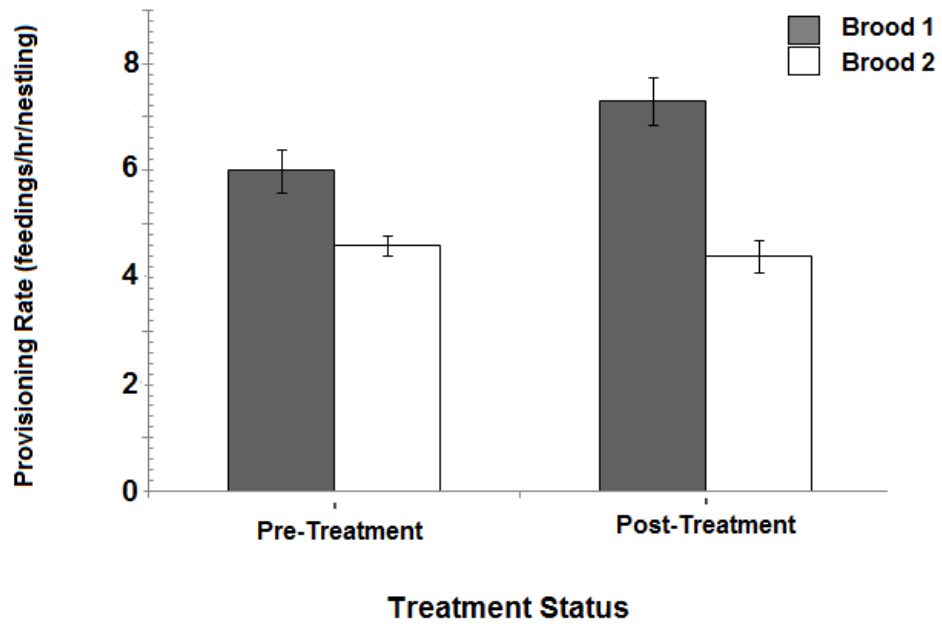reduction of nestling plumage on the provisioning behavior of adult Eastern

Phoebes.

Figure 3. Mean provisioning rates of male and female Eastern Phoebes for control and

UV-blocked nestlings combined in broods one and two. Error bars represent 95% CI.
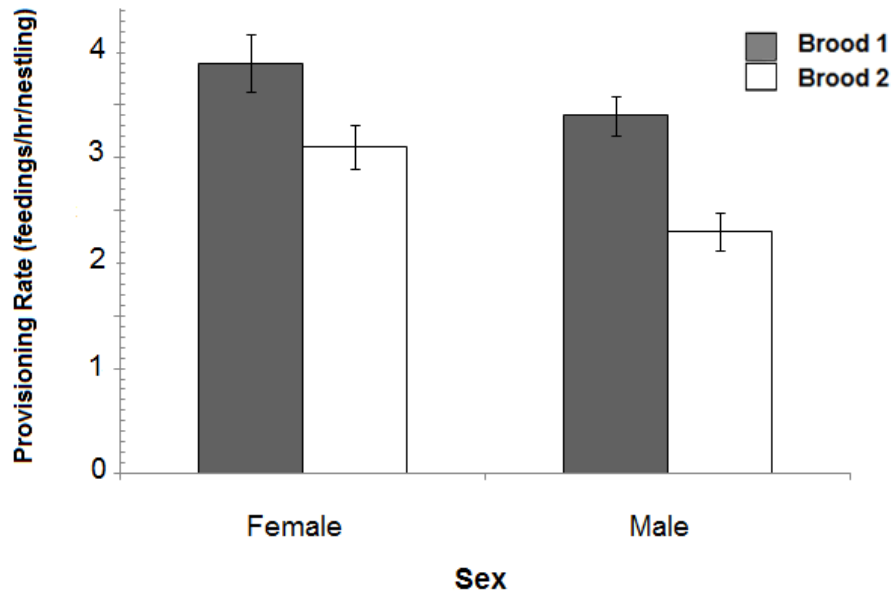
.

Figure 4. Mean provisioning rates of male and female Eastern Phoebes for broods one
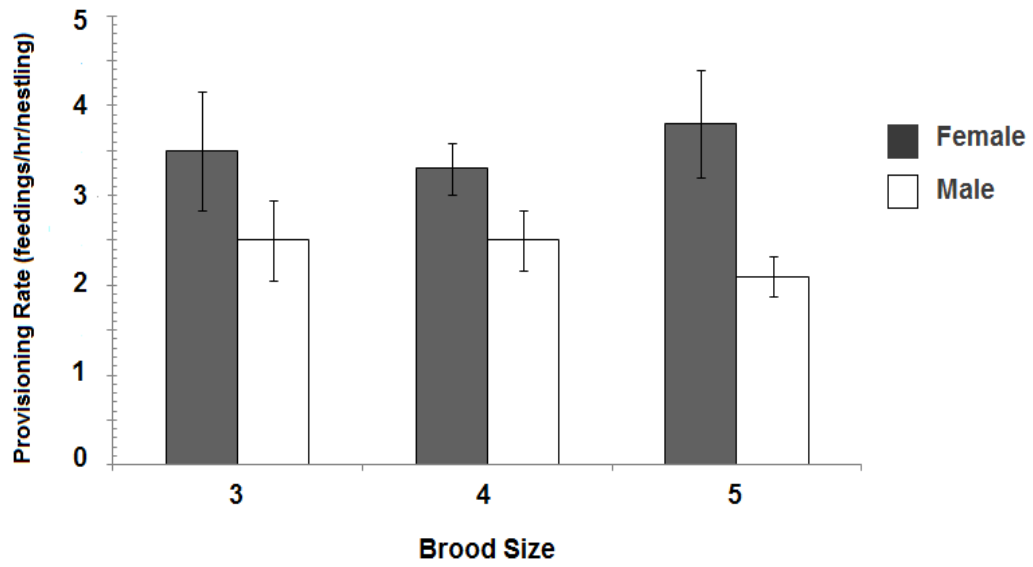
and two. Error bars represent 95% CI.

Figure 5. Mean provisioning rates of male and female Eastern Phoebes for broods of 3, 4, and 5 nestlings. Error bars represent 95% CI.
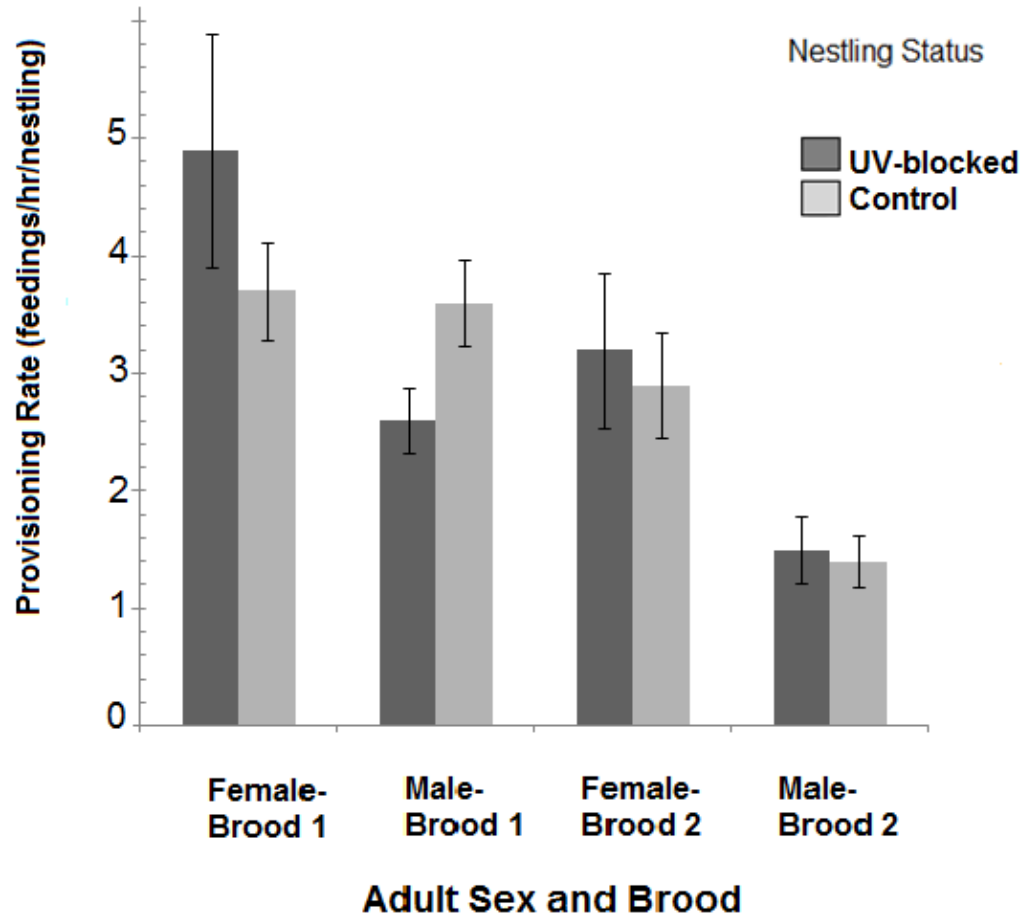
Figure 6. Mean provisioning rates for nestling Eastern Phoebes per hour by parental

males and females for both UV blocked and Control nestlings in broods one and two.

Error bars represent 95% CI.