**Biology Honors Thesis**

Do female Eastern bluebirds trade-off egg size with clutch size?

Caroline Balch

2017

APPROVED BY:

Director of Thesis: S B McRae
Susan B. McRae

Assessor: Chr Bal
Christopher N. Balakrishnan

Director of Undergraduate Studies:
Dr. Jean-Luc Scemama

On this day, 5/3/2017

DO FEMALE EASTERN BLUEBIRDS TRADEOFF EGG SIZE WITH CLUTCH SIZE?
by
Caroline Balch

A Senior Honors Project Presented to the
Honors College
East Carolina University
In Partial Fulfillment of the
Requirements for
Graduation with Honors
by
Caroline Balch
Greenville, NC
May 2017

Approved by:
Susan B. McRae
Department of Biology, College of Arts and Sciences

**Do female Eastern Bluebirds trade-off egg size with clutch size?**

Caroline G. Balch

A thesis submitted to the Department of Biology, East Carolina University, in partial fulfillment of the requirements for Biology Honors Thesis

and presented to the Honors College, East Carolina University in partial fulfillment of the requirements for Graduation with Honors

Advisor: Susan B. McRae, Ph.D
East Carolina University
Department of Biology

May 03rd, 2017

I hereby declare I am the sole author of this thesis. It is the result of my own work and is not the outcome of work done in collaboration, nor has it been submitted elsewhere as coursework for this or another degree.

Signed: Caroline Balch
Caroline G. Balch

Date: 05/03/17

**Do female Eastern Bluebirds trade-off egg size with clutch size?**

Caroline G. Balch

Department of Biology, East Carolina University, Greenville N.C. 27858-4353, U.S.A.

ABSTRACT - Egg size and clutch size are traits that show a fundamental trade-off in life history theory. Producing a larger number of offspring can come at the cost of being able to invest in those offspring. The degree of maternal flexibility in these traits remains poorly understood. As part of a long-term study, clutch data have been collected for the past six years for Eastern Bluebirds *Sialia sialis* breeding at East Carolina University's West Research Campus. In 2014, a spatial cluster of 2-egg clutches coincident with the occurrence of a late prescribed burn was observed. I measured eggs in these clutches from standardized clutch photographs taken in the field. The dimensions of eggs in these small clutches were larger than average, suggesting the mothers may have compensated for number by investing more in each egg. The additional observation that some of the 2014 2-egg clutches had brittle, misshapen eggshells led us to hypothesize that these mothers were resource limited, possibly lacking calcium due to the depletion of arthropod prey caused by the late burn. If calcium limits shell formation, then we might expect a negative relationship between clutch size and eggshell thickness more generally. We tested the prediction that shell thickness should be inversely correlated with clutch size. Based on six years' nest summary data, I examined the relationship between clutch size and egg size, and determined that small clutches occurred near areas of prescribed burn. I measured eggshell thickness of egg specimens laid by different females in clutches of different sizes in different years. I found that egg size was significantly negatively related to clutch size and burn status, providing

evidence of a trade-off between egg size and clutch size. Furthermore, clutch size was significantly negatively related to whether an area was burned during the previous winter. However, no significant relationship was found between eggshell thickness and clutch size. My results show that Eastern Bluebirds have an adaptive response in a life history trait in relation to prescribed burns. Further research should explore the effects of female age and condition in moderating the trade-off between egg size and clutch size.

**Acknowledgments**

I would sincerely like to thank the people and organizations that made this study possible: my fellow lab mates in the McRae and Balakrishnan labs, Dan Newhouse, my parents, Charles and Sally Balch, and the Department of Biology, East Carolina University. I am especially grateful to my project advisor, Dr. Susan B. McRae, for her knowledge, guidance, and time throughout this process. Funding was received from an East Carolina University Undergraduate Research and Creativity Award.

## Table of Contents

## List of Tables

## List of Figures

## Introduction

In any given reproductive attempt, parents must make the fundamental decision of whether to invest in as many offspring as feasible for them to provide care for, or to invest their care more judiciously in fewer offspring (Stearns, 1992). Such a decision involves a trade-off in life history theory. Life history refers to the traits that contribute the offspring production as well as survival (Reznick, Nunney and Tessier, 2010). For egg-bearing vertebrates, life history theory predicts that parents should trade-off egg size with clutch size (Lack, 1954). Breeding females within populations may be expected to vary in their investment decisions according to environmental variables including nutrient limitation and individual condition. When resources are limited, females cannot increase clutch size without limiting investment in each egg (Smith and Fretwell, 1974). While a negative correlation between egg size and clutch size is expected, it is not always observed (Ojanen, Orell, and Vaisanen, 1978).

An ongoing, long-term study of Eastern Bluebirds (*Sialia sialis*) initiated at East Carolina University's West Research Campus (WRC) near Greenville, North Carolina in Spring 2010 provides an excellent opportunity to investigate the trade-off between clutch size and egg size. Eastern Bluebirds at this latitude are multiple brooded. Each year, students monitor ~32 nest boxes through the birds' breeding season from mid-March to mid-August. In 2014, a spatial cluster of 2-egg clutches in the first breeding attempts of the season was observed following a late prescribed burn. This was second attempt at burning more efficaciously a 22-hectare segment of the site in February 2014, after a previous attempt 3 months earlier. The eggs in these clutches appeared visibly larger than the eggs in other clutches and some were misshapen. These observations led to the idea that the birds could

have laid smaller clutches in response to nutrient limitation affecting shell formation brought about by the late prescribed burn. For example, extreme heat or drought resulting from fire or other environmental perturbation could limit access to essential invertebrate prey.

Irregularly scheduled prescribed burns have been conducted at the WRC as part of the restoration of long-leaf pine savannah habitat. Burns, however, work best when performed at a specific time and intensity (Connell, 1978). When performed late, early, or at too great an intensity, an undesired decrease in diversity of nutrients and organisms could result. When resources are limited, females cannot increase clutch size without limiting investment in each egg (Smith and Fretwell, 1974). Reducing clutch size may therefore be a negative effect of such as disturbance on breeding Eastern Bluebirds, but females may compensate by investing more in each egg laid.

Low calcium intake could limit the reproductive output in birds. Most birds can use some stored calcium in their skeleton during egg laying, but the amount withdrawn is usually not enough to form even one egg (Graveland, 1996). As a result, most of the calcium has to be consumed daily during the egg laying period. The calcium can come from several sources including snail shells, other eggshells, and arthropods (Graveland, 1996). The diet of Eastern Bluebirds shows seasonal variation, with primarily arthropods being consumed in spring and early summer, and more berries being consumed in later summer and winter (Pinkowski, 1977). It seems likely that a disturbance in ground arthropod diversity or abundance could negatively affect Eastern Bluebird clutch size early in the breeding season.

Eastern Bluebirds nesting on the WRC are a good system to study this problem for several reasons. Firstly, as cavity nesters, Eastern Bluebirds are severely limited by nest sites, and will nest in the nest boxes provided. During the season, almost all of the boxes are

occupied by Eastern Bluebirds. Carolina Chickadees *Poecile carolinensis* are the only other species to nest in the boxes and they have never produced more than two early season clutches per year over the 2011 to 2016 seasons. Socially monogamous Eastern Bluebird pairs produce up to three broods per season providing a large sample size of clutches. Nest boxes mean that we can capture all breeding attempts by each breeding pair over the season. Natal philopatry has been documented among some breeders over the last 6-years of study. Eastern Bluebirds are relatively short-lived in the South (Patricia Gowaty, pers. comm.; unpublished data). This allows the opportunity to observe birds throughout their entire lives.

The guiding question of the study is whether female Eastern Bluebirds trade-off the number of eggs in their clutches with the size of their eggs, possibly due to calcium or other nutrient limitation resulting from arthropod reduction in areas exposed to late prescribed burns. Additionally, I tested whether eggshell thickness and color intensity differs in 2-egg clutches compared to modal clutch sizes (4- or 5-egg). This was performed with collected unhatched eggshell specimens from eggs laid by different females in clutches of different sizes from different years. I hypothesized that, if shell formation is a limiting factor, shell thickness would be inversely related to clutch size.

## Methods

### Research Site and Data Collection

East Carolina's West Research Campus (35º37'N, 77º28'W) covers over 202 hectares of mixed habitat comprised of old field, scrub, restored wetland, and long-leaf pine savannah. To support breeding Eastern Bluebirds, annually ~32 purpose-built nest boxes are installed in early March when pairs begin competing to claim a nest site. The boxes are set up in relatively consistent positions with adjustments being made only to alleviate problems experienced in previous years such as two boxes within the home range of a single pair (Figure 1). Initially, the boxes are monitored once weekly for nesting activity. Once egg laying begins, boxes are checked at least every three days, but usually more frequently. During checks, all nest changes are documented including: nest height and materials, number of eggs, egg color, number of chicks, their relative sizes and developmental stages. A complete summary nest chart is simultaneously kept to monitor critical dates of laying, hatching and fledging, and vital rates. Monitoring continues throughout the breeding season until mid-August.


Figure 1. Aerial view of ECU's West Research Campus showing locations of 31 Eastern Bluebird nest boxes. Nest boxes in the area with yellow points experienced the late prescribed burn on February 13, 2014. Boxes indicated by blue points were not affected.

Each clutch, upon completion, is photographed in a standardized manner on a black velvet background, including color standards (paint swatches and a set of all colors of plastic leg bands) and a size standard (15 cm ruler). All photos were taken in a shaded area using a (Sony Cyber-shot DSC-HX5V). Each chick was banded with a uniquely numbered aluminum United States Geological Service (USGS) band. Adults were captured using box traps (Stutchbury and Roberson, 1986; Friedman, Brasso, and Condon, 2008) and banded with an aluminum USGS band along with individually unique combination of colored leg bands for visual identification upon re-sighting. Unhatched eggs remaining in the nest at least 2 days after the last chick hatched were collected from nests, inspected for fertility, and the shell

cleaned, dried, and preserved in a light-proof box for future measurement. All of the information recorded was transcribed into an electronic nest file daily.

Since 2011, the WRC has been burned 3 times. Burns were conducted preceding the 2012, 2014, and 2015 breeding seasons. Before the 2012 breeding season, ~49 hectares were burned on February 9, 2012 over the lower eastern section and central portions of the site. Before the 2014 breeding season, there were two separate burns. The first burn occurred on November 21, 2013 over ~98 hectares (the north and east half of the site). The second part of the burn occurred on February 13, 2014 over ~22 hectares of the site (the northern quarter of the site). This second burn is the burn that preceded the cluster of 2-egg clutches that inspired the study (Figure 2). Lastly, the burn before the 2015 breeding season affected ~98 hectares (the entire western half of the site). This burn occurred on November 21, of 2014.

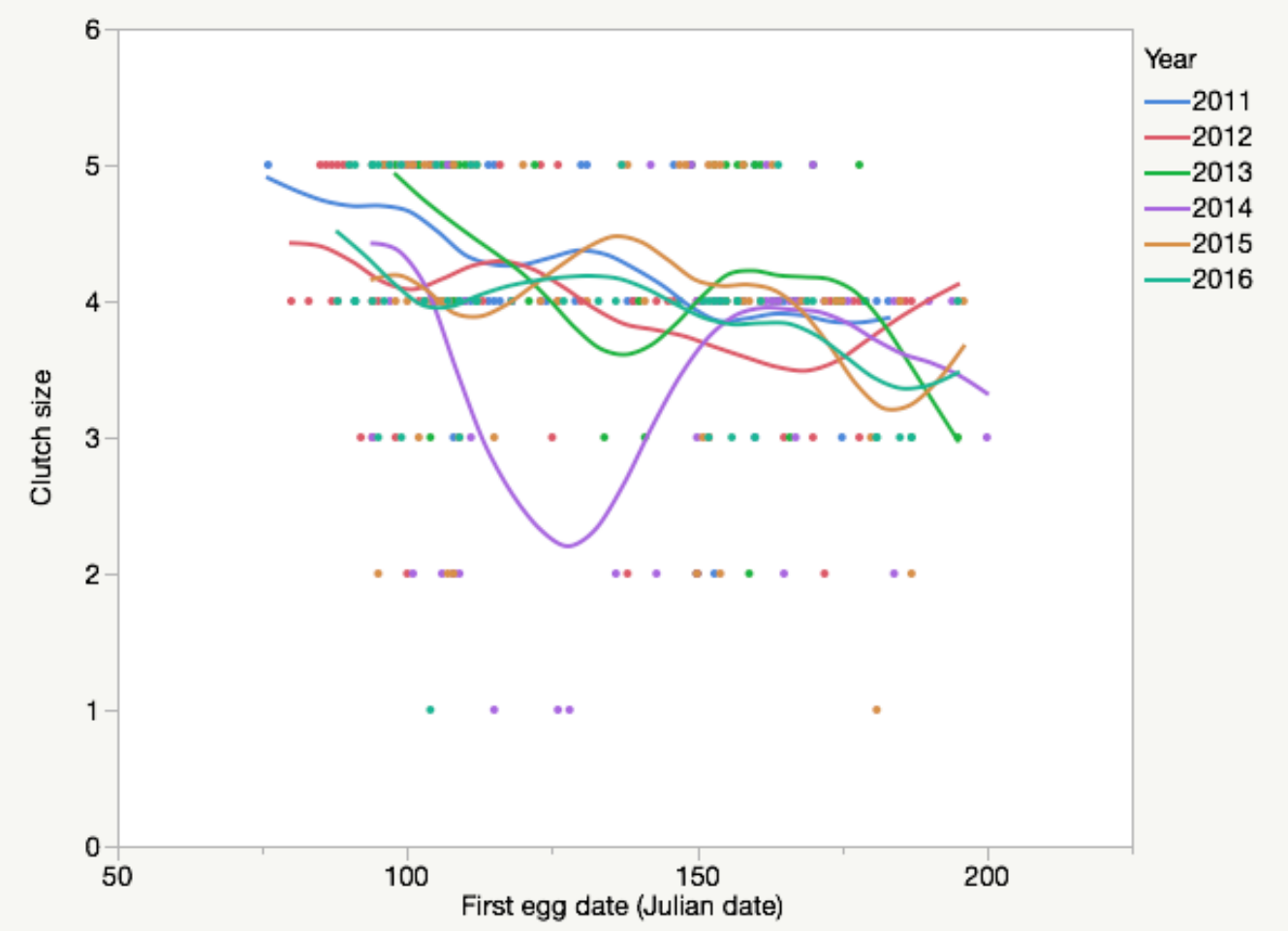


Figure 2: Clutch size in relation to first egg date with each year of the study represented by a different color. The dip in the purple line is representative of the cluster of 2-egg clutches observed early in the 2014 breeding season.

**Summary File**

I compiled and combined breeding data collected from the 2011 through 2016 seasons into a large summary file. Each nest attempt comprised a separate breeding record. The variables of interest to my study included: burn status (whether or not the vicinity of the nest box had been burned in the previous winter), year, box number, breeding attempt number, female and male parent identifications, first egg date (estimated within one day), clutch size, brood size, and the number of chicks fledged.

**Egg Measurements**

Clutch photos taken during the 2014-2016 breeding seasons were uploaded into ImageJ (Version 1.49v; National Institutes of Health, USA) for measurement. Both the length and width of 642 eggs from 60 clutches in 2014, 57 clutches in 2015, and 45 clutches in 2016 were measured in millimeters using the measuring tool in the software and the ruler in the photo for reference. The measurements were taken at the longest and broadest dimensions of each egg. The measures for length and width were then converted to centimeters and combined to find egg volume using the formula Volume = $0.051 * LB^2$, where L is the length and B is breadth or the maximum diameter (Hoyt, 1979).

**Eggshell Thickness Measurement**

Eggshell thickness was determined for 127 unhatched eggs collected during the 2011 through 2016 breeding seasons. Eggs were chosen that represented the range of clutch sizes seen on the site: 2 to 5, and based on whether the female parent at the nest had been captured and banded. No single egg clutches (5 in total) were measured in case they were dumped eggs (i.e. laid by a conspecific brood parasite). Eggshells were excluded if they were moldy. Mean eggshell thickness was determined by breaking off 3 small fragments of eggshell from the equator (broadest circumference) of each egg with tweezers and measuring the thickness using a Mitutoyo 342-361 LCD point micrometer (± 0.001). For consistency, shell thickness was recorded at the point of resistance. Measures of the 3 fragments were then averaged to represent the mean thickness of the shell of that egg. Mean eggshell thickness was then determined for each clutch. In most cases, collected eggs had their contents removed from a

hole in the broadest circumference of the shell. All of the fragments were collected from the perimeter of the opening, to preserve the integrity of the shell for spectral analysis. Since removing the (maternal) membrane from each fragment proved to be difficult and often resulted in breaking the fragment into unusable pieces, it was left on the fragments when they were measured. A single fragment of an eggshell measured both with and without the maternal membrane revealed that the difference was close to the measurement error of the micrometer (0.087 mm with membrane and 0.085 mm without the membrane with an error of ± 0.001 mm).

**Statistical Analysis**

Statistical analyses were performed using the program JMP Pro (Version 12, SAS Inc.). To determine if smaller clutches were laid in burned areas, General Linear Mixed Models (GLMM) were run to examine clutch size against first egg date (expressed as Julian date, where January 1 = 1), year, and burn status of the site. Fixed effects included the burn status of the site (burned or unburned), first egg date, and year. Female parent was included as a random effect to account for multiple clutches by the same female. First egg date was included to account for the expected decline in clutch size that occurs over any given season. Year was included to account for environmental variation that could occur. Next, another GLMM was run to examine the relationship between egg volume and clutch size and to identify any trade-off between the two traits. Fixed effects included clutch size, first egg date, burn status, and year. Once again, female parent was included as a random factor to account for multiple clutches laid by the same female. A GLMM was run to see the relationship between eggshell thickness and clutch size. The fixed effects were first egg date and clutch

size. Female parent was a random effect to account for eggs laid by the same female over all 6 years of the study.

## Results

### Clutch Size and Hatch Success

Between 2011 and 2016 there have been 341 active Eastern Bluebird nests on the West Research Campus ranging from 46 to 65 in a season. The mean clutch size over the 6 years was 4.02 eggs (Range: 1-5; $N = 339$) and the mean percentage of eggs hatched in successful nests was 82% (Range: 20-100%; $N = 281$). Over all 6 years there have been 23, 2-egg clutches, 10 of which were laid in the 2014 breeding season. Of the 2-egg clutches (all 6 years), 12 (17%) failed to hatch. The mean percentage of eggs from 2-egg clutches that hatched in successful nests was 73.1% (Range: 50-100%; $N = 11$).

Table 1: Summary of breeding data collected from 2011 to 2016 including number of nests, number of breeding pairs, mean clutch size, clutch size range, and the mean percentage of hatched eggs.

| Year | Total Number of Nesting Attempts | Number of Breeding Pairs * | Mean Clutch Size ± SD | Clutch Size Range | Mean Percentage of Hatched Eggs |
|---|---|---|---|---|---|
| 2011 | 46 | 26 | 4.20 ± 0.65 | 2-5 | 80.7% |
| 2012 | 61 | 29 | 3.98 ± 0.80 | 2-5 | 83.2% |
| 2013 | 56 | 30 | 4.29 ± 0.80 | 2-5 | 82.1% |
| 2014 | 65 | 32 | 3.72 ± 1.1 | 1-5 | 82.2% |
| 2015 | 64 | 32 | 4.02 ± 0.98 | 1-5 | 81.5% |
| 2016 | 49 | 27 | 3.98 ± 0.80 | 1-5 | 77.6% |

* Identities of one or both members of breeding pairs were not always known for certain.

### Clutch Size-Burn Status Relationship

Clutch size was significantly negatively related to whether an area was burned and first egg date but was not significantly related to year (Table 2). This indicated that environmental factors such as precipitation and temperature that can vary from year to year

did not have a significant effect on clutch size. However, clutches laid in burned areas were smaller than those laid in unburned areas.

Table 2: General Linear Mixed Model estimates, with standard errors, 95% confidence intervals, and *p* values of variables explaining clutch size in Eastern Bluebirds breeding on the WRC between 2011-2016. Maternal identification was included as a random factor. Statistically significant variables are bolded.

| Variables | Parameter Estimate | Std. error | CI (95%) | | *p* |
|---|---|---|---|---|---|
| **Burn Status** | **-0.17178** | **0.0553643** | **-0.280722** | **-0.062838** | **0.0021*** |
| **First Egg Date** | **-0.006452** | **0.0013728** | **-0.009156** | **-0.003749** | **<.0001*** |
| Year | -0.024764 | 0.0335183 | -0.090874 | 0.0413458 | 0.4609 |

**Egg Volume-Clutch Size Relationship**

Egg volume was significantly positively related to whether an area was burned (Table 3). From 2014 to 2016, the females in burned areas laid larger eggs than those in unburned areas indicating an environmental influence on egg size.

Table 3: General Linear Mixed Model estimate with standard error, 95% confidence interval, and *p* value explaining the relationship between egg volume and burn status in Eastern Bluebirds breeding on the WRC between 2014-2016. Maternal identification was included as a random factor. Statistically significant variable is bolded.

| Variables | Parameter Estimate | Std. error | CI (95%) | | *p* |
|---|---|---|---|---|---|
| **Burn Status** | **0.2233406** | **0.0339673** | **0.1563132** | **0.290368** | **<.0001*** |

Considering clutches from the 2014, 2015 and 2016 breeding seasons, egg volume was significantly inversely related to clutch size (Table 4). As clutch size increased over these years, egg volume decreased (Figure 3). This represents a clear trade-off in egg size and clutch size. Thus, there is a trade-off in egg size and clutch size that is influenced by the environment (burn status).

Table 4: General Linear Mixed Model estimate with standard error, 95% confidence interval, and *p* value explaining the relationship between egg volume and clutch size in Eastern Bluebirds breeding on the WRC between 2011-2016. Maternal identification was included as a random factor. Statistically significant variable is bolded.

| Variables | Parameter Estimate | Std. error | CI (95%) | | *p* |
|---|---|---|---|---|---|
| **Clutch Size** | **-0.109944** | **0.0301095** | **-0.169096** | **-0.050791** | **0.0003** |

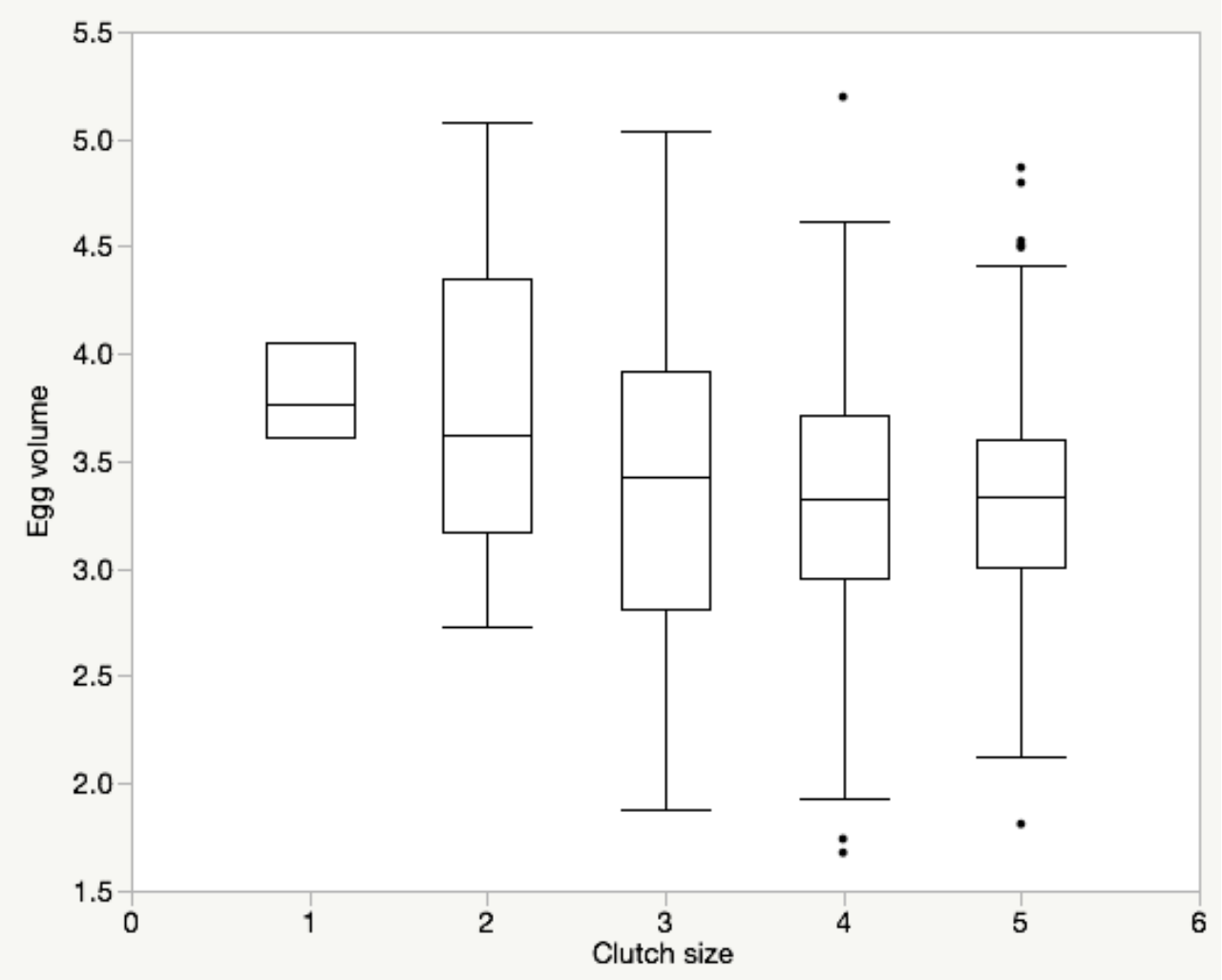


Figure 3: Mean egg volume was significantly negatively related to clutch size. Egg volumes were calculated from egg size measures (length and breadth) from standardized clutch photographs from 2014 (*N* = 60 clutches), 2015 (*N* =57 clutches), and 2016 (*N* = 45 clutches). Box plots indicate median, 25% and 75% confidence intervals, whiskers are 5$^{th}$ and 95$^{th}$ percentiles, and points represent outliers.

**Eggshell Thickness-Clutch Size Relationship**

There was no significant relationship between mean eggshell thickness and clutch size (Table 5). The 127 eggs measured showed no clear trend with thickness measures being consistent over 2 to 5-egg clutches (Figure 4). While I found no general overall trends in eggshell thickness in relation to clutch size, it was interesting to find that the thickest eggshell measured (0.0103 mm) was from a 2-egg clutch from the 2014 breeding season and the thinnest egg measured (0.055 mm) was from a 4-egg clutch in 2013.

Table 5: General Linear Mixed Model estimate, with standard error, 95% confidence interval, and *p* value explaining the relationship between eggshell thickness and clutch size in Eastern Bluebirds on the WRC between 2011-2016. Maternal identification was included as a random factor

| Variable | Parameter Estimate | Std. error | CI (95%) | | *p* |
|---|---|---|---|---|---|
| Clutch Size | 0.000709 | 0.0011452 | -0.001586 | 0.0030039 | 0.5384 |

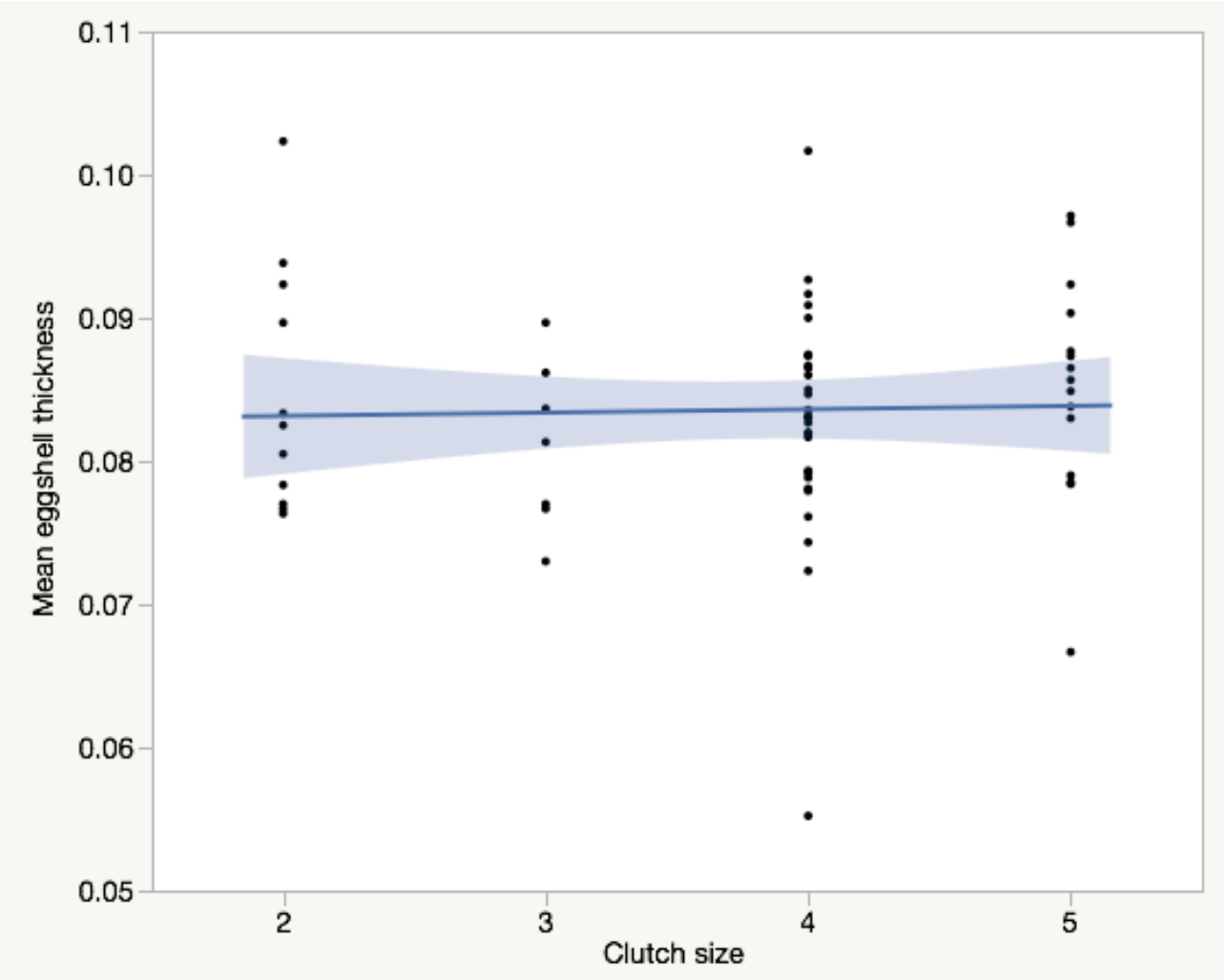


Figure 4: Mean eggshell thickness was not significantly related to clutch size. Means reported are based on clutch means representing 127 collected unhatched eggs from 62 clutches from all years. Linear regression line is shown with blue shaded area representing the standard error.

There was no significant relationship between eggshell thickness and burn status (Table 6). The model was run first generally distinguishing burned and unburned areas. It was then rerun differentiating only nests in the area that experienced a late burn from all the others. This yielded the strongest results, though non-significant. Distinguishing three categories with areas that were burned in early winter, versus burned late, or unburned was also not significant.

Table 6: General Linear Mixed Model estimate, with standard error, 95% confidence interval, and *p* value explaining the relationship between mean eggshell thickness in Eastern Bluebirds and whether an area was burned the previous winter or unburned on the WRC between 2011-2016.

| Variable | Parameter Estimate | Std. error | CI (95%) | | *p* |
|---|---|---|---|---|---|
| Burn Status | 0.0005742 | 0.0011382 | -0.001707 | 0.0028557 | 0.6159 |

## Discussion

Mean clutch size decreased in response to prescribed burns over all years but especially in response to the late burn in 2014. Also egg size was significantly negatively related to clutch size as well as whether or not an area was burned. This indicates evidence of a trade-off between egg size and clutch size that was influenced by the environmental condition of the burn. Lastly, there was no relationship between eggshell thickness and clutch size. This leads me to reject the hypothesis that females trade-off eggshell thickness with clutch size.

Egg production is costly and females are often limited by energy resources during egg formation (Bernardo, 1996). Because resources are limited, female birds cannot indiscriminately increase clutch size without a cost to the investment in each egg (Smith and Fretwell, 1974). The decrease of mean clutch size seen in response to prescribed burns could be a result of an added resource limitation. Calcium depletion, for example, may occur in addition to already limited resources as a result of prescribed burn leading to an inability to adequately invest in an average clutch size. In the case of late burns this is further exacerbated by the fact there is little time for resources to build up before breeding starts.

Since increasing egg size and clutch size both require an increase in nutrient acquisition and rely on a female's ability to locate resources, it may not be possible for most birds to produce large eggs in large clutches (Perrins, 1996). This can be especially difficult if resources are already limited by an environmental disturbance like a prescribed burn. This study revealed a trade-off in egg size and clutch size which was influenced by the burn status of the site. It has been seen that heavier eggs have higher hatching success and fledging success (Perrins, 1996). Females that possibly did not have adequate access to resources

benefited more by investing in smaller clutches of larger offspring in an attempt to maximize reproductive success.

The mean eggshell thicknesses measured in this study were comparable to means (±SD) of other North American passerines measured in a previous study (Eastern Phoebe *Sayornis phoebe*: 0.067 ± 0.003 mm; Eastern Kingbird *Tyrannus tyrannus*: 0.097 ± 0.009 mm; Great-crested Flycatcher *Myiarchus crinitus*: 0.109 ± 0.006 mm; Grey Catbird *Dumetella carolinensis*: 0.100 ± 0.013 mm; Northern Mockingbird *Mimus polyglottis*: 0.100 ± 0.011 mm) (Spaw and Rohwer, 1987). Although there was a trade-off seen in egg size and clutch size, this was not seen in eggshell thickness, at least with the micrometer used (scanning electron microscopy may be able to discriminate a more subtle difference in thickness.) The reasoning behind this could be that Eastern Bluebirds have a set amount of calcium devoted to egg formation. Decreasing clutch size does does not result in thicker eggs but it does result in larger eggs. Perhaps the excess calcium is instead used to increase egg size. Eggshell thickness could also be limited by the amount of time the egg takes to form. During laying, Eastern Bluebirds will lay an egg each morning (each egg takes about 24 hours to form) (Sturkie, 1986). This is consistent between individuals and could explain why average thicknesses were relatively consistent among clutches.

These results contribute to understanding how Eastern Bluebirds respond to prescribed burns. While the Eastern Bluebirds on the WRC decreased their clutch sizes in response to burns, they still experienced some reproductive success. However, the increase in two egg clutches following the February burn of 2014 indicates a more negative response. Even though brood reduction is observed in early broods at this site, the number of fledglings from successful first broods in other years was rarely fewer than 3. These results emphasize

the need for managers to evaluate the effects on plant and animal reproduction of differently timed burns in order to make more informed decisions concerning the optimal time to perform prescribed burns for management and restoration.

This study did not specifically address the hypothesis that the late, 2014 burn imposed extreme calcium limitation through the depletion of arthropod prey, resulting in females investing in small (2-egg clutches of thin-shelled eggs). While no evidence for a trade-off between eggshell thickness and clutch size was found in the study, this does not exclude the possibility that the eggs produced soon after the late burn in 2014 experienced a calcium deficiency or some other nutrient limitation. In order to determine whether calcium is impacting clutch size or misshapen eggs, supplemental calcium could be provided to the birds in areas affected by burns. Previous supplementation experiments have utilized various materials including snail shells, chicken eggshells, millipedes, and woodlice in both natural environments and aviaries (Bures and Weidinger, 2003).

This study also did not address every variable that has the ability to influence clutch size and egg size in breeding birds. Individuals often vary in their ability to acquire resources based on the environment but also because of variation in their individual foraging ability (Cam, et al., 2002; Jarvinen, 1995). This can lead to differential resource allocation to offspring. A higher quality female could be able to invest more in her offspring without harming her chances of survival (Christians, 2002). A study by Pellerin et al. (2016) found that the expected life history trade-off in egg mass and clutch size of Tree Swallows *Tachycineta bicolor* was reversed in the heaviest females from a population. Alternatively, the trade-off was present in average masses individuals and even stronger in the lightest individuals from the population. It would be interesting to see whether or not this variability

is present in the Eastern Bluebird population at the WRC. In most years, the majority of breeders in the long-term study were captured, banded and morphometrics taken. Since the weight and wing lengths of many banded adults have already been measured, examining how body condition of mothers affects the trade-off between egg size and clutch size will be a natural next step for the study.

In addition to female condition, several other traits could affect the trade-off including female age and temperature. It is expected that older, more experienced females should know more about the locations for optimal foraging opportunities. Pellerin et al. (2016) found that older females laid larger clutches. Age could also be taken into account on the WRC as some adults' ages are known (natally philopatric recruits from previous years), or can be estimated from attempts over several years. These future research opportunities can provide a more complete understanding of the trade-off between egg size and clutch size seen in the WRC's population of Eastern Bluebirds.

## Literature Cited


Bernardo, J. (1996). The particular maternal effect of propagule size, especially egg size: patterns, models, quality of evidence and interpretations. *American Zoologist*, 36, 216-236.

Bures, S. and Weidinger, K. (2003) Sources and timing of calcium intake during reproduction in flycatchers. *Behavioral Ecology*, 137, 634-647.

Cam, E., Link, W.A., Cooch, E.G., Monnat, J.Y. and Danchin, E. (2002). Individual covariation in life history traits: seeing the trees despite the forest. *The American Naturalist*, 159, 96-105.

Christians, J.K. (2002). Avian egg size: variation within species and inflexibility within individuals. *Biological Reviews*, 77, 1-26.

Connell, J.H. (1978). Diversity in tropical rain forests and coral reefs. *Science*, 199, 1302-1320.

Friedman, S.L., Brasso, R.L., and Condon, A.M. (2007). An improved, simple nest-box trap. *Journal of Field Ornithology,* 79, 99-101.

Graveland, J. (1996). Avian eggshell formation in calcium rich and calcium-rich and calcium-poor habitats: importance of snail shells and anthropogenic calcium sources. *Canadian Journal of Zoology*, 74, 1035-1044.

Hoyt, D.F. (1979). Practical methods of estimating volume and fresh weight of bird eggs. *The Auk*. 96, 73-77.

Jarvinen, A. (1995). Correlation between egg size and clutch size in the Pied Flycatcher *Ficedula hypoleuca* in cold and warm summers. *Ibis*, 138, 620-623.

Lack, D. (1954). *The Natural Regulation of Animal Numbers*. Oxford: Clarendon Press.

Ojanen, M., Orell, M., and Vaisanen, R.A. (1978). Egg and clutch sizes in four passerine species in northern Finland. *Ornis Fennica*, 55, 60-68.

Pellerin, S., Paquette, S.R., Pelletier, F., Garant, D., and Bélisle, M. (2016). The trade-off between clutch size and egg mass in Tree Swallows *Tachycineta bicolor* is modulated by female body mass. *Journal of Avian Biology*, 47, 500-507.

Perrins, C.M. (1996). Eggs, egg formation, and the timing of breeding. *Ibis,* 138, 2-15.

Pinkowski, B.C. (1977). Foraging behavior of the Eastern Bluebird. *The Wilson Bulletin*, 89, 404-414.

Reznick, D., Nunney, L., and Tessier, A. (2000). Big houses, big cars, superfleas and the costs of reproduction. *Trends in Ecology and Evolution*, 15, 421-425

Smith, C.C. and Fretwell, S.D. (1974). The optimal balance between size and number of offspring. *The American Naturalist*, 108, 499-506.

Spaw, C.D. and Rohwer, S. (1987). A comparative study of eggshell thickness in cowbirds and other passerines. *The Condor,* 89, 307-318.

Stearns, S.C. (1992). *The Evolution of Life Histories*. New York: Oxford University Press.

Sturkie, P.D. (1986). *Avian Physiology.* Berlin: Springer.

Stutchbury, B.J. and Robertson, R.J. (1986). A simple trap for catching birds in nest boxes. *Journal of Field Ornithology,* 57(1), 64-65.

East Carolina University

**Animal Care and Use Commitee**
212 Ed Warren Life Sciences Building
East Carolina University
Greenville, NC 27834

**252-744-2436** office
**252-744-2355** fax

November 20, 2013

Susan McRae, Ph.D.
Department of Biology
Howell Science Complex
East Carolina University

Dear Dr. McRae:

Your Animal Use Protocol entitled, "Reproduction, Behavior, and Population Dynamics of Eastern Bluebirds" (AUP #D257a) was reviewed by this institution's Animal Care and Use Committee on 11/20/13. The following action was taken by the Committee:

"Approved as submitted"

A copy is enclosed for your laboratory files. Please be reminded that all animal procedures must be conducted as described in the approved Animal Use Protocol. Modifications of these procedures cannot be performed without prior approval of the ACUC. The Animal Welfare Act and Public Health Service Guidelines require the ACUC to suspend activities not in accordance with approved procedures and report such activities to the responsible University Official (Vice Chancellor for Health Sciences or Vice Chancellor for Academic Affairs) and appropriate federal Agencies.

Sincerely yours,

Dorcas O'Rourke

Dorcas O'Rourke, DVM
University Veterinarian

DO/jd

Enclosure