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Vocal responses of adult Eastern Bluebirds (*Sialia sialis*) to potential nest predators and the behavioral responses of nestlings

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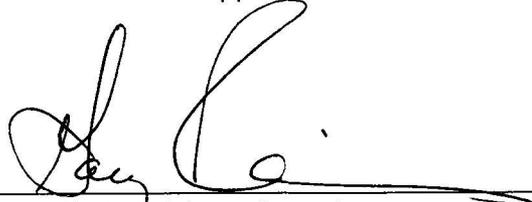
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Vocal responses of adult Eastern Bluebirds (*Sialia sialis*) to potential nest predators and
the behavioral responses of nestlings

By

Erin E. Grabarczyk

Thesis Approved:



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Vocal responses of adult Eastern Bluebirds (*Sialia sialis*) to potential nest predators
and the behavioral responses of nestlings

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Bachelor of Arts
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Submitted to the Faculty of the Graduate School of
Eastern Kentucky University
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DEDICATION

This thesis is dedicated to my family for encouraging me to do what I love,

To Jason, for his persistence and guidance,

And

To my mentors, Drs. Dave and Jill Russell for their continued inspiration and friendship.

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I would like to thank my advisor, Dr. Gary Ritchison, for his immeasurable patience, good advice, and ever-open office door. I would also like to thank my committee members, Dr. Charles Elliott and Dr. David Brown, for their comments, questions, and for challenging me as a student. Lastly, I would like to thank Sigma Xi and the Kentucky Society of Natural History for providing financial support.

ABSTRACT

The alarm calls of some birds are functionally referential and may provide nestlings with information about the threat posed by potential predators. However, few investigators have examined the responses of nestlings in cavity nests to the anti-predator vocalizations of adults. Therefore, the objectives of my study of cavity-nesting Eastern Bluebirds (*Sialia sialis*) were to examine (1) the vocal responses of adult Eastern Bluebirds to different predators, and (2) the behavioral responses of nestlings to those adult vocalizations. My study was conducted from April – July 2013 at the Blue Grass Army Depot in Madison County, Kentucky. Pairs of Eastern Bluebirds nesting in nest boxes were exposed to four potential nest predators, including taxidermy mounts of a raccoon (*Procyon lotor*) and an eastern chipmunk (*Tamias striatus*), a study skin of an American Kestrel (*Falco sparverius*), and a rubber model of a black rat snake (*Pantherophis obsoletus*). My control was a study skin of a Mourning Dove (*Zenaida macroura*). To assess responses during 3-min trials, predators or the control were placed adjacent to or on nest boxes with 12-19-day-old nestlings. During trials, adult vocalizations were recorded and the behavior of nestlings was simultaneously recorded with a camcorder. I conducted 48 trials at 27 nest boxes. Adult bluebirds did not respond vocally during 10 trials (20.8%), but did call during all 12 trials with the raccoon. In addition, adult bluebirds uttered alarm calls and chatter calls that were significantly longer in duration at significantly higher rates in response to the raccoon. Adult bluebirds uttered significantly more chatter calls and alarm calls during trials when

nestlings responded (23 of 39 trials [59%], excluding control trials) by crouching (21 trials), climbing the walls of the nest box (one trial), or fledging (one trial). Crouching may reduce the risk of predation by predators too large to enter the nest cavity, but potentially able to reach into a cavity. Remaining in a nest cavity is likely advantageous because premature fledging by young unable to fly or fly very well when a predator is nearby would increase the risk of mortality. My results indicate that adult Eastern Bluebirds do not produce predator-specific, functionally referential alarm vocalizations, but, by varying call characteristics and call rates, appear to provide nestlings with information about potential predators that generates appropriate anti-predator responses.

TABLE OF CONTENTS

CHAPTER	PAGE
I. INTRODUCTION.....	1
II. METHODS.....	4
Predator Presentations.....	5
Acoustic Analysis.....	7
Statistical Analysis.....	8
III. RESULTS.....	10
Adult vocal responses to predator and control models.....	10
Nestling responses to adult vocalizations.....	12
IV. DISCUSSION.....	14
Literature Cited.....	21
Appendix.....	25

LIST OF FIGURES

FIGURE	PAGE
1. Sonograms of vocalizations given by adult Eastern Bluebirds (<i>Sialia sialis</i>) in response to a mounted raccoon.....	26
2. Mean rate of calling (\pm SE) of alarm call vocalizations given by adult Eastern Bluebirds during predator presentations.....	27
3. Mean duration (\pm SE) of alarm calls of adult Eastern Bluebirds during 3-min predator-presentation trials.....	28
4. Mean (\pm SE) (a) number of notes per call and (b) mean duration of chatter calls of adult Eastern Bluebirds given in response to different potential predators near their nests.....	29
5. Image of fifteen-day-old Eastern Bluebird responding to adult alarm call vocalizations.....	30
6. Image of an American Kestrel predating fifteen-day-old nestling Eastern Bluebirds.....	32

CHAPTER I

INTRODUCTION

In response to the presence of potential nest predators, adult birds with nestlings typically give alarm calls. In open-cup nesting species, nestlings often respond to alarm calls by becoming quiet and crouching down in nests, thereby reducing the likelihood of detection (e.g., Yasukawa 1989, Gill and Sealy 2003, Platzen and Magrath 2004, Anderson et al. 2010). However, in response to adult alarm calls, older nestlings may also be able to obtain information about predators based on visual and auditory cues and vary their responses based on the perceived threat. For example, nestling Moustached Warblers (*Acrocephalus melanopogon*) respond to adult alarm calls by crouching in nests to avoid detection when threatened by an aerial predator, but, if old enough, leave nests in response to the presence of a terrestrial predator (Kleindorfer et al. 1996). Such responses are likely adaptive because aerial predators may be more of a threat to mobile fledglings whereas terrestrial predators approaching nests may be less likely to locate young that leave nests (Kleindorfer et al. 1996), e.g., by hiding in nearby vegetation.

The alarm calls of some birds are functionally referential and may encode information either about predator size (Templeton et al. 2005, Courter and Ritchison 2010) or about different predatory threats (Fasanella and Fernandez 2009, Suzuki 2011). Parental alarm calls that provide nestlings with information about the type of predator

approaching a nest could induce responses that increase their likelihood of surviving. For example, terrestrial predators represent the greatest threat to ground-nesting White-browed Scrubwrens (*Sericornis frontalis*) and, in response to parental alarm calls indicating the approach of a terrestrial predator, nestlings cease calling, reducing the likelihood of detection (Platzen and Magrath 2005). For species with domed nests, like White-browed Scrubwrens, and those that nest in cavities where nestlings may not perceive visual and auditory cues from approaching predators, alarm calls that provide information about predator type and degree of threat may be particularly important for nestling survival.

For some cavity-nesting species, the risk of predation for nestlings may be related to the ability of potential predators to enter nest cavities. However, few investigators have examined the possibility that cavity-nesting species use functionally referential alarm calls to elicit appropriate anti-predator behaviors by nestlings. Suzuki (2011) found that adult Great Tits (*Parus major*) produced different alarm calls in response to predators that could (Japanese rat snake, *Elaphe climacophora*) and could not (Jungle Crow, *Corvus macrorhynchos*) enter nest cavities. In response to calls given by adults in response to the crow, nestlings crouched down inside nest boxes; when responding to calls given by adults in response to the snake, nestlings jumped from nest boxes. These responses by nestlings would likely minimize predation risk because Jungle Crows extend their beaks into nest entrances when attempting to prey on nestlings, whereas snakes enter nest cavities to prey on nestlings (Suzuki 2011). Additional study

is needed to determine if other cavity-nesting species use functionally referential alarm calls, and the context in which the calls are elicited.

Eastern Bluebirds (*Sialia sialis*) are secondary cavity-nesters that breed throughout eastern North America (Gowaty and Plissner 1998). Adult bluebirds are known to utter at least two types of predator alarm calls, alarm calls (a complex medley of varying frequencies; Pinkowski 1971) and chatter calls (Gowaty and Plissner 1998). Gowaty and Plissner (1998) suggested that chatter calls were given in response to ground predators, but the contexts in which these alarm calls are used and if adults might vary the characteristics of these calls in response to different predators have not previously been examined.

I examined the possibility that, in response to different predatory cues, adult Eastern Bluebirds communicate with their nestlings using functionally referential alarm call vocalizations, and nestlings then respond in an adaptive and appropriate manner. I tested this possibility by exposing nesting pairs of Eastern Bluebirds to four different predator models and a control. As found by Suzuki (2011) for Great Tits, young bluebirds near fledging age might benefit from leaving nest boxes when a small predator that could enter boxes approaches, but by crouching down when large predators unable to enter boxes approach.

CHAPTER II

METHODS

Field work was conducted at the Blue Grass Army Depot in Madison County, Kentucky (37°41'58''N, 84°16'20''W). Prior to my study (December 2012 – January 2013), bluebird nest boxes (N = 64) were placed in open areas throughout the study area. Boxes were mounted on poles (EMT conduit) about 1.5 m above ground. Beginning on 1 April, nest boxes were checked at least twice weekly to determine if they were being used by bluebirds and, if so, to monitor nesting status. Once a nest was completed, boxes of focal pairs were checked at least every two days to determine clutch initiation dates. Because the incubation period is typically about 14 days (Gowaty and Plissner 1998), nests were again checked every other day after 10 days of incubation to determine hatch date.

For my experiments, I used a study skin of an American Kestrel (*Falco sparverius*) and a full-body taxidermy mount of a raccoon (*Procyon lotor*), both potential predators that would be too large to enter nest boxes, but able to reach in through cavity entrances with forelimbs (raccoon) or hindlimbs (American Kestrel). I also used a rubber model of a black rat snake (*Pantherophis obsoletus*) and a taxidermy mount of an eastern chipmunk (*Tamias striatus*), two potential predators small enough to enter boxes and prey on nestlings. My control was a study skin of a Mourning Dove (*Zenaida*

macroura). Each pair of bluebirds had the potential of being exposed to each predator and the control once during the 2013 breeding season.

Predator Presentations

Experiments began once nestlings reached 12 days old. At that age, nestling bluebirds are completely feathered (Gowaty and Plissner 1998), and may fledge prematurely if disturbed (G. Ritchison, pers. observ.). By day 14 post-hatching, young bluebirds are capable of weak, short-distance flight (Gowaty and Plissner 1998). Successive experiments at each nest were at least 48 hours apart. The order of predator model used at each nest was determined randomly.

The behavior of nestlings was recorded during experiments using a digital camcorder (HDR-XR100, Sony, Tokyo, Japan). To videotape nestlings inside nest boxes, plastic containers (60 cm x 30 cm x 30 cm) were attached to the back of nest boxes at least three days before experiments began. The backs of nest boxes were removed and replaced with wire mesh (1.3-cm x 1.3-cm mesh) to keep nestlings in the nest box and allow video-recording from behind the box. Prior to attaching the container to a nest box, a rectangular opening was cut slightly smaller than the back of nest boxes at the front of the plastic container, aligned with the back of the nest box, and secured with wood screws. Once the container was in place, a 'decoy' camcorder (small cardboard box similar in size and color to the camcorder I used) was placed at the back of the

plastic container so adults and nestlings could habituate to its presence. Flagging was placed bi-directionally every 2 m for 16 m radiating from the nest box to allow a better estimate when at least one adult was located within 10 m of a predator model or the control, signifying the start of a trial (described below).

Prior to each experiment, the decoy camcorder was removed from the plastic container and replaced with a camcorder that focused on the nestlings and recording began. After a minimum 30 min of pre-recording, predator models or the control were exposed when the focal pair was not present at the nest (and at least 30 m from the nest box). During experiments, the American Kestrel, eastern chipmunk, control (Mourning Dove), and snake model were attached to a 1.5-m-high adjustable pole located 1.5 m in front of nest boxes, whereas the raccoon was placed on the ground 1 m in front of nest boxes. To synchronize the video and audio recordings after placement of the predator or control, I waved my arm about 30 – 40 cm in front of the nest box so it would be seen on the camcorder located in the plastic container behind the nest box (but not by the nestlings) and simultaneously began audio-recording with the recorder and microphone (described below). I also noted the time the camcorder was turned on, when the predator was exposed, and the start and end time of the trials. Later, when videos and audio recordings were analyzed in the lab, this synchronization of the video and audio recordings allowed me to accurately determine the timing and characteristics of adult vocalizations and any corresponding responses by nestlings.

Experiments began once at least one adult bluebird moved within 10 m of the predator or control and were in a position where it could clearly see the predator. I noted the presence or absence of both the adult male and female throughout the trial. For the next 3 min, I recorded all vocalizations uttered by the adult bluebirds. Recordings were made with either a digital recorder (PMD661; Marantz, Kanagawa, Japan) or an analog cassette recorder (TCM-400DV; Sony, Tokyo, Japan) with a shotgun (directional) microphone (ME66; Sennheiser, Wedemark, Germany). As noted previously, the behavior of nestlings was recorded with a camcorder during experiments. After each 3-min experiment, I removed the predator and camcorder from the plastic container, and replaced it with the decoy camcorder (unless it was the last trial for that brood).

Acoustic Analysis

Audio recordings of adult Eastern Bluebirds were analyzed using Raven software (Cornell Lab of Ornithology, Ithaca, NY). For each 3-min experiment period, I determined the number of each type of vocalization uttered by adults, including loud songs, alarm calls, tu-a-wee calls, and chatter calls (Figure 1^{*}). In addition, I determined the characteristics of each vocalization, including frequency range, duration, and, for calls consisting of a series of repetitive notes (chatter calls), the number of notes per call. For

^{*} Refer to Appendix for all figures.

trials with both adults present I was unable to determine the sex of the adult uttering calls. Mean inter-note duration \pm SE was 0.05 ± 0.02 seconds (based on two randomly selected trials with each predator model, totaling 318 calls, of 14 different adult bluebirds). To standardize chatter calls, if inter-note duration was > 0.2 seconds, I considered it a different call. During experiments, no bluebirds uttered either soft calls or turring calls.

Video recordings of nestling Eastern Bluebirds were subsequently viewed. After synchronizing the audio and video recordings, I noted if the nestlings responded vocally (either by becoming quiet or beginning to call) or behaviorally (crouch, fledge, or no response) to adult vocalizations during each 3-min trial. Crouching was defined as a shift in position or lowering of the body into the nest (Kleindorfer et al. 1996).

Statistical Analysis

I used repeated measures analysis of variance to test the differences in call and song use, and vocalization characteristics (frequency range, duration, and number of notes per call). For significant results, I used a post-hoc Tukey's test to determine if call use differed based on the predator model presented. Further analysis was used to determine if nestlings responded significantly more when adults elicited alarm call vocalizations during a given trial. Statistical significance was accepted at $P < 0.05$. All

analyses were conducted using the Statistical Analysis System (SAS Institute 2006).

Values are presented as means \pm SE.

CHAPTER III

RESULTS

From 12 May to 29 July 2013, I conducted 48 trials at 27 nest boxes, with an average of 1.8 trials per box (range = 1 – 3). I conducted an average of 9.6 trials (range = 5 – 12) with each predator (N = 4) and control (N = 1). Mean brood size at nests when trials were conducted was 3.6 ± 0.4 (range = 2 – 5). The mean age of nestlings when trials were conducted was 15.2 ± 0.2 days post-hatching (range = 12 – 19 days post-hatching), with no difference in mean age of nestlings for trials conducted with different predators and the control ($F_{4,24} = 0.9$, $P = 0.48$). Both adults responded during 40 trials and one adult during eight trials. For trials where only one adult responded, only females responded during six trials and only males during two trials.

Adult vocal responses to predator and control models

Adult bluebirds did not respond vocally during 10 of 48 trials (20.8%), including during four of nine trials (44.4%) with the Mourning Dove, one of five trials (20%) with the Chipmunk, two of 12 trials (16.7%) with the snake, and three of 10 (30%) trials with the American Kestrel. Adults vocalized during all 12 trials with the raccoon.

Overall, for all 48 trials, bluebirds gave an average of 0.3 ± 0.1 tu-a-wee calls per min, 1.2 ± 0.4 loud songs per min, 1.2 ± 0.4 alarm calls per min, and 12.8 ± 2.5 chatter

calls per min. The rate at which loud calls ($F_{4,16} = 1.3$, $P = 0.32$) and tu-a-wee calls ($F_{4,16} = 0.9$, $P = 0.93$) were given by bluebirds did not vary with predator/control type. However, call rates for alarm calls ($F_{4,16} = 6.0$, $P = 0.004$) and chatter calls ($F_{4,16} = 12.8$, $P < 0.0001$) did vary with predator/control type (Figure 2). For both alarm calls and chatter calls, adult bluebirds called at the highest rates in response to the raccoon mount (Tukey's tests; $P < 0.05$; Figure 2).

The characteristics of loud songs did not vary with predator/control type (all $P \geq 0.12$); too few tu-a-wee calls were given during trials to permit analysis. No alarm calls were given during trials with the Mourning Dove and, in trials with the four predators, only the duration of alarm calls varied with predator type ($F_{3,1} = 89.1$, $P = 0.0046$, Figure 3; all $P \geq 0.58$ for the other characteristics); alarm calls given in response to the raccoon were longer in duration than those given in response to the other three predators (Tukey's test, $P < 0.05$; Figure 3). Only two chatter calls were given during trials with the Mourning Dove and, for the four predators, the frequency characteristics of chatter calls did not vary (all $P \geq 0.70$). However, the number of notes per call ($F_{3,5} = 5.4$, $P = 0.0495$) and call duration ($F_{3,1} = 7.6$, $P = 0.026$) did vary with predator type, with more notes per call and calls longer in duration during trials with the raccoon (Tukey's tests; $P > 0.05$; Figure 4).

Nestling responses to adult vocalizations

During trials, nestling bluebirds exhibited no apparent response during 25 of 48 (52.1%) trials. However, excluding nine control trials (Mourning Dove), nestlings failed to respond during 16 of 39 trials (41%). During 23 of 39 trials (excluding control trials; 59%), nestlings responded by crouching (N = 21), attempting to climb up a wall of their nest box (N = 1), or fledging (N = 1) (Figure 5). For analysis, I combined all responses (crouching, climbing, and fledging) into one category (i.e., responded).

Nestling bluebirds did not respond during trials with the Mourning Dove (N = 9). However, nestlings did respond during two of five trials (40%) with the chipmunk, four of 12 trials (33.3%) with the snake, six of 10 trials (60%) with the American Kestrel, and 11 of 12 trials (91.7%) with the raccoon. For predators that could potentially enter nest boxes (snake and chipmunk), nestling bluebirds responded during six of 17 trials (35.3%). For predators that could not enter nest boxes, but could reach in with legs and talons (American Kestrel) or forearms (raccoon), nestlings responded during 17 of 22 trials (77.3%).

During trials where they responded by crouching, climbing, or fledging (N = 23), nestlings were vocalizing prior to when adults first vocalized during nine trials (39.1%) and not vocalizing during 14 trials (60.9%). Nestlings that were not vocalizing previously also remained quiet after adults began vocalizing. When nestlings were vocalizing, nestlings stopped calling after adults began calling during six of nine trials (66.7%). However, during one trial when nestlings continued to call for several seconds, they

then responded by fledging and, during another trial where nestlings continued calling, the adults uttered only three tu-a-wee calls and no chatter calls. Only during one trial, with the snake as the predator, did nestlings continue to call throughout the trial after adults gave chatter calls (N = 61 calls).

Calling rates for loud songs ($F_{1,11} = 1.1$, $P = 0.45$) and tu-a-wee calls ($F_{1,11} = 2.0$, $P = 0.28$) did not differ between trials where nestlings did or did not respond. However, adult bluebirds uttered significantly more chatter calls ($F_{1,11} = 38.1$, $P < 0.0001$) and alarm calls ($F_{1,11} = 5.8$, $P = 0.034$) during trials when nestlings responded. For alarm calls, adult bluebirds uttered an average of 0.1 ± 0.05 calls per min during trials when nestlings did not respond and 2.3 ± 0.7 calls per min when nestling did respond. Adult bluebirds gave an average of 1.7 ± 0.8 chatter calls per min when nestlings did not respond and 24.9 ± 3.8 chatter calls per min during trials when nestlings responded.

CHAPTER IV

DISCUSSION

Nestling Eastern Bluebirds were more likely to respond, primarily by crouching and by either remaining or, if calling, becoming quiet, during predator trials when adults uttered chatter calls and alarm calls at higher rates. Studies of other species, including American Goldfinches (*Carduelis tristis*; Knight and Temple 1986), Moustached Warblers (*Acrocephalus melanopogon*; Kleindorfer et al. 1996), Red-winged Blackbirds (*Agelaius phoeniceus*; Madden et al. 2005), and Tree Swallows (*Tachycineta bicolor*; McIntyre et al. 2014), have also revealed that nestlings crouch in response to adult alarm calls. Similarly, nestlings in other species have also been found to cease calling in response to adult alarm calls (e.g., Knight and Temple 1986, Duckworth 1991, Platzen and Magrath 2004, Madden et al. 2005, McIntyre et al. 2014). As also noted by previous investigators (e.g., McIntyre et al. 2014), predators may be less likely to locate nests if nestlings cease calling. In addition, for cavity-nesting species, crouched nestlings may be more difficult for large predators to reach with their forelimbs (e.g., raccoon) or hindlimbs (American Kestrel; Figure 6).

Most nestling Eastern Bluebirds in my study responded to adult chatter and alarm calls uttered at high rates by crouching lower in their nests. In contrast, Suzuki (2011) and Suzuki and Ueda (2013) found that nestling Great Tits, also cavity-nesters, either fledged or crouched in response to different adult vocalizations (i.e., functionally

referential), one given in response to potential nest predators that could, and another to nest predators that could not, enter nest cavities and prey on nestlings. Adult Eastern Bluebirds did not use different calls when responding to different predators in my study (i.e., they do not have predator-specific, functionally referential calls). However, adult bluebirds did vary call rates and call characteristics in response to different predators, with chatter and alarm calls of longer duration and given at higher rates during trials with the raccoon mount, a predator unable to enter a nest box, but capable of reaching in a nest box or nest cavity to prey on nestlings (Radunzel et al. 1997, Gowaty and Plissner 1998). Thus, although adult Eastern Bluebirds do not provide their nestlings with information as specific as that provided to nestlings by the functionally referential calls of adult Great Tits, adults do, by uttering chatter and alarm calls that vary in duration and at different rates, appear to provide nestling bluebirds with information about potential predators that generate different nestling responses.

Previous investigators have reported that raccoons are major predators of the eggs and nestlings of Eastern Bluebirds (Petersen 1969, Pinkowski 1975a, Zeleny 1976, Radunzel et al. 1997), and sometimes also kill incubating or brooding females (Gowaty and Plissner 1998). As such, the vocal responses of adult Eastern Bluebirds and corresponding behavioral responses of nestlings could reduce the likelihood of nestlings being predated, with crouching nestlings more likely to be out of reach of a raccoon reaching into a nest box or cavity. In response to the other potential predators in my study (American Kestrel, chipmunk, and snake), adult Eastern Bluebirds uttered fewer

chatter and alarm calls that were shorter in duration, and nestlings responded by crouching during 12 of 27 trials (44.4%). Adult Eastern Bluebirds may perceive American Kestrels and eastern chipmunks as less threatening than raccoons because American Kestrels prey primarily (although not entirely; Figure 6) on ground-dwelling terrestrial arthropods and small mammals (Smallwood and Bird 2002) and eastern chipmunks feed primarily on seeds and fruits (Yerger 1955). Eastern chipmunks occasionally eat bird eggs and nestlings (e.g., Landry 1970, King and DeGraaf 2006), but likely represent less of a threat to 12-19-day-old nestling bluebirds than to eggs or smaller nestlings.

Snakes, including black rat snakes, are known predators of bluebird eggs, nestlings, and incubating or brooding adults (Hensley and Smith 1986, Gowaty and Plissner 1998, Bass 2011, G. Ritchison, pers. observ.), and adult Eastern Bluebirds in my study did respond vocally during 10 of 12 trials with the rubber snake. However, in response to the snake model, adult Eastern Bluebirds in my study called at significantly lower rates (chatter and alarm calls) with significantly shorter duration calls than when responding to the raccoon mount. In addition, nestling bluebirds only responded (by crouching) during four of 12 trials (33.3%) with the snake model.

One possible explanation for the limited response of Eastern Bluebirds to the snake in my study is that the rubber snake model was not sufficiently realistic and that they would respond more aggressively, and with more and longer duration chatter and alarm calls, to a live black rat snake. During four of 12 snake trials in my study, adult bluebirds uttered no chatter calls and, during another four trials, adults uttered only 3,

3, 8, and 8 chatter calls, respectively. During the remaining four trials, adults uttered 17, 19, 46, and 61 chatter calls, respectively. During the trial with 17 chatter calls the adult male was physically perched on top of the rubber snake model vocalizing, and in three of 12 trials adults continued to feed nestlings despite the presence of the rubber snake model. In addition, during six of 12 trials adult bluebirds flew > 30 m from the nest box before the end of the 3-minute trial. These results suggest that during eight of 12 trials, adult Eastern Bluebirds apparently responded as if the rubber snake was no threat or, at best, a minor threat (Figure 2). In response to live snakes near nests, adult Eastern Bluebirds typically respond more aggressively by uttering chatter calls and flying at and hovering near the snakes (Laskey 1946, Krieg 1971, Wetzel and Chandler 2008, Leonard 2009, Ritchison, pers. observ.).

During trials in my study when adult Eastern Bluebirds uttered chatter calls and alarm calls at higher rates, nestlings typically responded by crouching. Other investigators have also reported that nestling bluebirds crouch in response to adult chatter calls, as well as in response to movement of nest boxes (Laskey 1946, Krieg 1971). Laskey (1946:218) noted ‘that even 16-day-old nestling Eastern Bluebirds, potentially old enough to fledge, do not fly out at the approach of a possible enemy but crouch low, with heads bent downward.’ Nestling bluebirds do sometimes fledge when 16 or 17 days old, but typically do not fledge until 17 – 19 days old (Gowaty and Plissner 1998). Similarly, Pinkowski (1975) reported that nestling Eastern Bluebirds in most nests fledged when 18 or 19 days old (106 of 184 broods, 57.6%), no nestlings fledged at 15

days post-hatching or earlier, nestlings in 23 broods (12.5%) fledged at 16 or 17 days post-hatching, and nestlings in 55 broods (29.9%) fledged at 20-22 days post-hatching.

For many species of birds, an important factor in determining when nestlings fledge is their developmental state, particularly their wing development (Michaud and Leonard 2000, Johnson et al. 2004, Radersma et al. 2011, Schlicht et al. 2012). Wing development is likely important because fledglings generally have high mortality rates just after leaving nests (Naef-Daenzer et al. 2001, Rush and Stutchbury 2008) and better-developed wings may better allow fledglings to find cover and elude predators. Thus, for nestling Eastern Bluebirds that have not reached the developmental stage needed for fledging, crouching may be a better strategy than premature fledging because the risk of predation for a young bird unable to fly (or at least fly very well) would likely be high, especially when, based on the vocal behavior of adults, a potential predator is nearby. This may be particularly true for species like Eastern Bluebirds that typically nest in open habitats with no or little understory and sparse ground cover (Gowaty and Plissner 1998). In support of this hypothesis, McIntyre et al. (2014) found that 15-day-old nestling Tree Swallows, a cavity-nesting species that also breeds in open habitats, crouched in response to playback of adult alarm calls.

Most trials in my study were conducted at nest boxes where nestlings were ≤ 16 days old (28 of 39, excluding trials with the Mourning Dove), including eight of 12 trials (66.7%) with the raccoon mount that elicited the strongest vocal responses by adult Eastern Bluebirds, and possibly not sufficiently developed to fledge. Of the 11 trials

conducted with nestlings 17-19 days old, five were with either the snake or chipmunk to which adult bluebirds exhibited little response. Of the remaining six trials with 17-19-day-old nestling bluebirds, two were with the American Kestrel and four with the raccoon. During one trial with the American Kestrel, adults did not vocalize and nestlings exhibited no response. Thus, during five trials with 17-19-day-old nestling bluebirds where adults vocalized, nestlings crouched three times and either fledged or possibly attempted to fledge (climbing the side of the nest box) during two trials. These results suggest that, when nestling Eastern Bluebirds are likely sufficiently developed, or nearly so, for fledging (and at least short-distance flights), they may, in some cases, fledge rather than crouch in response to adult alarm calls.

In summary, my results indicate that the vocal repertoires of adult Eastern Bluebirds do not include functionally referential calls, i.e., different calls for use in the presence of different potential nest predators. However, adult bluebirds did vary call rates and call characteristics in response to different predators, with chatter and alarm calls of longer duration given at higher rates in response to the predator that apparently posed the greatest threat to nestlings (raccoon). These calls, particularly chatter calls, when longer in duration and given at higher rates appear to provide nestlings with information about the presence of potential predators to which they typically respond by crouching, behavior that might reduce the likelihood of predation by predators too large to enter a cavity, but able to reach in with forearms (raccoon) or talons (American Kestrel). However, older nestling bluebirds sufficiently developed, or nearly so, to fledge

(≥ 17 days old) may either crouch or fledge in response to the chatter and alarm calls of adults.

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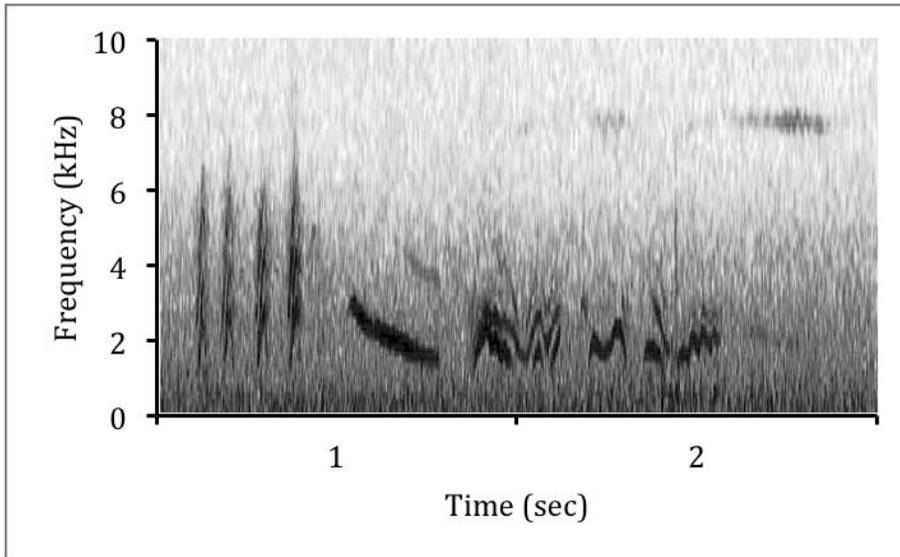
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APPENDIX

(a)



(b)

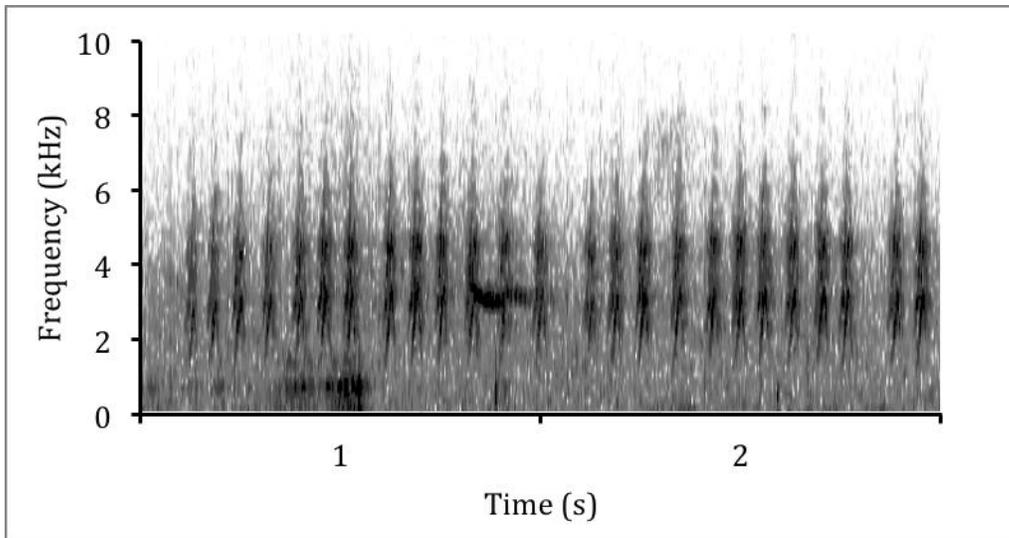
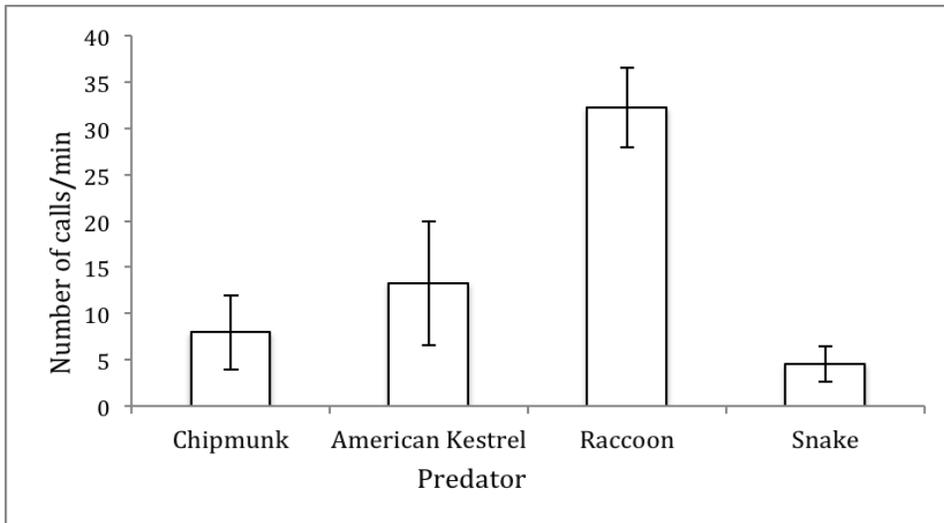


Figure 1. Sonograms of vocalizations given by adult Eastern Bluebirds (*Sialia sialis*) in response to a mounted raccoon.

(a) Alarm calls began with a variable number of chat notes. (b) Chatter calls consisted of a series of short duration notes that extend over a wide range of frequencies.

(a)



(b)

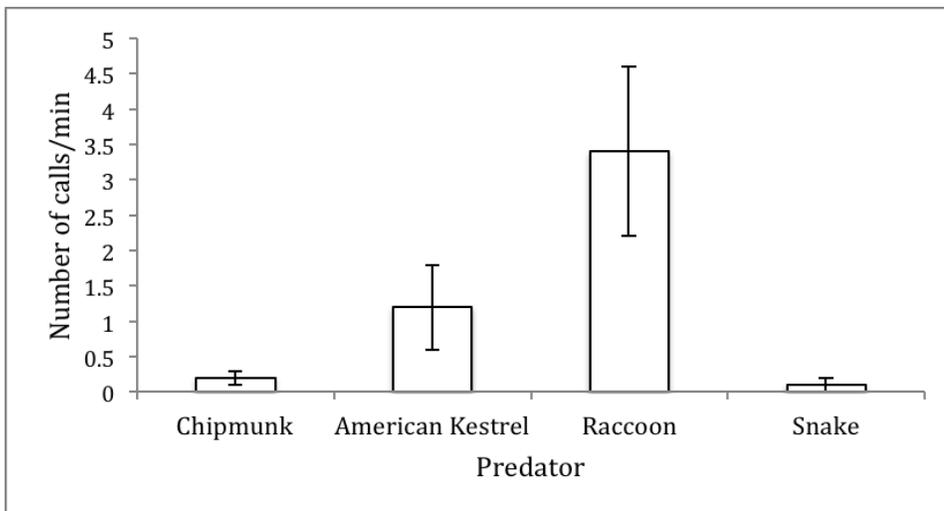


Figure 2. Mean rate of calling (\pm SE) of alarm call vocalizations given by adult Eastern Bluebirds during predator presentations. For both (a) chatter calls and (b) alarm calls the rate of calling was significantly greater in response to the raccoon predator model. No alarm calls and only two chatter calls were given in response to the control (Mourning Dove)

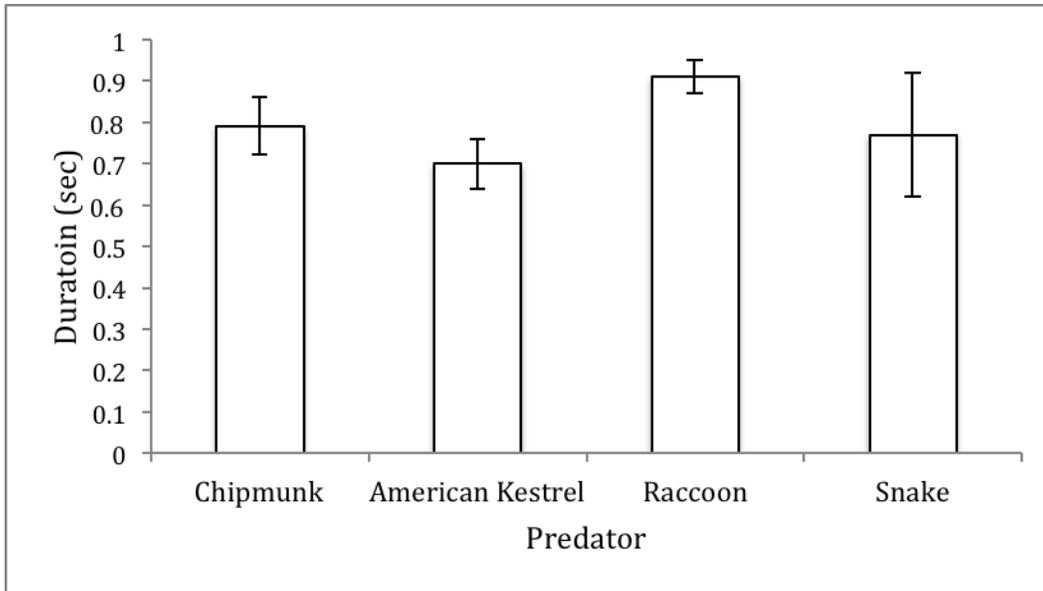
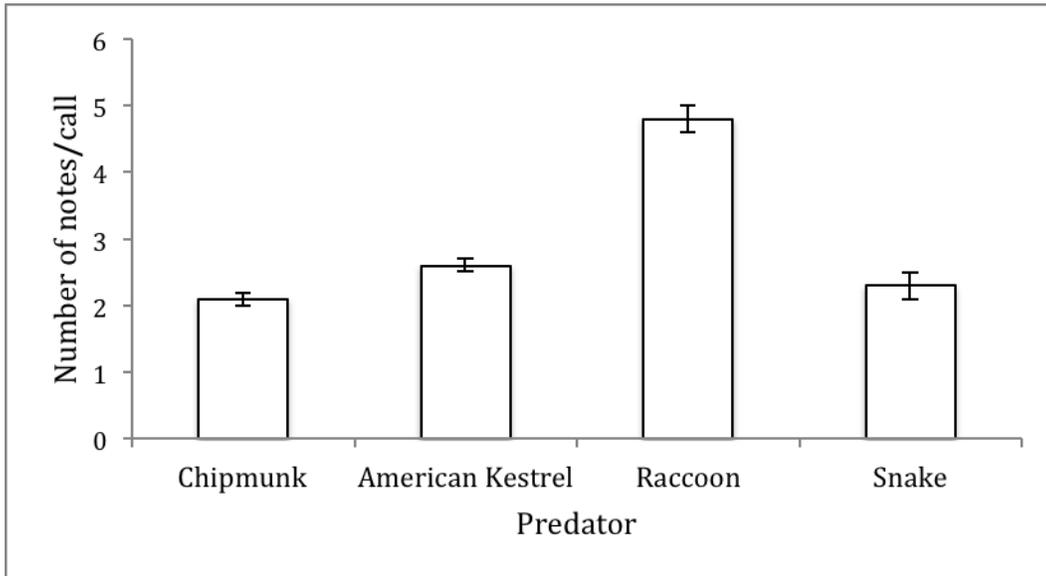


Figure 3. Mean duration (\pm SE) of alarm calls of adult Eastern Bluebirds during 3-min predator-presentation trials.

Nestlings were significantly more likely to respond to adult alarm calls that were longer in duration and given at a higher rate.

(a)



(b)

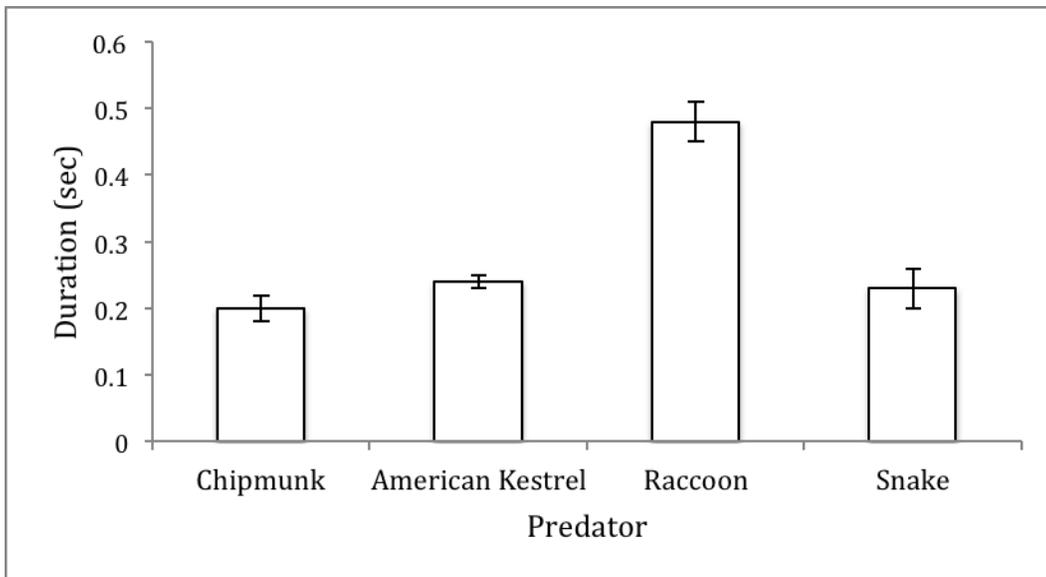


Figure 4. Mean (\pm SE) (a) number of notes per call and (b) mean duration of chatter calls of adult Eastern Bluebirds given in response to different potential predators near their nests. Bluebirds gave longer calls, both in terms of number of notes and call duration, during trials with the raccoon mount.

(a)



(b)



Figure 5. Image of fifteen-day-old Eastern Bluebird responding to adult alarm call vocalizations.

Fifteen-day-old nestling Eastern Bluebird (a) prior to a trial, and (b) crouching in the nest in response to adult chatter call. (c) Nestling climbing the side of the nest box wall while another nestling crouches during an experiment with the raccoon mount. Images of nestlings were selected from video footage recorded during predator presentations.

(c)



Figure 5. (Continued).

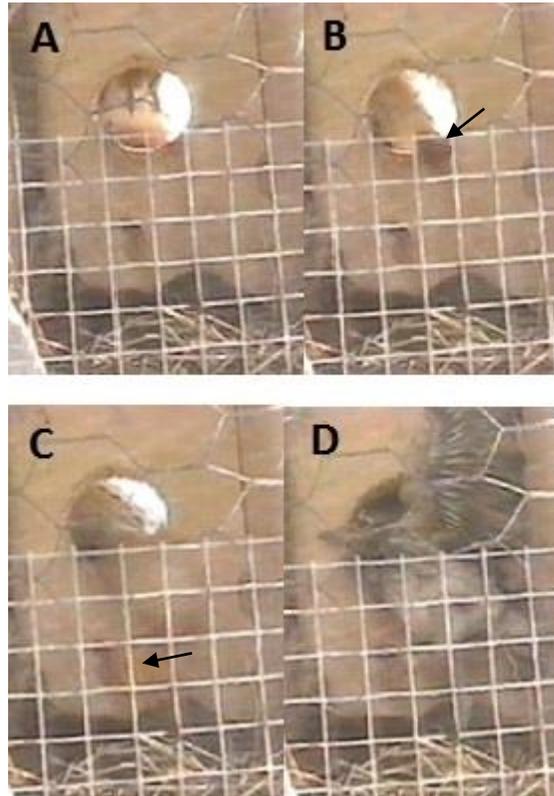


Figure 6. Image of an American Kestrel predated fifteen-day-old nestling Eastern Bluebirds.

Image of an American Kestrel, after four unsuccessful attempts, finally manages to grab a nestling and pull it out of the nest box. The remaining nestlings eventually fledged so if the subsequently American Kestrel returned and attempted to remove additional nestlings, it was unsuccessful. (A) American Kestrel looking into nest box with nestling Eastern Bluebirds crouching in the nest. (B) American Kestrel reaching into nest box with left leg and foot (arrow) in an unsuccessful attempt to grab a nestling. (C) Another unsuccessful attempt by the American Kestrel (arrow points to left foot just above the crouching nestlings). (D) *Source*: Kieffer, B. 2011. Effect of nestling sex ratio on the provisioning behavior of adult Eastern Bluebirds. M. S. thesis, Eastern Kentucky University, Richmond, KY.