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Effect of predator type, season, brood size, and West Nile Virus infection on the nest defense behavior of male and female Eastern Bluebirds

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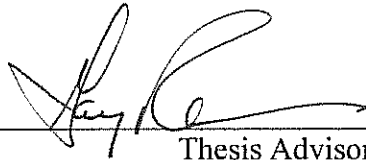
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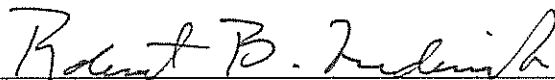
By

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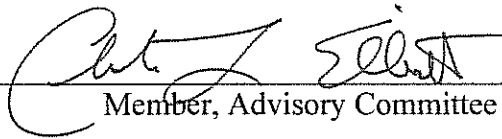
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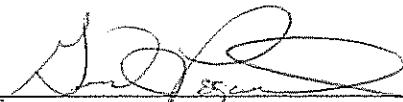
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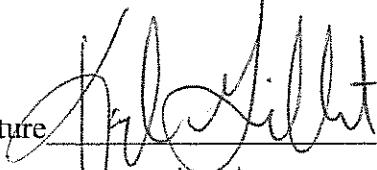


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Effect of predator type, season, brood size, and West Nile Virus infection
on the nest defense behavior of male and female Eastern Bluebirds

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Submitted to the Faculty of the Graduate School of
Eastern Kentucky University
in partial fulfillment of the requirements
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ABSTRACT

The intensity of nest defense by birds can be influenced by many factors, including a parent's sex, brood size, stage of breeding season, type of predator, and physical condition. Because previous studies have produced conflicting results concerning the effects of these factors on the nest defense behavior of birds, additional studies are needed to better clarify how and why such factors influence behavior. No one to date has examined the possible effect of a viral infection on avian nest defense behavior. Thus, my objectives were to determine the effect of adult sex, brood size, stage of the breeding season, predator type, and infection with West Nile Virus (WNV) on the nest defense behavior of male and female Eastern Bluebirds (*Sialia sialis*). Eastern Bluebirds were studied from March to August 2003 at the Blue Grass Army Depot. Adult and nestling Bluebirds were captured, measured, banded, and blood was drawn. Nest defense was examined when nestlings were 15-18 days old. Pairs of bluebirds were presented with two predators, a human and an Eastern Screech-Owl (*Megascops asio*), and nest defense behaviors were recorded.

Analysis revealed that nest defense intensity differed significantly with predator type, with bluebirds responding more vigorously to an Eastern Screech-Owl than to a human ($P < 0.0001$). Nest defense intensity also differed between the sexes, with male bluebirds defending with greater intensity than females ($P = 0.031$). However, analysis revealed that brood size ($P = 0.70$) and stage of breeding season ($P = 0.11$) did not influence nest defense intensity of Eastern Bluebirds. There was also no difference in the intensity of nest defense between pairs where one adult was infected with West Nile Virus and pairs where neither adult was infected ($P = 0.24$). My results indicate that male

and female Eastern Bluebirds responded more vigorously to an Eastern Screech Owl than a human, possibly because an avian (aerial) predator like an Eastern Screech-Owl, in contrast to a terrestrial predator, represents a threat not only to nestlings, but to adults as well. Intensity of nest defense may not vary with brood size because the value of a given number of young may vary with the reproductive potential of parents and, therefore, parents capable of raising fewer young might be expected to defend their smaller brood as intensively as parents with greater reproductive potential defend their larger brood. The intensity of nest defense by bluebirds may remain constant throughout the breeding season because the declining value of offspring as the season progresses may be balanced by the effect of declining re-nesting potential. Finally, my results suggest that WNV infection, at least during the viremic stage, did not affect the physical condition of Eastern Bluebirds enough to affect their nest defense behavior.

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CHAPTER I

INTRODUCTION

Parent birds may benefit by defending nests from potential predators if such behavior increases the likelihood that their young will survive. However, such behavior may also be costly, with some risk of injury or even death. Thus, because birds seek to maximize lifetime reproductive success rather than current reproductive success, parents must assess the danger posed by a potential nest predator and then choose appropriate responses (Radford and Blakey 2000).

The intensity of nest defense by birds can be influenced by many factors, including a parent's sex, brood size, and stage of the breeding season. However, the relative importance of these factors has been found to vary among species and even among individuals within a species. For example, females defend nests more vigorously than males in some species (Weatherhead 1989), males more vigorously than females in other species (Winkler 1992), and males and females with equal vigor in still other species (Nealen and Breitwisch 1997). Similarly, the intensity of nest defense has been found to increase with brood size in some species (Radford and Blakey 2000), but not others (Halupka 1999), and intensity varies with stage of the breeding season in some species (Redmond et al. 2009), but not others (Hobson et al. 1988).

Another factor that can influence the nest defense behavior of birds is the type of predator. For example, Tree Swallows defended nest sites more vigorously against a ferret (*Mustela putorius*) than a black rat snake (*Elaphe obsoleta*; Winkler 1992). Brunton (1990) found that Killdeer (*Charadrius vociferous*) defended nests more intensely against ground-based predators than aerial predators. Such differences in

response might be influenced by the relative risk posed by a predator to both parents and offspring (Brunton 1990), but other factors, such as previous experience with potential predators, could also influence the behavior of adults (Maloney and McLean 1995).

Another factor that may affect nest defense behavior is a bird's physical condition and, specifically, whether a bird has been exposed to a pathogen and is immune-challenged. Previous studies suggest that birds responding to induced immune challenges (i.e., caused by injecting non-pathogenic antigens) may increase reproductive investment (Bonneaud et al. 2004). Exposure to a pathogen could potentially influence nest defense behavior because birds and other animals invest more in current reproductive effort if the chance of surviving to reproduce again is low, i.e., the terminal investment hypothesis (Clutton-Brock 1984).

Because previous studies have produced conflicting results concerning the effects of factors such as sex, brood size, stage of the breeding season, and predator type on the nest defense behavior of birds, additional studies are needed to better clarify how and why such factors influence behavior. In addition, although investigators have induced immune challenges to study how such challenges might influence reproductive investment (e.g., clutch sizes and likelihood of re-nesting), no one to date has examined the possible effect of a viral infection on avian nest defense behavior. Thus, my objectives were to determine the effect of adult sex, brood size, stage of the breeding season, predator type, and infection with West Nile Virus on the nest defense behavior of male and female Eastern Bluebirds (*Sialia sialis*).

CHAPTER II

MATERIALS AND METHODS

Eastern Bluebirds were studied from March - August 2003 at the Blue Grass Army Depot (BGAD). The BGAD consists of 5,907 hectares of open grassland and scattered woodlots and is located in Madison County, Kentucky. Lab work was conducted at the University of Kentucky from August 2003 - December 2004.

Prior to nest building and territory establishment by male Eastern Bluebirds, I placed nest boxes (N = 100) in open habitats on the BGAD. Once territories had been established and nest boxes occupied, I captured bluebirds by using mist nets. Bluebirds were lured into nets either by using playback of the songs of Eastern Bluebirds or by placing nets near occupied boxes. Captured birds were measured to obtain mass, wing chord length, tarsus length, and tail length. A blood sample (40 – 70 μ l) was also collected from each captured bird. Finally, captured bluebirds were banded with a U. S. Geological Survey aluminum band plus a unique combination of three colored plastic bands to permit individual identification.

Nest boxes were monitored every two to three days to determine their status. Blood samples were also drawn from nestlings when they were about 7 – 12 days old. For each nest, I determined clutch size, number of nestlings, and number of fledglings. All blood samples were analyzed to determine the presence of West Nile Virus (WNV). Blood samples were analyzed for the virus by using a reverse transcription-nested polymerase chain reaction (RT-nPCR) assay. This assays had been used previously to detect West Nile Virus in several species, including birds (Lanciotti et. al. 2000, Johnson

et. al. 2001). A blood sample testing positive with the RT-nPCR indicated that the bird had WNV.

Nest defense behavior of adult bluebirds was examined when nestlings were 15 – 18 days old. Pairs of bluebirds were presented with two predators. During separate trials, at least 24 hrs apart, a human and a live Eastern Screech-Owl (*Megascops asio*) were presented at each site. Predators moved to or were placed 0.5 m in front of nest boxes when the adults were not present. Trials began when at least one adult came within 30 m of the nest site. Nest defense behavior was recorded for three minutes. Behaviors recorded for each bluebird included (1) the closest distance of approach to the predator (± 0.5 m), (2) mean distance from the predator (with distances recorded every 30 seconds), (3) number of songs, (4) number of alarm calls (the number of ‘chit’ calls; Gowaty and Plissner 1998), (5) number of flights (the number of times each adult flew between three to 30 meters of the predator), (6) number of flybys (the number of flights each adult made within 1 -2 m of the predator), (7) number of attacks (the number of times each adult flies to within one meter of the predator), and (8) number of hits (the number of times a bluebird struck the predator). For variables 1 and 2, I assumed larger numbers (i.e., staying further from the predator) indicated a weaker response, whereas, for variables 3 through 8, I assumed higher numbers indicated a stronger response. I also assumed that attacks and hits represented the strongest response and bluebirds engaging in such behavior, by approaching a potential predator so closely, were taking the greatest risk. As such, for analysis, I used this formula:

Nest defense intensity (NDI) = (number of songs + number of calls + number of flights + number of flybys + number of attacks x 2 + number of attacks x 3) – (closest distance + mean distance),

to generate a single variable that quantified the intensity of nest defense by male and female Eastern Bluebirds.

I examined the possible effect of predator type (human vs. screech-owl), month (May, June, July, and August), and brood size (3, 4, or 5 young) on the nest defense behavior of Eastern Bluebirds. In addition, to examine possible effects of WNV infection on bluebird behavior, I compared the intensity of nest defense of (1) bluebirds infected with WNV to that of bluebirds not infected, and (2) bluebirds with at least one nestling infected with WNV to that of bluebirds with no nestlings infected with WNV. All analyses were conducted using analysis of variance, and all analyses were conducted using the Statistical Analysis System (SAS Institute 1989). Significance was accepted at $P < 0.05$, and values are presented as means \pm standard error.

CHAPTER III

RESULTS

During the 2003 field season, I conducted predator trials with 65 pairs of Eastern Bluebirds. For all variables examined, analysis revealed no differences in the responses of bluebirds with different-aged nestlings (all $P \geq 0.08$; all trials were conducted with pairs that had 15 – 18 day-old nestlings) so nestling age was not included in subsequent analyses. Analysis revealed that the intensity of nest defense differed significantly with predator type, with bluebirds responding more aggressively to an Eastern Screech-Owl (mean NDI = 35.9 ± 3.5) than to a human (mean NDI = 0.1 ± 2.8 ; Tables 1 and 2). The intensity of nest defense also differed between the sexes (Table 1), with male bluebirds defending with greater intensity (mean NDI = 23.1 ± 3.3) than females (mean NDI = 13.2 ± 3.8). However, further analysis revealed that the responses of male and female bluebirds were similar, with the only exception being number of songs (Table 2). The number of young (3, 4 or 5) did not influence the intensity of nest defense by male and female Eastern Bluebirds (Table 1). Finally, the intensity of nest defense did not vary among months (May, June, July, and August), and no interactions were significant (Table 1).

Compared to their response to a human, Eastern Bluebirds responding to an Eastern Screech-Owl approached closer and initiated more flybys and attacks (Table 3). Among months, Eastern Bluebirds remained closer to predators (mean distance) during July and August than during May and June (Table 4). In addition, in response to potential nest predators, bluebirds sang and called less in May than during the other months, and

initiated more attacks in August and, especially, July than during May and June (Table 4).

Of the 130 adult bluebirds at nests where I conducted trials, 10 were infected with WNV (7.7%; 5 males and 5 females, with the other member of the pair not infected in all cases). In addition, at least one nestling was infected with WNV in nine of the 65 nests (14%). I found no difference in the intensity of nest defense (NDI) between pairs where one adult was infected with WNV and pairs where neither adult was infected ($F_{1, 212} = 1.4, P = 0.24$). Similarly, for pairs where one adult was infected and the other was not, I found no difference between them in the intensity of nest defense ($F_{1, 27} = 0.1, P = 0.72$). Finally, the intensity of nest defense did not differ between pairs with no infected nestlings and pairs with at least one infected nestling ($F_{1, 212} = 0.1, P = 0.86$).

Table 1. Effects of sex, month, predator type and number of young on the intensity of nest defense by male and female Eastern Bluebirds defending nestlings near fledging age (15-18 days old).

Effect	SS	df	MS	F	P
Sex	4844.9	1	4844.9	5.0	0.031
Month	6047.5	3	2015.8	2.1	0.11
Predator	51908.8	1	51908.8	53.1	< 0.0001
Number of young	707.9	2	354.0	0.1	0.70
Month x number of young	3459.3	4	864.8	0.9	0.47
Month x predator	1695.3	3	565.1	0.5	0.65
Number of young x predator	3083.2	2	1541.6	1.6	0.21
Sex x predator	612.8	1	612.8	0.6	0.43
Sex x month	5590.6	3	1863.5	1.9	0.13
Sex x number of young	503.7	2	251.9	0.3	0.77
Sex x predator x month	1962.5	6	327.1	0.3	0.92
Sex x number of young x month	487.2	4	121.8	0.1	0.97
Month x number of young x predator	1003.5	6	250.9	0.2	0.91
Error	256021.5	187			

Table 2. Responses of male and female Eastern Bluebirds to two potential nest predators, a human and an Eastern Screech-Owl.

Variable	<u>Responses to screech-owl</u>		<u>Responses to human</u>	
	mean	SE	mean	SE
Closest approach (m)***	4.0	0.5	12.1	0.9
Mean distance (m)***	8.8	1.1	16.5	0.9
Number of songs**	5.4	0.6	3.3	0.5
Number of calls**	22.8	0.8	19.9	1.0
Number of flights**	1.8	0.2	3.3	0.3
Number of flybys***	2.9	0.4	0.5	0.2
Number of attacks***	7.4	1.0	0.2	0.2
Numbers of hits*	0.1	0.06	0	—

*P < 0.05, **P < 0.01, and ***P < 0.0001

Table 3. Responses of male and female Eastern Bluebirds to potential nest predators.

Variable	Males		Females	
	mean	SE	mean	SE
Closest approach (m)	7.3	0.8	8.7	0.9
Mean distance (m)	11.7	0.9	13.9	1.3
Number of songs*	5.4	0.6	2.6	0.5
Number of calls	19.9	1.1	17.9	1.1
Number of flights	2.2	0.2	2.1	0.3
Number of flybys	1.7	0.4	1.2	0.3
Number of attacks	3.2	0.7	3.0	0.7
Numbers of hits	0.05	0.04	— ^a	—

*P < 0.0001

^aOne female hit a screech-owl during one trial (out of 99 trials)

Table 4. Variation among months (mean (SE)) in the responses of male and female Eastern Bluebirds to potential nest predators (human and Eastern Screech-Owl combined).

Month	Closest approach (m)	Mean distance (m)	No. of songs	No. of calls	No. of flights	No. of flybys	No. of attacks
May	7.1 (1.2)	15.8 (1.6)	1.6 (0.6)	14.9 (1.7)	2.6 (0.6)	2.2 (0.7)	3.0 (1.0)
June	9.2 (1.4)	14.0 (2.1)	5.3 (0.9)	20.1 (0.9)	2.3 (0.3)	3.4 (0.8)	2.3 (1.0)
July	7.0 (1.1)	11.1 (1.2)	3.7 (0.6)	21.1 (1.1)	3.0 (0.4)	1.4 (0.5)	6.1 (1.4)
August	8.2 (0.9)	11.2 (1.0)	5.5 (0.8)	25.9 (1.2)	2.3 (0.3)	0.4 (0.1)	3.6 (0.9)

CHAPTER IV

DISCUSSION

Adult sex

My results indicate that male and female Eastern Bluebirds defended nests with nestlings with equal intensity, responded with greater intensity to an Eastern Screech-Owl than a human, and tended to respond with less intensity early in the breeding season than later in the breeding season. Although male bluebirds did utter more songs than females during nest defense trials, that difference may have been more the result of the tendency of males to sing more than females (Gowaty and Plissner 1998) than a different response to nest predators. Previous studies have provided conflicting results concerning the relative intensity of nest defense by males and females. As with Eastern Bluebirds in my study, male and female Northern Cardinals (*Cardinalis cardinalis*; Nealen and Breitwisch 1997) and male and female Northern Flickers (*Colaptes auratus*; Fisher and Wiebe 2006) defended nests with equal intensity. In contrast, studies of a number of other species have revealed that males defend nests more vigorously than females, including Mountain Bluebirds (*Sialia currucoides*; Gibson and Moehrensclager 2008), Fieldfares (*Turdus pilaris*; Hogstad 2005), Killdeer (*Charadrius vociferous*; Brunton 1990), Eastern Kingbirds (*Tyrannus tyrannus*; Redmond et al. 2009), and European Blackbirds (Kryštofková et al. 2011). In yet other species, females defend nests more vigorously than males (e.g., Song Sparrows, *Melospiza melodia*; Weatherhead 1989).

Males in some bird species may defend nests more vigorously and take more risks than females when doing so because only females incubate eggs and brood young and, as a result, are essential for nest success (Redmond et al. 2009, Kryštofková et al. 2011).

Being injured would, of course, be maladaptive for both sexes (Montgomerie and Weatherhead 1988), but, if a female is severely injured or killed, nest failure would be inevitable. However, the likelihood of nest failure if a female is injured or killed varies with nest stages. During incubation and early in the nestling period when young must be brooded, the loss of a female in species where only females incubate eggs and brood young would almost certainly mean the loss of the nest. However, I conducted nest defense trials when young bluebirds were near fledging age (15-18 days post-hatching). For young near the age of fledging and for species like Eastern Bluebirds where both adults provision young and fledglings (Gowaty and Plissner 1998), injury or death of the adult female would likely not result in nest failure. In such cases, as was the case in my study, females may defend nests as vigorously as males.

Another factor that could potentially influence the intensity of avian nest defense by males and females is certainty of parentage. For example, Weatherhead (1989) found that female Song Sparrows defended nests more vigorously than males, possibly because males are less certain of their parentage than females. However, male Eastern Bluebirds in my study defended nests as vigorously as females even though females are known to engage in extra-pair copulations (thereby reducing the certainty of paternity for males; Gowaty and Plissner 1998). Studies of other species where females are known to engage in extra-pair copulations have revealed similar results, males still defend nests as vigorously, or even more vigorously, than females (e.g., Winkler 1992, Gibson and Moehrensclager 2008, Redmond et al. 2009). One possible explanation for such results, particularly for cavity-nesting species like Eastern Bluebirds, is that males are not just defending nestlings, but are also defending nest sites. For example, Winkler (1992)

suggested that male Tree Swallows may defend their cavity nests more vigorously than females because they are typically more aggressive in territory defense. For secondary-cavity-nesting species, like Eastern Bluebirds and Tree Swallows, availability of suitable cavities may be limited and if so, males may vigorously defend nest sites. This may be due, in part, to the continued presence of a predator near those sites, and for females, may reduce the quality of those nest sites and increase the likelihood that females might leave the territory to seek mates with higher-quality nest sites.

Male birds may also vigorously defend nests, regardless of their certainty of paternity, because nest defense is an epigamic signal used by females during mate choice (Curio et al. 1984, Redmond et al. 2009). Thus, if females choose mates or stay paired with males based on male quality, which may be based in part on how vigorously they defend nests, then males that defend nests vigorously may be more successful at pairing with, and retaining as mates, higher quality females.

Predator type

Eastern Bluebirds in my study defended nests more vigorously in response to an Eastern Screech-Owl than a human. Previous studies have revealed that other species of birds also respond differently to different potential nest predators (Veen 1977, Kleindorfer et al. 2005, Morrison et al. 2006). For example, Tree Swallows defending nest sites responded more vigorously to a ferret (*Mustela putorius*) than a black rat snake (*Elaphe obsoleta*; Winkler 1992). Brunton (1990) reported that Killdeer defending nests responded more intensely to ground-based predators than aerial predators.

Several factors may influence how birds respond to different potential nest predators, including nest stage (eggs vs. nestlings), the likelihood that predator defense can be effective, and the degree of threat a potential predator poses to adults. Eastern Bluebirds in my study may have responded more aggressively to an Eastern Screech-Owl than a human because an avian (aerial) predator represents a threat not only to nestlings, but to adults as well. Similarly, the intensity of nest defense by Black-billed Magpies (*Pica pica*) was also found to vary with type of predator, with the most vigorous defense directed toward raptors regardless of nest stage (Buitron 1983). Such aggression toward raptors may be beneficial because they represent a threat to adult magpies as well as nestlings (Buitron 1983). In addition, raptors as aerial predators would also represent a greater threat to young birds than terrestrial predators, like humans, after they fledge. For cavity-nesting species like Eastern Bluebirds, a raptor like an Eastern Screech-Owl may not represent a serious threat to nestlings because they would likely be too large to enter most bluebird nest cavities. However, I examined the behavior of Eastern Bluebirds defending nests with young near the age of fledging, and an Eastern Screech-Owl would pose a potentially serious threat to young bluebirds after they leave the nest. Thus, if an aggressive response by Eastern Bluebirds toward an Eastern Screech-Owl causes the owl to leave the area (move-on hypothesis; Curio 1978), the risk of predation for both adults and fledglings might be reduced.

The response of Eastern Bluebirds in my study to a human was significantly less vigorous than that to an Eastern Screech-Owl. One possible explanation for the reduced response to a human is that nest boxes were checked every two to three days once brooding began. As a result, bluebirds were exposed to a human approaching nests and

checking nest contents as many as five or six times before predator trials were conducted. It is possible, therefore, that bluebirds habituated to human presence and activity and, as a result, perceived a human as a less threatening predator. Similarly, Lord et al. (2001) found that New Zealand Dotterels (*Charadrius obscurus aquilonius*) nesting on beaches with more human activity exhibited a decreased intensity of response to a human approaching nests than did dotterels at more remote beaches. In contrast, Knight and Temple (1986:322) suggested that repeated visits by humans to bird nests can result in an increased intensity of response, i.e., after repeated visits by a human where no adults or nestlings are harmed, adults can 'lose fear of the predator' and, as a result, increase the intensity of their responses. Other investigators, however, have reported that repeated visits by humans to nests do not affect the intensity of responses by adult birds (e.g., Weatherhead 1989, Winkler 1992). Given the conflicting results of previous studies, the possible effect of my repeated visits to nests on the responses of adult Eastern Bluebirds during nest defense trials remains unclear.

Another possible explanation for the less vigorous response by Eastern Bluebirds to a human near their nests (compared to that of an Eastern Screech-Owl near nests) is that bluebirds may make judgments concerning their ability to successfully drive different predators away from nests and respond accordingly. Thus, because a large predator like a human is unlikely to be driven from nests, bluebirds may exhibit a less vigorous response. Similarly Patterson et al. (1980) suggested that the responses of White-crowned Sparrows (*Zonotrichia leucophrys*) to potential nest predators varied with their ability to drive them away. For example, adult White-crowned Sparrows exhibit

reduced responses to snakes, possibly because sparrows are unable to drive snakes away from nests (Patterson et al. 1980).

Brood size

I found that brood size did not influence the intensity of nest defense by male and female Eastern Bluebirds. Similar results have been reported for several other species of birds, including Tree Swallows (Winkler 1992), Aquatic Warblers (*Acrocephalus paludicola*; Halupka 1999), Red-backed Shrikes (*Lanius collurio*; Tryjanowski and Golawski 2004), Willow Ptarmigans (*Lagopus lagopus*; Sandercock 1994). In other species of birds, the intensity of nest defense has been found to increase in increasing brood size in several species of birds, including Great Tits (*Parus major*; Radford and Blakey 2000), Merlins (*Falco columbarius*; Wiklund 1990), and Tawny Owls (*Strix aluco*; Wallin 1987). Montgomerie and Weatherhead (1988) suggested that the intensity of nest defense should increase with increasing brood size because the benefits of deterring a predator increase with the number of young. At least two factors may contribute to differences among species in the effect of brood size on the intensity of nest defense. First, the value of a given number of young may vary with the reproductive potential of parents (Montgomerie and Weatherhead 1988) and, therefore, parents capable of raising fewer young might be expected to defend their smaller brood as intensively as parents with greater reproductive potential defend their larger brood. As a result, the results of studies where only natural variation in brood size is considered may not reveal any differences in the intensity of nest defense among pairs with different brood sizes (Montgomerie and Weatherhead 1988).

A second factor that might explain differences among studies in the effect of brood size on nest defense behavior is the type of predator used in experiments. As noted previously, some predators represent a threat to both adults and young (e.g., Eastern Screech-Owl in my study) and, because inducing such predators to leave the area is beneficial to adults, responses to such predators may be similar regardless of brood size. In contrast, given that the benefits of deterring a predator increase with the number of young, the intensity of nest defense by adults may be more likely to vary with brood size when responding to predators that only threaten young.

Stage of breeding season

I found no seasonal (monthly; May - August) variation in the intensity of nest defense by Eastern Bluebirds. Similar results have been reported for Redwings (*Turdus iliacus*; Bjerke et al. 1985) and Yellow Warblers (*Dendroica petechia*; Hobson et al. 1988). However, previous studies have revealed a decline in the intensity of nest defense as the breeding season progresses for some species of birds, including Eastern Kingbirds (Redmond et al. 2009), Meadow Pipits (Halupka and Halupka 1997), and Song Sparrows (Weatherhead 1989), whereas others have reported an increase in intensity as the breeding season progresses, e.g., Great Tits (Regelmann and Curio 1983). A possible explanation for a decline in intensity of nest defense later in the breeding season is the declining value of nestlings later in the season (in terms of adult fitness) because of the reduced likelihood of successful recruitment of such nestlings into the breeding population late in the season (Montgomerie and Weatherhead 1988). In contrast, an increase in the intensity of nest defense as the breeding season progresses may occur

because of a decline in re-nesting potential, i.e., with a reduced likelihood of being able to re-nest later in the season, adults should be willing to take greater risks to defend current nests (Montgomerie and Weatherhead 1988). For species like Eastern Bluebirds and others where the intensity of nest defense remains constant throughout the breeding season, Weatherhead (1989) proposed that the declining value of offspring as the season progresses may be balanced by the effect of declining re-nesting potential. However, another possible explanation is that, as with responses by parents with different-sized broods described previously, responses to predators like Eastern Screech-Owls that threaten both adults and young may remain constant throughout the breeding season because, regardless of time of year, inducing such predators to leave the area is always beneficial for adults as well as offspring.

Effect of WNV infection

The nest defense behavior of Eastern Bluebirds infected with WNV did not differ from that of non-infected bluebirds and, in addition, the behavior of adult bluebirds with an infected nestling did not differ from that of adults with no infected nestlings. Previous studies suggest that birds responding to induced immune challenges (i.e., caused by injecting non-pathogenic antigens) may increase reproductive investment (e.g., Bonneaud et al. 2004, Hanssen 2006, Velando et al. 2006, Bowers et al. 2012). Because increased effort in current reproduction can negatively impact future reproduction, animals should generally restrict current efforts to maximize lifetime reproductive success (Curio 1983). However, Clutton-Brock (1984) suggested that animals should invest more in current reproductive effort if the chance of surviving to reproduce again is

low, i.e., the terminal investment hypothesis. My results suggest that WNV infection, at least during the viremic stage, did not affect the physical condition of Eastern Bluebirds enough to affect their nest defense behavior. Similarly, Hill et al. (2010) found that being seropositive for WNV had no negative effects on the reproduction or survival of Eastern Bluebirds in Alabama.

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VITA

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