

EFFECTS OF RED IMPORTED FIRE ANTS ON SONGBIRD NEST SURVIVAL

A Thesis

by

ANDREW J. CAMPOMIZZI

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

May 2008

Major Subject: Wildlife and Fisheries Sciences

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ABSTRACT

Effects of Red Imported Fire Ants on Songbird Nest Survival. (May 2008)

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Chair of Advisory Committee: Dr. Michael L. Morrison

Invasive species are often implicated in population declines of native species through competition and predation. Red imported fire ant (*Solenopsis invicta*) predation of songbird nestlings and eggs has been documented. I conducted a replicated manipulative experiment to determine the magnitude of the decrease in nest survival caused by *S. invicta* in addition to other predators. I conducted mensurative experiments to quantify the frequency of *S. invicta* foraging near active songbird nests and factors that influence the susceptibility of songbird nests to *S. invicta* predation. I hypothesized that predation by *S. invicta* reduced nest survival by 10%, potentially biologically significant, and that songbird nests would be more susceptible to *S. invicta* predation that were located: (1) closer to the ground, (2) closer to an edge, (3) closer to disturbed soils, and (4) initiated later in the breeding season. I monitored 235 songbird nests including 45 black-capped vireo (*Vireo atricapilla*), 67 white-eyed vireo (*V. griseus*), and 123 northern cardinal (*Cardinalis cardinalis*) nests on 9 patches of 36–103 ha each on private land in east-central Texas, USA in 2006–2007. I found preventing *S. invicta* from preying upon songbird nests increased nest survival 20% for white eyed vireos and 1% for black-capped vireos. I detected *S. invicta* near songbird nest on 60% of food lures on the ground and 7% of food lures 1 m high in vegetation ($n = 122$). Vireo nests

<2 m high and <4 m from an edge were more susceptible to *S. invicta* predation indicating potential threshold conditions, below which songbird nests may be more susceptible. If my results are applicable to other areas then songbird populations of some species nesting below 2 m may have substantially lower nest survival in areas occupied by *S. invicta*. I suggest the negative impacts of *S. invicta* on songbird nest survival may be reduced by applying integrated pest management methods and increasing woody vegetation cover in breeding areas of songbird species susceptible to *S. invicta* nest predation.

ACKNOWLEDGEMENTS

I thank Dr. M. L. Morrison, Dr. R. N. Wilkins, Dr. J. M. Packard, and Dr. B. M. Drees for supporting my thesis research. I thank fellow graduate students including: S. Farrell, J. Butcher, T. Pope, T. Conkling, C. Lituma, J. Groce, C. Cocimano, and A. Knipps for advice, suggestions, and ideas. I thank Dr. B. Collier for guidance with analyses. My project was supported with funding from United States Department of Defense, Environmental Readiness Program, and the United States Department of Agriculture, Natural Resources Conservation Service. I thank the landowners and managers for allowing access to their properties for field work; S. Farrell, T. Conkling, T. Pope, J. Kruse, T. Westcott, J. Assmus, T. Lucas, Z. Lebrun-Southcott, J. Shewan, C. Lituma, C. Turner, L. Moulton, and C. Curry for assistance collecting field data; A. Calixto for assistance with ant identification in the field; B. Summerlin for identifying ant samples in the lab; B. Hays, S. Manning, D. Petty, L. Law, V. Buckbee, and M. Rubio for logistic support.

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INTRODUCTION

Invasive species are often implicated in population declines of native species through competition and predation (summarized by Caughley and Gunn 1996:71–147). Invasive ant species can negatively impact various native species because of their relatively high abundance and intense foraging ability compared with native ants (Holway et al. 2002). The red imported fire ant (*Solenopsis invicta*) is an invasive ant considered a threat to native species in the USA (Taber 2000, Allen et al. 2004), the Caribbean (Davis et al. 2001), Australia (Moloney and Vanderwoude 2002;2003), New Zealand (Pascoe 2001), and China (Zhang et al. 2005). Successful land management for susceptible, native prey and competitor species requires focused conservation efforts where *S. invicta* has already been introduced and anticipation of conservation needs where *S. invicta* are expected to colonize (Morrison et al. 2004, Sutherst and Maywald 2005).

S. invicta were accidentally introduced to North America in the 1930s from South America (Wilson 1951, Lofgren et al. 1975). Subsequently, researchers have documented the detrimental effects of *S. invicta* in the USA on native arthropods (Porter and Savignano 1990, Gotelli and Arnett 2000), birds, mammals, and herpetofauna (reviewed by Allen et al. 2004). *S. invicta* have also been implicated in the extinction of the tree snail (*Orthalicus reses reses*) in the USA (Forys et al. 2001). *S. invicta* are known nest predators of several songbird species in the Mississippi alluvial valley

This thesis follows the style of The Journal of Wildlife Management.

(Twedt et al. 2001), and barn swallows (*Hirundo rustica*) and black-capped vireos (*Vireo atricapilla*; Stake and Cimprich 2003) in Texas. Removal of *S. invicta* from breeding areas of ground nesting birds increased nest or fledgling survival for colonial nesting water birds (Drees 1994), least tern (*Sterna antillarum*; Lockley 1995), and northern bobwhites (*Colinus virginianus*; Allen et al. 1995, Mueller et al. 1999). These studies suggest that *S. invicta* likely reduce nest survival of songbirds in addition to losses from native nest predators.

Nest predation is the primary cause of nest failure for many songbird species (Nice 1957, Ricklefs 1969, Martin 1993). Management action to improve the nest survival of threatened or endangered songbird species is often suggested or undertaken to aid in recovering a species with small populations (e.g., Fish and Wildlife Service 1991, Cain et al. 2003). Predator-prey interactions involving songbird nests are complex systems, some predator removal experiments have resulted in nest survival increases (Jackson 2001, Schmidt et al. 2001) whereas others resulted in little change in nest survival (Beauchamp et al. 1996, Schmidt et al. 2001).

It is likely that active songbird nests, especially a nest with young, are identified as a food source by foraging *S. invicta* in the same manner as other food sources. *S. invicta* forage alone, walking in exploratory loops in search of food (Wilson 1962). When a forager finds food it consumes the food, carries the food back to the colony, or recruits other members of the colony to aid in recovering larger food items (Taber 2000:32–45). *S. invicta* recruit to food sources in large numbers (hundreds, Porter and

Tschinkel 1987) up to 40 m from their colony (Martin et al. 1998), subduing prey and out competing other species with their abundance and venomous sting.

The susceptibility of songbird nests to *S. invicta* predation is likely to vary spatially and temporally according to patterns of *S. invicta* distribution, abundance, and foraging. The higher a nest is located from the ground, the more likely that a forager would have located a food item closer to the ground before finding the nest. *S. invicta* foragers were more commonly detected in areas with less canopy cover and more direct sunlight (Porter et al. 1988, Porter and Savignano 1990, Stein et al. 1990, Stiles and Jones 1998). Summerlin et al. (1976) found *S. invicta* were more common in areas with more disturbed soils from grazing and Tschinkel (1987) found *S. invicta* were more common near paved roads, unpaved roads, and agriculture. *S. invicta* have been found to be more active (Porter and Tschinkel 1987, Porter and Savignano 1990) and prefer protein food sources during warmer months (Stein et al. 1990). It is important to note that the studies mentioned above found that *S. invicta* were more common or more active under certain conditions, but were also present and less active in other areas. Thus, any songbird nest may potentially be at risk of predation by *S. invicta*, but susceptibility of nests may follow certain patterns.

I investigated the effect of *S. invicta* on nest survival of the federally endangered black-capped vireo and 2 more common songbird species, white-eyed vireos (*V. griseus*) and northern cardinals (*Cardinalis cardinalis*). I selected these species because *S. invicta* have been identified as a primary predator of black-capped vireo nests in east-central Texas (Stake and Cimprich 2003). Also, both white-eyed vireos and northern

cardinals co-occur with black-capped vireos, nesting in the same vegetation. Major factors contributing to population declines of black-capped vireos were habitat loss and nest parasitism by brown-headed cowbirds (*Molothrus ater*; U.S. Fish and Wildlife Service 1991). Native predators of black-capped vireo nests include species of reptiles, mammals, and birds (Graber 1961, Stake and Cimprich 2003). *S. invicta* was an additional nest predator in this ecological system and was currently found throughout much of the southern USA including most of black-capped vireo breeding range (Figure 1). I conducted a replicated manipulative experiment to determine if *S. invicta* caused a $\geq 10\%$ decrease in nest survival in addition to native predators, and mensurative experiments to quantify the frequency of *S. invicta* foraging near active songbird nests and factors that influence the susceptibility of nests to *S. invicta* predation. I tested a reduction in nest survival of $\geq 10\%$ because sensitivity analyses for other songbird species (Porneluzi and Faaborg 1999, Powell et al. 1999) have suggested it may be biologically significant for population dynamics. Also, I hypothesized that songbird nests would be more susceptible to *S. invicta* predation for nests: (1) closer to the ground, (2) closer to an edge, (3) closer to disturbed soils, and (4) initiated later in the breeding season.

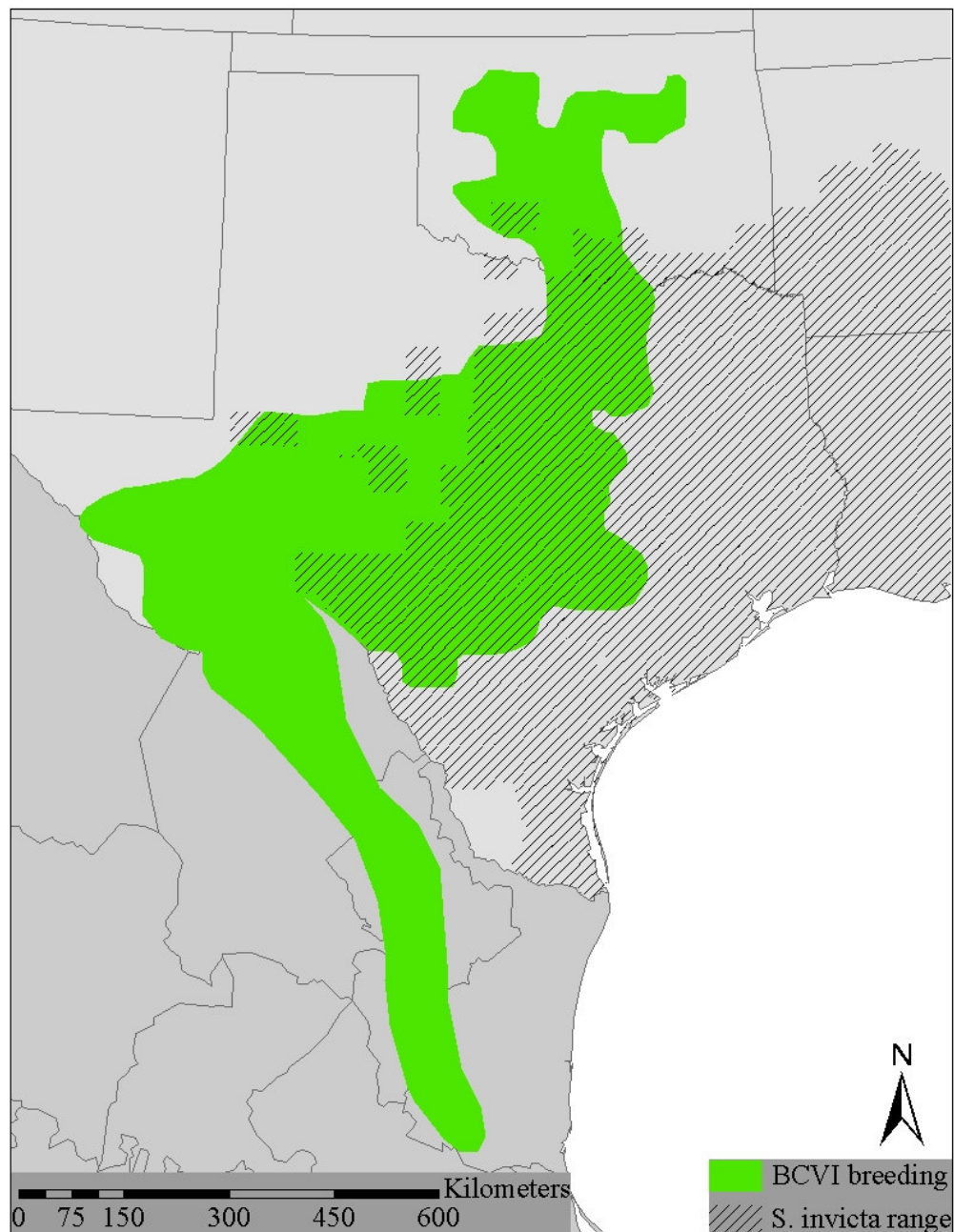


Figure 1. Overlap of black-capped vireo (BCVI) breeding range and *Solenopsis invicta* range in the southern USA and north-eastern Mexico. Black-capped vireo range estimate from Wilkins et al. (2006) and *S. invicta* range estimate from USDA (<http://www.aphis.usda.gov/>).

STUDY AREA

I used 9 sampling units located on 11 private land parcels in the Leon river watershed in Coryell County in east-central Texas, USA. Permission to access private land limited sampling unit selection because most land in this region was privately owned. I used the results of previous presence-absence surveys for all avian species in 2006 on 21 private properties and 1 state park and in 2007 on 32 properties and 1 state park within a 140,000 ha area to select our 9 sampling units of 36–103 ha. These 9 sampling units were the only patches of vegetation where black-capped vireos were detected. Vegetation on sampling units consisted of mid-successional stage woody vegetation similar to areas occupied by black-capped vireos in the nearby Lampasas Cut Plains (see Grzybowski et al. 1994, Bailey and Thompson 2007) and ecotones between mature oak-juniper (*Quercus-Juniperus*) woodland and grassland. Landscape topography in the study area includes hills and mesas with elevation range 200–500 m. Primary land uses on private lands in the study area were ranching, farming, and hunting.

METHODS

My target population was nesting black-capped vireos in the study area. I included white-eyed vireos and northern cardinals that co-occurred with black-capped vireos to broaden the information collected on effects of *S. invicta* on nesting songbirds in general and to increase sample size. I assumed *S. invicta* would potentially prey upon any bird nest found while foraging (i.e., not selecting one species' nest over another) because songbird nests would provide a similar source of protein (Stein et al. 1990). I included black-capped vireo, white-eyed vireo, and northern cardinal nests found 0.4 to 4.2 m high in woody vegetation in our sample. I used nests of these heights because it was within the height range of black-capped vireo nest placement in our study area and mostly typical of black-capped vireo nest placement in general (Graber 1961, Grzybowski 1995).

Nest Survival

I used behavioral cues and systematic searching (Martin and Geupel 1993) to locate active songbird nests from 15 March to 31 July during 2006 and 2007. I visited active nests every 3–4 days to determine outcome (i.e., nest fledged ≥ 1 young, or failed) and presence or absence of *S. invicta*. I considered a nest successful if we saw adults carrying food to fledglings or we detected fledglings by sight or sound while visiting nests after a penultimate visit with large nestlings near fledging age. I considered nests failed if we did not observe fledglings or adults carrying food when visiting nests that previously had nestlings.

I assigned each nest to either the treatment or control group using a probabilistic starting point followed by systematic assignment. Assignment of treatment or control for the first nest found for each species was decided by a coin toss. Assignment to treatment or control group alternated for each additional nest found. I used this method to assign treatments and controls to intersperse treatment nests and control nests in space and time within each sampling unit (sensu Hurlbert 1984). I treated individual nests rather than reducing *S. invicta* abundance in areas with ant-specific broadcast poison baits, as is typically done in *S. invicta* research (e.g., Martin et al. 1998, Calixto et al. 2007). This method allowed me to intersperse treatments thus reducing spatial effects, increasing sample size, and avoiding the unknown affects of removing *S. invicta* from the nest predator assemblage (e.g., cause a population response of other nest predators).

I prevented *S. invicta* from preying upon treatment nests by applying a chemical barrier (Spiral Wrap Arinix™, Nix of America, San Jose, CA) and a physical barrier (Tree Tanglefoot® Pest Barrier, The Tanglefoot Company, Grand Rapids, MI) to branches supporting nests. The Spiral Wrap is a 5 cm long flexible plastic which contains 8.6% permethrin and was originally designed to prevent small insects from entering automobile vents. Permethrin is a low toxicity pesticide used in outdoor clothing to repel small insects (e.g., ticks, mosquitoes). The Spiral Wrap slowly releases permethrin from the plastic and stops ants from crossing the chemical barrier (B. M. Drees, Texas A&M University, unpublished data). Tanglefoot is a natural gum resin that passively catches crawling insects, stopping them from climbing trees and damaging agricultural products (e.g., fruits, nuts). I applied the Tanglefoot Pest Barrier to the

branch supporting a treatment nest ≥ 0.25 m from each nest. I wrapped a Spiral Wrap around the branch on top of the Tanglefoot Pest Barrier allowing the Tanglefoot to fill gaps between the branch and Spiral Wrap. I assumed the barrier did not deter other predators (e.g., snakes, birds, mammals) from preying upon nests because these predators could easily maneuver past the insect-specific, 5 cm barrier. If the barrier deterred other nest predators then observed treatment effects would be due to treatment nests being protected from ants plus other nest predators. To control for any potential effects of applying the spiral wrap or its presence at nests, we attached an inert spiral wrap to branches supporting control nests.

Vireo nests were built on a single isolated branch, enabling the use of the ant barrier to block the only access point to the nest available to ants. I was not able to successfully deploy ant barriers at northern cardinal nests because nests were supported by many branches allowing ants to access the nest from multiple locations. Thus, I did not include northern cardinal nests in the manipulative experiment because the ant barrier was ineffective. I did, however, include northern cardinal nests in mensurative experiments below.

I determined the magnitude of effect of *S. invicta* nest depredation on black-capped and white-eyed vireo nest survival both separately and combined. I analyzed nest survival separately for each vireo species to examine potential differences in the treatment effect between species. I analyzed nest survival for both vireo species combined to enable analysis of nest stage survival and between-year differences in nest survival. I defined nest survival (\hat{S}^t) as the probability that a nest successfully fledged at

least 1 young bird, daily survival rate as the probability that a nest survived one day, and nest stage survival as the probability that a nest would remain active during the incubation or nestling stage. I used a modified Mayfield (1961;1975) method to calculate estimates of daily survival rate and nest survival corrected for exposure days. I modified Mayfield's method by using the number of days nests were active under treatment rather than the total number of exposure days nests were observed active. I made this modification to ensure that the effect of the treatment on nest survival was being measured. I calculated 2 SE for nest survival estimates using Johnson's (1979) method. I used the estimates of nest survival and associated error to compare nest survival between treatments, species, and nest stages.

***S. invicta* Activity Near Nests**

I measured *S. invicta* foraging activity relative to active songbird nests using food lures to determine if *S. invicta* were actively foraging near nests. I measured foraging activity at as many nests as possible, however, many nests failed before I was able to sample for ants. Food lures have been used to detect ant species and monitor fluctuations in the number of foragers over time (see Drees 1994, Barr and Best 2002). I placed 1 food lure (i.e., 4 cm² peanut oil soaked index card) on the ground and 1 placed 1.0 m high in woody vegetation. I placed food lures about 10 m from each active songbird nest assuming that both the active songbird nest and food lure to be within the estimated 40 m range that *S. invicta* forage from each colony (Martin et al. 1998). I collected food lures after 40–60 min and recorded if the lure was discovered by foraging *S. invicta* and estimated the number of *S. invicta* on discovered lures. When *S. invicta*

were not detected on food lures during initial sampling at a nest, I resampled for *S. invicta* 3 to 4 days later if the nest was still active. I did not resample at a nest once *S. invicta* were detected on food lures. I collected samples of ants found on food lures and in songbird nests and had them identified by a technician at the Center for Urban and Structural Entomology, Department of Entomology, Texas A&M University. I summarized *S. invicta* activity by calculating the proportion and 2 SE of food lures with *S. invicta* detections on the ground and 1 m high. I compared *S. invicta* activity between the ground and 1 m high, and between years using the mean and 2 SE.

Nest Susceptibility to *S. invicta*

I recorded if *S. invicta* were detected in nests during nest monitoring visits. I measured nest height (i.e., distance from the ground to the top of the nest) and distance to edge (i.e., horizontal distance from the nest to the nearest location where branches and leaves of woody vegetation did not overlap) once nests became inactive. I recorded the location of each nest using a hand held GPS (Global Positioning System) accurate to 6 m. I used our GIS (Geographic Information System, ESRI® ArcMap™ 9.1, Redlands, CA) to measure the distance from each nest to the nearest soil disturbance (i.e., trail, road, or agriculture) visible on a 2006 National Agricultural Imagery Program aerial photograph downloaded from <<http://datagateway.nrcs.usda.gov/>>. I classified songbird nests as initiating during a particular week of the 15 week nesting season based on the date the first host egg was laid in each nest.

I analyzed nest susceptibility data by examining box plots, scatter plots, histograms, and calculating mean and 2 SE of nest susceptibility variables. I tested for

statistical significance of nest susceptibility variables between nests with and without *S. invicta* detections using Mann-Whitney U tests ($\alpha = 0.05$). I did not use logistic regression because while I had data for 122 songbird nests, I detected ants in only 8 of these nest making it difficult for this type of analysis to detect relatively small differences between nests with and without *S. invicta* detections. I used SPSS 14.0.2 (SPSS Inc., Chicago, Illinois, USA) for statistical analyses.

RESULTS

I found nests for black-capped vireos, white-eyed vireos, and northern cardinals on all 9 sampling units. I monitored 235 songbird nests including 45 black-capped vireo, 67 white-eyed vireo, and 123 northern cardinal nests.

Nest Survival

I monitored 71 nests for our manipulative experiment comprised of 27 black-capped vireo and 44 white-eyed vireo nests. I found nest survival for black-capped and white-eyed vireos was 10% lower for control nests ($\hat{S}^t = 0.038$, $n = 40$) than for treatment nests ($\hat{S}^t = 0.138$, $n = 31$; Table 1). I found nest survival varied between years. Nest survival was 7% lower for control nests in 2006 ($\hat{S}^t = 0.018$, $n = 19$) than 2007 ($\hat{S}^t = 0.081$, $n = 21$; Table 1). Nest survival was 0.3% lower for treatment nests in 2006 ($\hat{S}^t = 0.120$, $n = 15$) than 2007 ($\hat{S}^t = 0.154$, $n = 16$; Table 1). I found that the magnitude of the effect of the treatment varied between when the nest was in the incubation stage and the nestling stage. I found nest stage survival was 7% lower during incubation for control nests ($\hat{S}^t = 0.23$, $\pm 2SE = 0.224\text{--}0.238$) than for treatment nests ($\hat{S}^t = 0.30$, $\pm 2SE = 0.284\text{--}0.312$; Table 2). Nest stage survival during nestling stage was 37% lower for control nests ($\hat{S}^t = 0.19$, $\pm 2SE = 0.184\text{--}0.206$) than for treatment nests ($\hat{S}^t = 0.56$, $\pm 2SE = 0.524\text{--}0.594$; Table 2). I found that the magnitude of the effect of the treatment on nest survival was different for black-capped vireos than for white-eyed vireos. I found nest survival was 1% lower for black-capped vireo control nests ($\hat{S}^t = 0.027$, $n = 14$) than for treatment nests ($\hat{S}^t = 0.040$, $n = 13$; Table 3). Nest survival was 20% lower for white-

eyed vireo control nests ($\hat{S}^t = 0.044$, $n = 26$) than for treatment nests ($\hat{S}^t = 0.246$, $n = 18$; Table 3).

Table 1. Modified Mayfield estimates of daily survival rate (DSR) and nest survival (probability of a nest successfully fledging ≥ 1 bird) combined for black-capped and white-eyed vireo nests on private land in 2006 and 2007 in east-central Texas, USA. Treatment nests were protected from ant predation.

	DSR	Nest survival	± 2 SE	<i>n</i>
2006				
Control	0.8623	0.012	0.011–0.013	19
Treatment	0.9317	0.120	0.105–0.137	15
2007				
Control	0.9194	0.081	0.075–0.087	21
Treatment	0.9396	0.154	0.139–0.170	16
Total				
Control	0.8968	0.038	0.037–0.039	40
Treatment	0.9361	0.138	0.132–0.144	31

Table 2. Modified Mayfield estimates of daily survival rate (DSR) and stage survival (probability that a nest survived the stage with ≥ 1 young) during incubation and nestling stages combined for black-capped and white-eyed vireo nests monitored 2006–2007 in east-central Texas, USA.

	DSR	Stage survival	± 2 SE
Incubation			
Control	0.9125	0.23	0.224–0.238
Treatment	0.9271	0.30	0.284–0.312
Nestling			
Control	0.8618	0.19	0.184–0.206
Treatment	0.9483	0.56	0.524–0.594

Table 3. Modified Mayfield estimates of daily nest survival (DSR) and nest survival (probability of a nest successfully fledging ≥ 1 bird) for black-capped (BCVI) and white-eyed vireo (WEVI) nests during 2006–2007 in east-central Texas, USA. Treatment nests were protected from ant predation.

	DSR	Nest survival	± 2 SE	<i>n</i>
BCVI				
Control	0.887446	0.027	0.024–0.032	14
Treatment	0.898618	0.040	0.034–0.048	13
WEVI				
Control	0.901288	0.044	0.042–0.047	26
Treatment	0.954338	0.246	0.225–0.269	18

***S. invicta* Activity Near Nests**

I sampled for ant activity using food lures near 122 active black-capped vireo, white-eyed vireo, and northern cardinal nests. I detected *S. invicta* near songbird nest on 60% of food lures on the ground and 7% of food lures 1 m high in vegetation during both years of research ($n = 122$). Detections of *S. invicta* on food lures varied between 2006 (71% of food lures on the ground and 5% of food lures 1 m high [$n = 56$]) and 2007 (50% of food lures on the ground and 8% of food lures 1 m high [$n = 66$]). I detected *S. invicta* on 21% more food lures in 2006 than 2007 (Figure 2). I identified 5 genera of ants foraging on food lures near active songbird nests: *S. invicta*, red harvester

ant (*Pogonomyrmex barbatus*), pharaoh and little black ants (*Monomorium* spp.), cheese ants (*Forelius* spp.), and big-headed ants (*Pheidole* spp.).

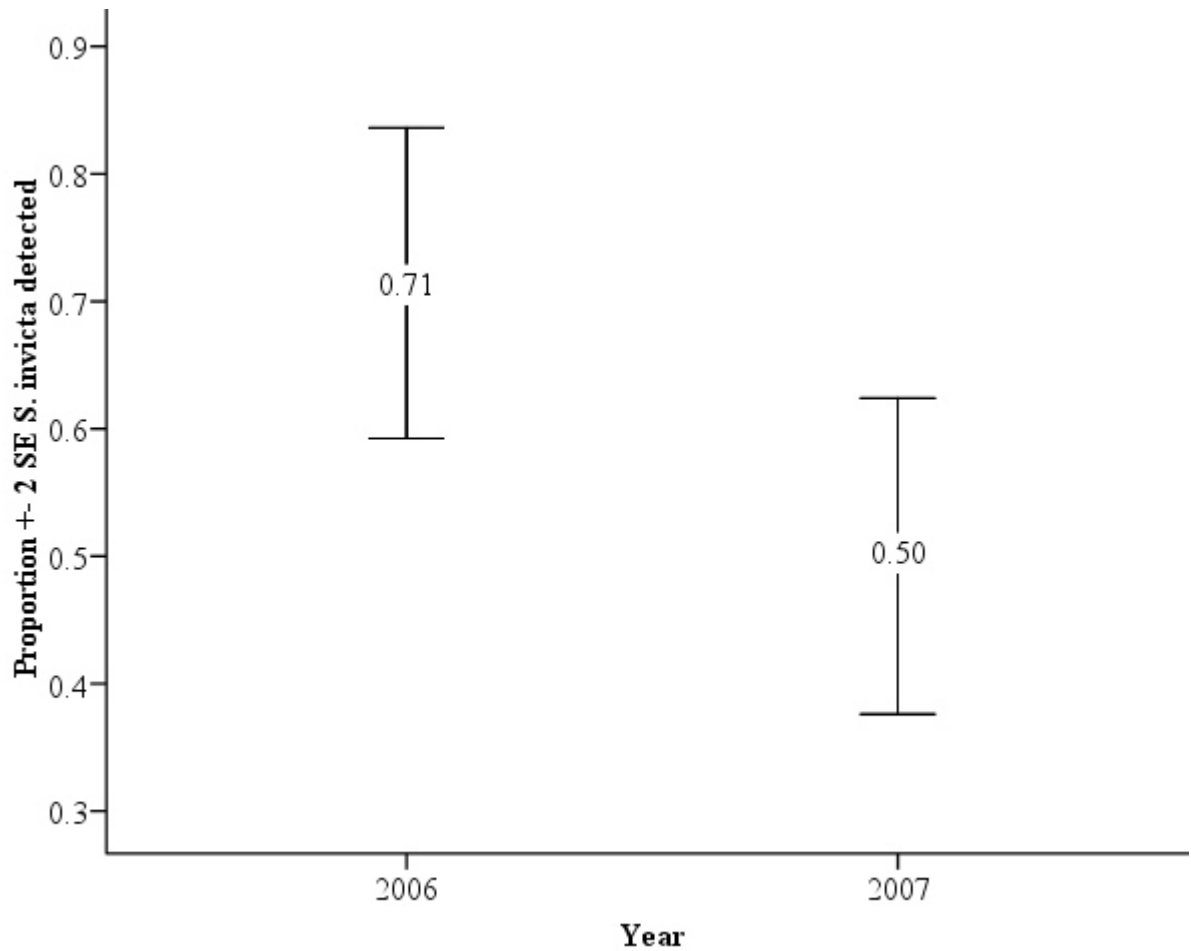


Figure 2. The proportion of food lures with *S. invicta* detections and 2 SE for food lures placed 10 m from active songbird nests (black-capped vireo, white-eyed vireo, and northern cardinal) monitored 2006–2007 in east-central Texas, USA.

Nest Susceptibility to *S. invicta*

I detected *S. invicta* in 8 of the 122 black-capped vireo, white-eyed vireo, and northern cardinal nests monitored for nest susceptibility. I found that nests with *S. invicta* detections were 14% lower ($\bar{x} = 1.2$ m, $n = 8$) than nests without *S. invicta* detections ($\bar{x} = 1.4$ m, $n = 114$), but the difference was not statistically significant ($U = 385.5$, $P = 0.46$; Table 4). I did not detect *S. invicta* in nests above 2 m high despite monitoring 19 nests above 2 m. I found that distance to edge was not different between nests with ($\bar{x} = 7.4$ m, $n = 8$) and without *S. invicta* detections ($\bar{x} = 3.2$ m, $n = 114$; $U = 405.5$, $P = 0.60$; Table 4). I noted, however, that 6 of the 8 nests with *S. invicta* detected in the nest were <4 m from the edge. I found that distance to soil disturbance ($U = 391.0$, $P = 0.50$, $n = 114$) and first egg week ($U = 403.5$, $P = 0.59$, $n = 114$) were not different between nests with and without *S. invicta* detections (Table 4).

Table 4. Mean and 2SE for nest height, distance to edge, distance to soil disturbance, and first egg week of nest initiation for songbird nests (black-capped vireo, white-eyed vireo, and northern cardinal) with and without *S. invicta* detected in nests in 2006–2007 in east-central Texas, USA.

	Nest height		Distance to edge		Distance to disturbance		First egg week		
	\bar{x}	± 2 SE	\bar{x}	± 2 SE	\bar{x}	± 2 SE	\bar{x}	± 2 SE	
No ants	1.4	1.2–1.5	3.2	2.2–4.2	40.4	34.9–45.9	6.8	6.1–7.4	114
Ants	1.2	0.8–1.5	7.4	0.0–15.2	52.0	25.5–78.5	7.6	4.6–10.7	8

DISCUSSION

Nest Survival

I hypothesized that *S. invicta* would cause a $\geq 10\%$ reduction in nest survival and thus, potentially negatively impact songbird populations. I found that preventing ants from preying upon vireo nests increased estimates of nest survival by 10%, suggesting *S. invicta* nest depredation has a biologically significant impact on black-capped and white-eyed vireo populations on our study sites in central Texas (Porneluzi and Faaborg 1999, Powell et al. 1999). The 10% increase in nest survival I found through preventing *S. invicta* from preying upon songbird nests corresponds to the frequency of 10–11% that researchers have observed *S. invicta* in nests. For example, Stake and Cimprich (2003) found that *Solenopsis* spp. accounted for 11% of nest failures in black-capped vireos using video cameras on Fort Hood, Texas. Similarly, Twedt et al. (2001) observed that *S. invicta* caused nest failure at 10% of songbird nests where predators could be identified on cottonwood plantations in Louisiana and Mississippi. Although our treatment method acted as a barrier to all ant species, *S. invicta* were the most common and abundant ant in the study area, detected at 83% of food lures where ants were detected, suggesting they pose the greatest threat to songbird nests.

I found *S. invicta* had the largest impact on nest survival during the nestling stage, reducing survival of this stage by 37% in control nests not protected from *S. invicta* (Table 2). These results suggest that vireo nests with nestlings may be more easily located by and recruited to by *S. invicta* foragers. Video monitoring of nests have shown that fire ant ants swarmed black-capped vireo nests with nestlings more often

than nests with eggs (Stake and Cimprich 2003). Researchers have observed *S. invicta* preying upon nestlings of several birds species including: least tern, black rail (*Laterallus jamaicensis*), barn swallow, cliff swallow (*Hirundo pyrrhonota*), crested caracara (*Caracara plancus*), northern bobwhite, and wood duck (*Aix sponsa*; summarized by Suarez et al. 2005). Our data suggest that *S. invicta* were important nest predators in this ecological system, however, most nests I monitored did not fail because of *S. invicta*. There were many possible reasons for nest failure in our system including other nest predators, brood parasitism, inclement weather, abandonment, infertile eggs, and nestling starvation.

I found that preventing *S. invicta* from preying upon songbird nests showed an increase in nest survival for both black-capped and white eyed vireos, however, the increase was 20% for white-eyed vireos and 1% for black-capped vireos (Table 3). I were unsure why the response in nest survival was different for these species considering they share many similar life history characteristics including overlap in spatial and temporal nesting characteristics (Grzybowski 1995, Hopp et al. 1995). Nests included in our experiment were interspersed both spatially and temporally on each sampling unit and nest heights averaged 1.2 m ($\pm 2SE = 1.0-1.4$; $n = 27$) for black-capped vireos and 1.5 m ($\pm 2SE = 1.3-1.7$; $n = 44$) for white-eyed vireos. These similarities between black-capped and white-eyed vireo nesting ecology suggest that they were subjected to similar causes of nest failure. Nest survival was lower for black-capped vireos than for white-eyed vireos possibly due to higher frequency of nest parasitism by brown-headed cowbirds on black-capped vireos in our study area (Farrell 2007). I suggest that subtle

differences in breeding behavior or nest placement may lead to lower nest survival in black-capped vireos than white-eyed vireos.

I found that nest predation by *S. invicta* reduced nest survival for endangered black-capped vireos and more common white-eyed vireos in addition to native predators of songbird nests in our study area in central Texas. If our results are applicable to other areas then populations of some songbird species nesting within 2 m of the ground may be negatively impacted within the 320,000,000 ha currently occupied by *S. invicta* in the USA (USDA 2007). I suspect the effects of *S. invicta* on nest survival of songbirds to vary spatially and temporally considering the complex interactions of nest predator assemblages (Beauchamp et al. 1996, Jackson 2001, Schmidt et al. 2001) and other reasons for nest failure.

***S. invicta* Activity Near Nests**

I did not know how common *S. invicta* would be in our study area. I found that *S. invicta* were present in all sampling units and were nearly ubiquitous. Our finding of higher nest survival of control nests in 2007 than 2006 was correlated with lower *S. invicta* activity in 2007 than 2006 (Table 1, Figure 2). Decreased *S. invicta* activity is likely due to different weather conditions between years. Weather in 2006 was hot (20.8 °C) and dry (37.2 cm) compared with cooler (18.3 °C) rainy (102.7 cm) weather in 2007 (30 yr normals were 19.1 °C for January – July and 50.8 cm precipitation; NOAA 2007). I observed *S. invicta* tending to larvae and rebuilding mounds between frequent the rain events of 2007, presumably reducing foraging effort and subsequent predation on songbird nests. *S. invicta* activity is dependent on temperature and rainfall (Porter and

Tschinkel 1987, Porter and Savignano 1990) suggesting that *S. invicta* impact on songbird nests during cool rainy years may be less than during hot dry years.

Nest Susceptibility to *S. invicta*

I hypothesized that songbird nests located closer to the ground, nearer to an edge, nearer to soil disturbance, and initiated later in the breeding season would be more susceptible to predation by *S. invicta*. My small sample size of songbird nests with *S. invicta* detected in the nest made data analysis for biological meaningful effects difficult, but I found several interesting trends in the data. My data suggested that nests <2 m high and <4 m from an edge were more susceptible to *S. invicta* predation indicating potential threshold conditions, below which songbird nests may be more susceptible (sensu Lindenmayer and Luck 2005, Luck 2005). My ability to detect *S. invicta* in nests may have been limited because I checked higher nests with hand-held mirrors and I visited nests once every 3 to 4 days. It may be beneficial in similar, future studies to reduce these potential detection problems either by visiting nests more often, monitoring nests with cameras, or using sticky traps to capture foraging ants.

My findings of a potential threshold of nest height, below which songbird nests are vulnerable to predation by *S. invicta*, is supported by several video camera studies of nest predators. Stake and Cimprich (2003) found that 11% ($n = 142$) of black-capped vireo nests were lost to *Solenopsis* spp. compared to Stake et al. (2004) and Reidy (2007) who found that 0% ($n = 61$) and 2% ($n = 67$), respectively, of golden-cheeked warbler (*Dendroica chrysoparia*) nests were lost to *Solenopsis* spp. Median height for black-capped vireos has been reported as 1.0 m (range 0.2, 3.0) compared to 5 to 7 m for

golden-cheeked warblers (Grzybowski 1995, Ladd and Gass 1999). These studies support a threshold of nest height susceptibility, but there are other potential explanations including different habitat requirements for the 2 species and associated land uses that could affect *S. invicta* distribution, abundance, and foraging.

Nest predation is often found to be higher near edges although not in all landscapes (Tewksbury et al. 1998). It is likely that landscape structure and natural history characteristics of nest predators determine if songbird nests near edges are more susceptible to predation. My results suggest that nests near edges of woody vegetation (<4 m) are more likely to be preyed upon by *S. invicta* which is supported by studies of *S. invicta* distribution and abundance (Porter et al. 1988, Porter and Savignano 1990, Stiles and Jones 1998).

The potential effects of *S. invicta* on songbird nest survival is substantial because of the extensive and expanding range of *S. invicta* in the USA and worldwide (Morrison et al. 2004, Sutherst and Maywald 2005). More studies to quantify the effects of *S. invicta* and other invasive species on songbird nest survival are needed. For example, I found that nest survival for 2 co-occurring congeners responded differently to our treatment for excluding ants as nest predators. Further investigation to determine why similar songbird species may respond differently to invasive nest predators would be helpful. Building this body of knowledge will enable biologists to understand which avian species are susceptible to invasive predators and aid in directing conservation efforts to those species that are susceptible to nest losses by invasive species (sensu: Parker et al. 1999).

SUMMARY OF MANAGEMENT IMPLICATIONS

My findings suggest *S. invicta* predation can reduce nest survival up to 20% for some songbird species. Thus, suppression of *S. invicta* populations in songbird breeding areas with susceptible nests and populations of concern (i.e., threatened, endangered, locally rare) may be a management action to consider to increase songbird productivity. Suppression of *S. invicta* populations in songbird breeding areas may be accomplished through integrated pest management (Drees and Gold 2003, Pereira 2003) and increasing woody vegetation cover to provide nesting areas for songbirds distant from edges and less fragmented. It may be useful and more feasible to focus suppression of *S. invicta* specifically around the edges of woodland and shrubland breeding patches of susceptible songbirds because I found nests near edges were more susceptible to predation. I emphasize that my methods excluded *S. invicta* from nests altering the functional, but not numerical response of *S. invicta*. Suppression of *S. invicta* populations in songbird breeding areas may have ecological consequences on the nest predator assemblage that are not yet realized (e.g., resulting in an increase in rodent or snake populations).

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