Invasive Fire Ant (Solenopsis invicta) Predation of Eastern Fence Lizard (Sceloporus undulatus) Eggs

CHRISTOPHER J. THAWLEY1 AND TRACY LANGKILDE

Department of Biology, Intercollege Graduate Degree Program in Ecology, and Center for Brain, Behavior and Cognition, Pennsylvania State University, University Park, Pennsylvania USA

ABSTRACT.—Invasive species are a threat to biodiversity, and understanding their impacts on native ecosystems is a research priority. Imported red fire ants (Solenopsis invicta) are invasive in the southeastern United States and have multiple effects on a variety of native species. In some species and particular life stages (e.g., juveniles and eggs), native species may be especially vulnerable to fire ants, but research on these impacts has been limited. Fire ants occupy microhabitats used for nesting by Eastern Fence Lizards (Sceloporus undulatus) across much of their range. We examined the extent of fire ant predation on fence lizard eggs by constructing artificial nests at a fire ant–invaded location and monitoring their predation for up to 20 days. During this period, 24% of nests were predated by fire ants, and survival curves suggest 61% of nests may be vulnerable to fire ant predation over the entire incubation period. Distance of nests to the nearest fire ant mound and canopy cover above nests were not significant predictors of predation, indicating that nest site choice by fence lizards may not be able to avert fire ant predation. Invasive fire ants likely represent a novel level of predation pressure on many species, and these effects should be accounted for in management and conservation strategies.

Invasive species are a major threat to biodiversity worldwide and have important ecological and economic impacts (Wilcove et al., 1998). Nonnative invaders have been implicated as causative agents of changes in nutrient cycling, alterations in community structures, loss of ecosystem services, reductions in abundance in affected species, and species extirpations and extinctions (Pyšek and Richardson, 2010). Research into the mechanisms by which invasive species impact and interact with native species is key to understanding the extent and strength of their effects on ecosystems and making informed and accurate predictions and management decisions concerning invaders (Sax et al., 2005).

Ants are one of the most successful taxa of animal invaders and have diverse and extensive ecological impacts worldwide (Cole et al., 1992; Holway et al., 2002). These effects include changes in the abundance and distribution of native invertebrates and vertebrates and corresponding alterations to mutualisms, pollination, seed dispersal, and other ecological processes (Holway et al., 2002). Imported red fire ants (Solenopsis invicta) are native to South America and have become invasive in over seven countries, including in the southeastern United States (Tschinkel, 2006). Previous research has revealed both direct and indirect impacts of fire ants on native species at both local and biogeographical scales (reviewed in Allen et al., 1994; Gotelli and Arnett, 2000; Wojcik et al., 2001).

Many of the direct effects of fire ants on native species are the result of these ants responding quickly and in large numbers to defend their nest mounds or capture prey, resulting in both sublethal and lethal interactions with organisms, including vertebrates (Allen et al., 2004; Tschinkel, 2006). Fire ant venom has both hemolytic and neurotoxic effects, and stings can lead to paralysis, infections, and loss of digits or vision (Wojcik et al., 2001; dos Santos Pinto et al., 2012). Encounters with fire ants can cause species to alter habitat use (Killian et al., 1995; Holtcamp et al., 1997) and change activity levels (Pedersen et al., 1996) and can result in altered physiological (Graham et al., 2012) and behavioral responses to stress (Trompeter and Langkilde, 2011). Attacking fire ants also can overwhelm and kill vertebrates, and direct predation by fire ants has been observed on multiple species (reviewed in Allen et al., 2004).

Many native species have life stages that lack defenses, either behavioral or otherwise, to invasive fire ants and, therefore, are particularly vulnerable (reviewed in Allen et al., 2004). Fire ants pose the greatest threat to immobile individuals (such as the sick or young, Allen et al., 2004) and to species that respond to threats by becoming immobile (e.g., Box Turtles, Montgomery, 1996; deer fawns, Allen et al., 1997; hognosed snakes, Tuberville et al., 2000; and fence lizards, Langkilde, 2009a). Juveniles of some species, such as turtles or nestling birds, have limited mobility or opportunity to escape attack by foraging fire ants (Drees, 1994; Epperson and Heise, 2003), and hatchlings are particularly vulnerable after they have pipped their eggs but not yet emerged (Allen et al., 2004). Fire ants also are capable of penetrating intact eggs of some species (Moulis, 1997; Wojcik et al., 2001). Reptile eggs seem to be particularly vulnerable, and fire ants have penetrated the eggs of many reptile species in both the laboratory (Diffie et al., 2010) and field (Mount et al., 1981; Thawley, 2014); however, studies looking at the potential impacts of fire ants on nesting and reproductive success in lizards are rare (but for effects of native Solenopsis, see Chalcraft and Andrews, 1999).

Eastern Fence Lizards (Sceloporus undulatus) are vulnerable to fire ants as both juveniles and adults (Langkilde, 2009a; Robbins and Langkilde, 2012), and fire ants can penetrate and consume fence lizard eggs during staged, field encounters (Newman et al., 2014); however, we currently lack knowledge about the prevalence of fire ant predation on lizard eggs in the field and its contributing factors. By constructing artificial nests in areas invaded by fire ants and monitoring their survival, we conducted a field study to 1) quantify the predation pressure of fire ants on fence lizard nests and 2) determine whether nest site conditions (canopy cover) and location (distance from fire ant mound) affect levels of fire ant predation.
We conducted egg predation trials at Solon Dixon Forestry Education Center, Escambia County, Alabama, where *S. undulatus* nests successfully (CJT, pers. obs.). We placed artificial nests in edge habitats where mixed pine/hardwood forests dominated by longleaf (*Pinus palustris*) and loblolly pine (*Pinus taeda*) graded into mowed field habitats and areas around roadsides and outbuildings. In these habitats, fire ant mounds were spaced an average of 10 m apart (Langkilde, 2009b); mound densities were comparable to other disturbed, fire ant-invaded sites (Tschinkel, 2006). Trials were conducted from 26 June to 17 July 2013, a period during which *S. undulatus* eggs were naturally incubating at this site.

We obtained eggs for trials from female fence lizards caught across the eastern United States at sites with (Alabama, Mississippi) or without (Arkansas, Tennessee, Pennsylvania, and New Jersey) a history of fire ant invasions. Lizards were housed in tubes with moist sand allowing for nest construction, and enclosures were checked twice daily for freshly laid eggs. We incubated eggs in moist vermiculite (~200 kPa) for 7–27 days before placing them in artificial field nests.

Artificial *S. undulatus* nests were constructed by modifying the methods of Buhlmann and Coffman (2001) to allow for daily observations of nests without continual soil disturbance likely to attract fire ants. Nests were placed in open, sandy soils that *S. undulatus* prefers for nesting (Angilletta et al., 2009) and were constructed by digging 10-cm diameter holes 15 cm deep into the soil. We inserted clear, acrylic tubes (7-cm diameter, 30.5-cm length; Uline S-7017) with white vinyl endcaps (S-14134, Uline, Inc., Pleasant Prairie, WI) into these holes and placed six *S. undulatus* eggs (a realistic clutch size, Du et al., 2014; CJT, pers. obs.) 7–9 cm below the surface and in contact with the outer wall of the tubes (Fig. 1). Small pieces of plastic transparency were placed above the eggs to prevent soil entering the immediate space around them, and soil was carefully replaced around the eggs and tube. This allowed for a small amount of empty space to remain around the eggs and provided for viewing eggs from the interior of the tube. To prevent sunlight from entering the aboveground portions of the tubes and heating the eggs to levels above soil temperatures, each tube was lined with white plastic to reflect sunlight, capped and filled with a plastic bag of soil to ground level. If *S. invicta* entered an artificial nest during construction, we relocated the nest as a nesting female would likely do.

For each artificial nest, we measured distance to nearest fire ant mound as well as percent canopy cover using a spherical densitometer (Model C, Forestry Suppliers Inc., St. Jackson, MS), a cheap, simple method of estimating wide-angle light penetration (Fiala et al., 2006). Pilot trials revealed that Nine-Banded Armadillos (*Dasypus novemcinctus*) will dig next to observation tubes inserted into the ground and prey on lizard eggs; therefore, we surrounded each artificial nest with an exclosure 60 cm in diameter and made from galvanized fencing that did not exclude fire ants.

We monitored nests daily for 15–20 days by removing upper tube caps and soil inserts and lowering a small digital video camera (Pentax Optio W90) into each tube. We filmed eggs from multiple angles and analyzed the video footage in the field to verify the condition of eggs. If ants were found on eggs during videotaping, we allowed several hours for the attack to progress before returning and excavating eggs. We interrupted ant attacks before all eggs had been consumed to identify ant species and assess whether excavated eggs had been penetrated. Because these interruptions may have preempted ants penetrating additional eggs, we considered nests as predated if at least four of the six eggs were punctured. Therefore, we report predation of nests rather than of individual eggs.

We tested for effects of distance to nearest fire ant mound and canopy cover on whether nests were predated by fire ants using logistic regression. We generated estimates of nest predation for the entire incubation period by fitting survival curves to predation data collected during our observational period (15–20 days) and extrapolating to an estimated incubation period of 56 days at this site (CJT, pers. obs.). All statistical analyses were conducted using program R v3.1.1 (R Foundation for Statistical Computing, Vienna, Austria, http://www.R-project.org, 2014).

**RESULTS**

Seven of the 25 artificial nests were preyed on over the 20-day course of the study. Of these, fire ants were confirmed as nest predators at five nests via egg excavation and were observed via camera (but not collected) as predators of a sixth nest. In a seventh nest, fence lizard eggs were preyed on by a thief ant (*Solenopsis* sp.); this nest was omitted from further analyses. Of the six fire ant-predated nests, three contained eggs from female lizards of fire ant-invaded sites (*N* = 11), and three contained eggs from females of ant-uninvaded sites (*N* = 13).

The environmental and spatial variables we measured did not affect predation rates. Artificial nest sites had a mean of 37.5%
FIRE ANT PREDATION ON EASTERN FENCE LIZARD EGGS

Fig. 2. Survival of fence lizard nests over time. Solid line shows Kaplan–Meier curve fit to survival data (20 days) with 95% confidence intervals as dashed lines. Dotted line represents fitted exponential survival curve. Estimated incubation time at study site is 56 days.

canopy cover (range = 9–62%) and were a mean of 4.3 m (range = 1.5–10.5 m) from the nearest fire ant mound. Neither canopy cover nor distance to nearest fire ant mound were significant predictors of fire ant predation on nests ($\beta = -0.022$, df = 1, $P = 0.57$; $\beta = -0.076$, df = 1, $P = 0.32$, respectively).

We tested the fit of exponential and Weibull survival curves to nest data and selected the exponential curve as having the best fit ($LRT; \chi^2 = 0.63$, df = 1, $P = 0.43$; Fig. 2). Extrapolating from the exponential survival curve provided an estimate of 61% nest mortality attributable to fire ants over the 56-day incubation period.

**DISCUSSION**

Invasive fire ants likely represent a strong predation pressure on Eastern Fence Lizard eggs. Although juvenile and adult fence lizards are capable of behavioral avoidance of fire ants (Freidenfelds et al., 2012), fence lizard eggs have little defense against these predators. Fence lizard eggs are rich in protein and are present during late spring and summer, when fire ants actively seek out high protein foods to support growth of their brood (Sorenson et al., 1983; Stein et al., 1990). Therefore, these eggs likely are an attractive food source to fire ants. Our results indicate that up to 61% of lizard nests may be at risk of predation by fire ants, similar to levels of mortality found for turtle nests (45%; Buhllmann and Coffman, 2001). This result is based on extrapolation of a survival curve rather than monitoring eggs throughout incubation, and it may be inaccurate if fire ant predation rates vary significantly over time. In fact, our estimate of predation may be conservative, because pipped or hatched *Sceloporus* may remain underground until soil conditions favor emergence, extending the period when they are at risk of predation by fire ants (Buhllmann and Coffman, 2001). However, even within the first 20 days of incubation, 24% of nests were predated by fire ants, representing a significant mortality cost.

Although our estimates of predation on nests by invasive fire ants are high (24–61%), these lizards likely experienced some historic level of nest predation by native fire ants (*Solenopsis geminata* and *Solenopsis xyloni*) prior to the invasion of *S. invicta*. These native fire ants have similar predatory modes to *S. invicta* and are known to prey on hatching birds (Kroll et al., 1973; Delmicki and Bolen, 1977) and likely on sea turtle eggs and hatchlings (Moulis, 1997). Although fence lizards may have adapted to the historical presence of native fire ants, invasive fire ants likely pose a greater threat for several reasons. Colonies of *S. invicta* are larger than those of *S. geminata* and *S. xyloni* (Tschinkel, 1988), and *S. invicta* workers recruit aggressively to food sources (Morrison, 2000). After displacing native fire ants, *S. invicta* now occur at higher densities than native fire ant species historically did (Porter et al., 1988; Tschinkel, 2006). This increased density likely both increases the proportion of available habitat occupied by fire ants, especially in disturbed areas, and within those areas, produces a stronger predation pressure on native species including fence lizards (Vinson, 1994).

Although fence lizards may reduce fire ant predation by selecting nest sites with low or no fire ant presence, this is unlikely for several reasons. Our results show that neither canopy cover (up to 62%) nor distance from nearest fire ant mound (up to 10 m) had a significant effect on nest survival. Although fire ants avoid sites with high canopy density (Tschinkel, 2006), fence lizards do not use these sites for nesting (Angilletta et al., 2009). Also, fire ant mounds often are densely spaced, being an average of 10 m apart (range 1–35 m) at this and other fire-invaded sites (Langkilde, 2009b). Fire ant colonies generally expand to occupy space until they contact workers from other colonies, ensuring that most microhabitats suitable for nesting by fence lizards are occupied by foragers from at least one fire ant colony (Adams, 2003; Tschinkel, 2006). Additionally, fence lizard nests represent microclimates preferred by fire ants; fence lizards nest in sandy soils at depths that are commonly occupied by foraging tunnels of fire ants (Markin et al., 1975; Angilletta et al., 2009). Fence lizard nests also maintain temperatures favorable for fire ant activity (Lofgren et al., 1975; Angilletta et al., 2009) and may represent a sheltered, thermally optimal food source when surface temperatures are unfavorable for foraging (Porter and Tschinkel, 1987). As such, fire ants likely occupy and forage in most edge and patchy habitats suitable for fence lizard nest habitat within fire ant–invaded areas.

Of the six nests predated by fire ants, three were from fire ant–invaded sites, and three were from uninvaded sites. Although this is a small sample, it suggests that eggs produced by fence lizards at fire ant–invaded sites do not have special adaptations to prevent or deter fire ant attack. This result corresponds with patterns of thickness in fence lizard eggshells, which showed no adaptive thickening of eggshells produced by lizards at fire ant–invaded sites (M. Goldy-Brown, pers. obs.).

Because estimates of nest failure are not available for *S. undulatus* in the absence of fire ants, we do not know the extent of the effects that fire ant predation on nests may have on fence lizard populations. Estimates of nest failure rates (including nest predation) in congeners, however, range from 32% in *Sceloporus virgatus* (Vinegar, 1975) to 78% in *Sceloporus olivaceus* (Blair, 1960). Blair (1960) suggests that vertebrates, especially snakes and armadillos, account for the majority of nest predation and may find lizard nests via scent left by mothers during laying. Although fire ants may be replacing the predation pressure of other nest predators (such as armadillos, excluded during this study), fire ants in our study entered nests via underground
tunnels, suggesting they may detect nests via different modes than vertebrate predators. Also, the predation rates we observed (24–61%) would encompass a large portion of the nest failure expected naturally in similar species. These observations suggest that fire ants may replace or potentially add to other sources of nest mortality.

Also, we lack data on whether fire ants may reduce abundance of S. undulatus at fire ant–invaded sites. Although fire ant induced mortality has been observed in many species (Allen et al., 2004), population level effects have been demonstrated experimentally in only two vertebrates: bobwhite quail and white-tailed deer (Allen et al., 1995, 1997; reviewed in Tschanz, 2006). Ultimately, many fence lizard populations persist despite long-term (up to 80 years) invasion by fire ants, suggesting they have compensated for fire ant–induced mortality via demographic processes or adaptation (Langkilde, 2009b). Large-scale, experimental efforts to determine impacts of fire ants on fence lizard populations would illuminate this issue.

In conclusion, fire ants may represent a strong and potentially novel pressure on fence lizards and other species, including some of conservation concern, which have life-history strategies resulting in high vulnerability to predation by fire ants (e.g., egg-laying or delayed emergence from nests, Landers et al., 1980; Allen et al., 1994; Forrys et al., 2001). Although fence lizard populations persist in fire ant–invaded areas despite potentially high predation of eggs (and possibly juveniles and adults; Langkilde, 2009a) by fire ants, other species may not be so fortunate. Indeed, fire ants have been surmised to contribute to enigmatic population declines in several reptile species, including Southern Hog-Nosed Snakes (Heterodon simus; Tuberville et al., 2000) and Eastern Kingsnakes (Lampropeltis getula; Winne et al., 2007). Our method could be adapted to studies of predation on many subterranean nesting species because it is simple to implement, inexpensive (< $5/nest, assuming possession of a suitable camera), quick (< 5 min/nest/day), and allows monitoring of many nest replicates. Future studies should experimentally verify both the ability of fire ants to prey on eggs in natural scenarios and the frequency at which they do so. These results, combined with models investigating how this predation may alter fitness of affected populations, will allow strong inferences about how fire ants may affect the persistence of species with vulnerable life stages.

Acknowledgments. —Thanks to M. Goldy-Brown, C. Norjen, M. Herr, and J. Williams for help collecting eggs and constructing nests, the Solon Dixon Forestry Education Center for logistical support, and B. Chitterlings and two anonymous reviewers for constructive comments on the manuscript. Animal collection was authorized by the respective state’s permits and research approved by the Institutional Animal Care and Use Committees of Penn State University and Auburn University. Funding was provided by the National Science Foundation (DEB-0949483) to TL.

**Literature Cited**


**References**


Accepted: .