Invasive ants influence native lizard populations

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Abstract. The red imported fire ant (*Solenopsis invicta*; hereafter RIFA) is an invasive predator found on four continents, namely South America, North America, Australia, and Asia. Red imported fire ants are implicated in the decline of native invertebrates and vertebrates throughout their invaded range. We used the eastern fence lizard (*Sceloporus undulatus*) as a model species to understand the influence of RIFAs on native reptiles in the southeastern United States. Our objective was to quantify the effects of RIFAs on fence lizard recruitment and survival. We experimentally stocked populations of fence lizards into eight enclosures with either ambient or reduced numbers of RIFAs from May 2012 to October 2013. Fitting Link-Barker models, we found that the RIFA treatment affected fence lizard recruitment (f), but not survival (Φ). Recruitment was 1.6 times greater in the enclosures with reduced numbers of RIFAs than in those with ambient numbers. Red imported fire ants likely affect reptiles with analogous life history strategies to those of fence lizards similarly. Consequently, RIFAs may have undesirable consequences for the biodiversity of reptiles in the southeastern United States and on other continents with established RIFA populations.

Key words: invasive species; recruitment; *Sceloporus undulatus*; *Solenopsis invicta*; survival.

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INTRODUCTION

Non-native species are one of the greatest threats to global biodiversity (Wilcove et al. 1998, Clavero et al. 2009) and are considered a major cause of animal extinctions worldwide (Clavero and Garcia-Berthou 2005). Of particular concern are the impacts of invasive predators on native fauna because of their potential to have both direct (e.g., predation) and indirect (e.g., physiological, behavioral, and morphological changes) effects (Parker et al. 1999, Preisser et al. 2005, Sih et al. 2010, Lockwood et al. 2013). Collectively, the direct and indirect effects have been hypothesized to, and in some cases empirically shown to, cause population declines in native fauna (Lockwood et al. 2013). Still, we have little understanding of how invasive species influence the demography (e.g., survival, recruitment, and population growth) of the majority of native species, although these data are central to determining how invasive species threaten native species. Understanding the influence of invasive species on the population demographics of native species will help identify potential mechanisms of decline, delineate the severity of the problem, and inform conservation.

The red imported fire ant (*Solenopsis invicta*; hereafter RIFA) is an invasive predator that was introduced into the southeastern United States in

the 1930s (Tschinkel 2006). More recently, RIFA populations in the southeastern United States have been the source of introduced populations in California, Australia, New Zealand, Taiwan, Hong Kong, Macao, and China (Ascunce et al. 2011). The RIFA is a generalist predator that forages on seeds, carrion, and live vertebrates and invertebrates (Allen et al. 2004, Tschinkel 2006). They are able to overwhelm larger vertebrates due to their aggression, large population sizes, and venom (MacConnell et al. 1971, Brand et al. 1972). Since their establishment in the United States, RIFAs have been linked to the decline of several native species including the Houston toad (*Bufo houstonensis*; Brown et al. 2012), bobwhite quail (*Colinus virginianus*; Allen et al. 1995), Texas horned lizard (*Phrynosoma cornutum*; Goin 1992), and southern hognose snake (*Heterodon simus*; Tuberville et al. 2000). However, these accounts have largely been speculative (e.g., Mount et al. 1981, Tuberville et al. 2000), based on correlative and/or descriptive studies (e.g., Ferris et al. 1998, Brown et al. 2012, Parachú Marcó et al. 2015), laboratory studies (e.g., Allen et al. 2001, Parachú Marcó et al. 2014), or focused on changes in morphology or behavior (e.g., Orrock and Danielson 2004, Langkilde 2009). Excluding birds (e.g., Allen et al. 1995, Mueller et al. 1999, Dabbert and Mitchell 2002), few studies have empirically assessed the effects of RIFAs on the population demographics (e.g., survival and recruitment) of native species outside of a laboratory setting (e.g., Allen et al. 1997*b*, Long et al. 2015).

Reptiles have several life history characteristics that increase their vulnerability to RIFAs. Foremost, many reptiles are oviparous and RIFAs can depredate individuals of some species pre- and post-hatching (Mount et al. 1981, Allen et al. 1997*a*, 2001, Dziadzio 2015). Second, many species inhabit disturbed areas that are the preferred habitat of RIFAs (e.g., eastern fence lizard; *Sceloporus undulatus*; Trauth et al. 2004, Tschinkel 2006). Some reptiles (e.g., turtles and lizards; Ackerman 2003) also excavate nests in soil and may provide scent and disturbance attractive to RIFAs (Allen et al. 1994, Tschinkel 2006, Dziadzio et al. 2016). Additionally, many reptiles act as both a predator and prey of RIFAs, and research indicates that consumption of RIFAs can cause mortality through envenomation (Long 2013, Robbins et al. 2013). Thus, reptiles are not only susceptible to mortality by RIFAs via direct depredation, but also when foraging. Nonetheless, most studies have focused on individual-level effects of RIFAs on reptiles and less has been done to understand the effects of RIFAs on reptile populations.

To quantify the population-level effects of RIFAs on an insectivorous, oviparous reptile, we used eastern fence lizards as a model species. The specific objective of our research was to determine the effects of RIFAs on fence lizard survival and recruitment. Fence lizards prefer disturbed habitats and have a diet largely comprising Formicidae (DeMarco et al. 1985, Parker 1994, Trauth et al. 2004), making it likely that they interact with RIFAs regularly. Additionally, fence lizards are oviparous and their thin-shelled eggs may be particularly susceptible to RIFAs (Trauth et al. 2004). Red imported fire ants have exerted selective pressures on fence lizards resulting in morphological (e.g., longer hind limb length) and behavioral (e.g., twitching to escape depredation) adaptations and they likely have a negative effect on fence lizard populations (Langkilde 2009). Although fence lizards have epidermal scales, RIFAs are able to sting lizards by using their mandibles to grasp a scale, lifting the edge of the scale with their abdomen, and then inserting their sting shaft into the soft tissue beneath the scale (Langkilde 2009). Research has established that RIFAs can depredate hatchling and juvenile fence lizards (Langkilde 2009) and their eggs (Newman et al. 2014, Thawley and Langkilde 2016), that the consumption of RIFAs causes mortality in juveniles (Boronow and Langkilde 2010), and that RIFAs may alter their behavioral response to stress (Trompeter and Langkilde 2011). Accordingly, we predicted that RIFAs would decrease survival and recruitment of eastern fence lizards.

MATERIALS AND METHODS

Study site

We conducted our study at Ichauway, the 12,000-ha research site of the Joseph W. Jones Ecological Research Center. Ichauway is located approximately 20 km south of Newton, Georgia, in Baker County, United States, and is dominated by a longleaf pine (*Pinus palustris*) and wiregrass (*Aristida beyrichiana*) ecosystem. The longleaf pine and wiregrass ecosystem has a relatively open canopy of longleaf pine, a sparse or absent

midstory, and a diverse understory (Van Lear et al. 2005).

We completed our experiments within eight 0.2-ha (45 × 45 m) enclosures located on the southwest portion of the property in a 10-year-old longleaf pine plantation. We located the enclosures in areas with similar vegetation to minimize effects of differences in vegetation composition on the results of our study. The enclosures had an understory largely comprising *Rubus* sp., *Vernonia gigantea*, and *Ambrosia artemesiifolia* and a few scattered shrubs <1.5 m tall. Over 23 species of ant occur on Ichauway (e.g., *Dorymyrmex* sp., *Pheidole* sp., *Camponotus* sp.), but RIFAs are the dominant ant on site (Carroll and Hoffman 2000, Stuble et al. 2009, 2011).

Each enclosure was fenced with Galvalum metal siding buried in a 1 m deep trench along the perimeter of the plots to prevent organisms from entering or exiting the enclosures. Specifically, fence lizards were unable to exit or enter the enclosures because their nails would not allow them to grasp the metal sides. The above-ground portion of the siding was 1 m high. We maintained a 1-m mowed buffer on the inner and outer perimeter of each enclosure to discourage movement in and out of the enclosures using vegetation.

Fence lizards require basking sites, such as logs, to provide suitable habitat (Trauth et al. 2004). To standardize available basking sites in the enclosures, we placed 24 piles of 1–1.25 m long live oak (*Quercus virginiana*) logs with 10–20 cm diameter into each enclosure in 2012. Each pile consisted of two logs forming the bottom with one placed on top, centered on the two bottom logs, to form an opening to provide both a basking site and shelter. We placed the basking sites between intersections on a 4 × 4 grid with 10 m spacing centered in each enclosure. All other large woody debris was removed from the enclosures prior to the experiment. Additional details on the enclosures can be found in Long et al. (2015).

Stocking

We stocked each enclosure with three male and three female adult fence lizards of similar size (snout-vent length [SVL] >50 mm; SVL range: 50–60 mm; weight range: 5–12 g) and reproductive condition from 1 May 2012 to 29 May 2012. We marked lizards on the epidermis with small spots of acrylic outdoor paint (Folkart) and reapplied paint as necessary throughout the study. From 4 April 2013 to 14 May 2013, we stocked an additional male and female lizard into each enclosure and added replacements for individuals that had not been recaptured for more than 3 months. Based on Tinkle and Ballinger (1972), the natural density of lizards in populations found in Ohio, Colorado, Texas, and South Carolina ranged from 0.4 to 4.4 individuals/0.2 ha. Additionally, densities of approximately 14.4 individuals/0.2 ha were found in Mississippi (Parker 1994). Consequently, an initial density of 6–8 individuals/0.2 ha was chosen to balance our need for sufficient mark–recapture data and the applicability of our results to natural fence lizard populations.

Treatments

Our experiment consisted of a control with ambient numbers of RIFAs (*n* = 4 enclosures) and a treatment where we reduced RIFA numbers (*n* = 4). We used Amdro, a conventional fire ant bait formulation, to reduce RIFA numbers. We applied 1.7 kg/ha of Amdro using a broadcast treatment, as this has been shown to be more effective than individual mound treatments, killing 85–95% of colonies (Apperson et al. 1984, Collins et al. 1992). We applied Amdro in the morning before 11:00 hours by walking along paths on the 4 × 4 grid described above within each enclosure and evenly distributing Amdro across the enclosures by hand. We reapplied Amdro when RIFAs were present at 30–40% of the bait stations used to sample RIFA foraging pressure.

Invertebrate monitoring

We quantified RIFA foraging activity monthly from May 2012 to October 2013 using bait sampling (Agosti et al. 2000) to monitor the effectiveness of the Amdro treatment and to determine the necessity of and timing for reapplication of Amdro in treated plots. Details on sampling design and data showing a reduction in RIFAs within the treated enclosures are provided in Long et al. (2015).

To monitor the influence of the Amdro treatment on other invertebrates, we completed pitfall trapping within the enclosures. We sampled once pre-Amdro application (7 April 2012 to 9 April 2012) and again approximately 1 and 4 months following treatment (23 May 2012 to 25 May 2012 and 25 August 2012 to 27 August 2012,

respectively). The pitfall traps consisted of a 19 mm length of 19.05-mm PVC pipe buried in the ground at each grid intersection (16 traps/enclosure; Agosti et al. 2000). For each sampling period, we placed a 19 × 125 mm glass test tube filled with a mixture of water and Dawn dish detergent into the PVC tube for 48 h. After 48 h, we collected the test tubes and positioned a rubber stopper into each piece of PVC pipe. We counted all invertebrates and identified RIFAs to species, other ants to genus, and all other invertebrates to order.

Statistical analyses.—We assessed the influence of Amdro treatment on the total abundance of invertebrate orders and ant genera and for each individual order and genus/species with >100 captures. Additionally, we used package Biodiversity R (Kindt and Coe 2005) to calculate Shannon diversity (H'), evenness indices (J'), and species richness (S). We used the log of the count of each invertebrate group, H', J', and S as our dependent variables and fit linear mixed models in the package NLME (Pinheiro et al. 2016) within Program R (R Core Team 2014) for each dependent variable to determine the influence of Amdro treatment on the invertebrate community. We completed the analyses separately for pre-treatment vs. 1 and 4 months because we were interested in immediate (1 month) and longer-term (4 months) impacts, not the differences between months 1 and 4. We included the interaction between *Treatment* and *before/after treatment* as fixed effects and *Trap* nested within *Enclosure* as a random effect. We considered $P \leq 0.05$ to indicate a significant difference.

Mark–recapture

We sampled for fence lizards every 4 weeks over an 18-month period from May 2012 to October 2013. We did not sample January–February 2013 as fence lizards exhibit reduced activity during the winter (Trauth et al. 2004). Each mark–recapture session included a morning and afternoon survey each day for four consecutive days (eight surveys/session). We captured fence lizards by systematically walking the 1-m mowed path on the inner perimeter of each enclosure followed by checking each log pile for fence lizards. Each survey was completed within approximately 20 min. Fence lizards are territorial and usually found on the same basking site within and between days (Haenel et al. 2003), which facilitated capture and

recapture of individuals. We did not traverse unmowed areas to minimize observer effects on vegetation structure within enclosures through compaction of vegetation. We captured new individuals by hand and determined sex, assessed them for reproductive condition, weighed, measured their SVL, and marked them with a unique paint code and toe clip. To reduce stress from capture, we only recaptured painted individuals by hand if their paint code had worn away; otherwise, they were simply resighted and no measurements were taken. All applicable institutional and/or national guidelines for the care and use of animals were followed. Specifically, all mark–recapture methods followed recommendations of the American Society of Ichthyologists and Herpetologists (ASIH), the Herpetologists' League, and the Society for the Study of Amphibians and Reptiles guidelines on the use of amphibians and reptiles in field research (ASIH et al. 2004) and were approved by the University of Florida Institutional Animal Care and Use Committee (Approval number 201207414).

Statistical analyses.—To compare fence lizard survival and recruitment between treatments, we fit Link-Barker models (Link and Barker 2005) in Program Mark (White and Burnham 1999). We accounted for capture heterogeneity using finite mixture models (Pledger 2000, Pledger et al. 2003) with two groups of animals. Due to low capture probabilities, we combined each four-day sampling period for the analysis. Our encounter histories included one dummy session, where we set capture probability to one to account for the stocked individuals, 14 mark–recapture sessions, and eight groups. The first two groups included the adults in the enclosures with ambient RIFA conditions and those in the enclosures with reduced RIFA numbers, the second four groups accounted for the individuals that we stocked into the enclosures in 2013 (capture probabilities were set to zero until the session that they were stocked), and the last two groups accounted for the juveniles in the enclosures with ambient and reduced RIFA populations.

We completed a goodness-of-fit (GOF) test to assess model fit using our most parameterized model in Program U-CARE (Choquet et al. 2009). We assessed a Cormack-Jolly-Seber model because there is no GOF test for Link-Barker recruitment and survival models. The GOF test indicated that

Table 1. A model comparison table for capture–mark–recapture analysis to formulate a base model to estimate survival (Φ), capture probability (p), and recruitment (f) of eastern fence lizard (*Sceloporus undulatus*) populations located within eight enclosures on Ichauway, the research site of the Joseph W. Jones Ecological Research Center, in Newton, Georgia, United States.

Model	AIC$_c$†	ΔAIC$_c$†	k†	w_i†
Φ‡				
Age + Year	1728.2	0.0	13	0.59
Age	**1729.0**	**0.8**	**12**	**0.40**
Year	1736.0	7.8	12	0.01
[.]	1745.7	17.5	11	0.00
p‡				
Hetero + Age + Season	**1726.1**	**0.0**	**12**	**0.74**
Hetero + Age + Year + Season	1728.2	2.1	13	0.26
Hetero + Season	1746.5	20.4	11	0.00
Hetero + Year + Season	1748.5	22.4	12	0.00
Age + Season	1757.7	31.6	11	0.00
Age + Year + Season	1759.8	33.6	12	0.00
Season	1762.5	36.3	10	0.00
Hetero + Age + Year	1763.3	37.1	11	0.00
Year + Season	1764.5	38.3	11	0.00
Hetero + Age	1769.2	43.1	10	0.00
Hetero + Year	1778.2	52.0	10	0.00
Hetero	1779.9	53.7	9	0.00
Age + Year	1790.0	68.8	10	0.00
Age	1792.5	66.4	9	0.00
Year	1792.9	66.7	9	0.00
[.]	1793.4	67.3	8	0.00
f‡				
BP 3–4 and 12–14 + Year	**1725.7**	**0.0**	**13**	**0.77**
BP 2–4 and 12–14 + Year	1728.2	2.6	13	0.22
BP 2–4 and 12–14	1734.4	8.8	12	0.01
BP 3–4 and 12–14	1745.5	19.8	12	0.00
[.]	1873.0	147.3	11	0.00

Note: The variables in boldface were selected to form the base model for each parameter.

  † From left to right: Akaike's information criteria corrected for small sample sizes (AIC$_c$), the difference between a model's AIC$_c$ and the lowest AIC$_c$ (ΔAIC$_c$), the number of model parameters (k), and model weights (w_i).

  ‡ Effects of age and year on survival (Φ), heterogeneity (*Hetero*), age, year and season on capture probability (p), and breeding peaks (BP) including sessions 3–4 and 12–14 or 2–4 and 12–14 and year on recruitment (f) were modeled sequentially for each parameter while using the most general model for the other parameters.

our data were over-dispersed ($ĉ$ = 1.36; a $ĉ$ of 1 indicates perfect model fit) and that trap dependence was present. When trap dependence was incorporated into the model, the model fit was slightly under-dispersed, but improved ($ĉ$ = 0.93). Because of the reasonable model fit when trap dependence was included, we included no quasi-likelihood adjustment in our analyses.

Prior to assessing the effects of RIFAs, we built a base model to determine survival (Φ), recruitment (f), and capture probability (p) of fence lizards. We included the effects of age (*Age*), capture heterogeneity (*Hetero*), and year (*Year*) on Φ, *Age*, *Hetero*, *Year*, and season (*Season*) on p, and

breeding peaks (*BP*; including sessions 2–4 and 12–14 or 3–4 and 12–14) and *Year* on recruitment (f). We did not include the variable time in estimating Φ, p, or f because the models did not provide reliable estimates or provided estimates with high standard errors. *Season* was not included when modeling Φ because the model did not provide reliable estimates. Moreover, we used *BP* rather than *Season* for recruitment because fence lizards have a distinct breeding period. We formed a base model by sequentially assessing each of these effects on Φ, p, and f (Table 1). First, we considered effects on Φ while modeling p and f using the most general model for each. We

Table 2. A model comparison table for capture–mark–recapture analysis to assess the effects of red imported fire ants (*Solenopsis invicta*; RIFA) on survival (Φ) and recruitment (*f*) of eastern fence lizard (*Sceloporus undulatus*) populations located within enclosures with reduced (*n* = 4) or ambient (*n* = 4) numbers of RIFA on Ichauway, the research site of the Joseph W. Jones Ecological Research Center, in Newton, Georgia, United States.

Model†	ΔAIC$_c$‡	AIC$_c$‡	*k*‡	w_i‡
Φ (*Age* + *Year*) *f* (*BP* 3–4 and 12–14 + *Year* + RIFA)	1721.2	0.0	12	0.56
Φ (*Age* + *Year* + RIFA) *f* (*BP* 3–4 and 12–14 + *Year* + RIFA)	1722.6	1.3	13	0.29
Φ (*Age* + *Year*) *f* (*BP* 3–4 and 12–14 + *Year*)	1724.5	3.2	11	0.11
Φ (*Age* + *Year* + RIFA) *f* (*BP* 3–4 and 12–14 + *Year*)	1726.5	5.3	12	0.04

Note: BP, breeding peaks.
  † Capture probability (*p*) was modeled as *p* (heterogeneity + season + age) for all models.
  ‡ From left to right: Akaike's information criteria corrected for small sample sizes (AIC$_c$), the difference between a model's AIC$_c$ and the lowest AIC$_c$ (ΔAIC$_c$), the number of model parameters (*k*), and model weights (w_i).

completed the same process for *p* and *f*. We selected the top model for each parameter using an information theoretic approach and assessed model likelihood with Akaike's information criteria corrected for small sample size (AIC$_c$; Akaike 1973). We determined our best approximating models based on the relative difference to the smallest AIC in each model set (ΔAIC; Burnham and Anderson 2002). We considered models with a delta AIC of <2 competing models (Burnham and Anderson 2002). If we did have competing models, we used the least parameterized of the models to form the base model rather than model averaging to decrease model complexity and allow for more precise parameter estimates.

Following formulation of a base model, we assessed the effects of RIFAs on Φ and *f*. We added RIFA treatment as an effect on Φ and *f*, Φ only, and *f* only and selected the top model as described above (Table 2). We also used model weights (w_i; the weight of evidence for a given model being the best given the candidate models and data set) to determine our top model.

RESULTS

Invertebrate monitoring

We captured 18 different classes/orders of invertebrates and 10 ant genera (Appendix S1: Table S1). Abundance of arthropod classes/orders and ant genera decreased following Amdro application (Appendix S1: Table S2, Figs. S1, S2). This difference was largely due to RIFAs comprising 33% of all invertebrate captures pre-Amdro application. Nonetheless, 4 months after treatment, only 4 of 11 ant genera (*Brachymyrmex* sp.) and invertebrate orders (Hemiptera, Hymenoptera,

and Acari) showed reductions in abundance and treatments had a positive influence on the diversity and evenness of ant genera and invertebrate orders, but not richness (Appendix S1: Table S2, Figs. S1–S4).

Mark–recapture

From 11 June 2012 to 11 October 2013, we completed 14 mark–recapture surveys for fence lizards. Overall, we captured 31 new juveniles within the enclosures with ambient RIFA conditions and 74 within enclosures with reduced numbers of RIFAs. Developing base models, we found that Φ was best described by *Age*, *p* by *Hetero*, *Age*, and *Season*, and *f* by *BP* including sessions 3–4 and 12–14 and *Year* (Table 1).

We found that the model with RIFAs affecting *f* only was more than two times likely to explain demographic variability than the next best model (Table 2). We found that *f* was 3.5 times greater in 2012 than in 2013 for all enclosures (Fig. 1), but consistently 1.6 times greater in the enclosures with reduced RIFAs (Fig. 1). Survival of juvenile fence lizards was approximately 15–18% greater than that of adult lizards, but Φ did not differ between enclosures with reduced and ambient RIFA conditions (Fig. 2).

DISCUSSION

Our study experimentally demonstrated a negative population-level effect of RIFAs on a native reptile via decreasing recruitment, but not survival. Although we determined that RIFAs reduce recruitment of fence lizards, the mechanisms underlying this decrease are still unknown. Field studies on artificial fence lizard nests indicated
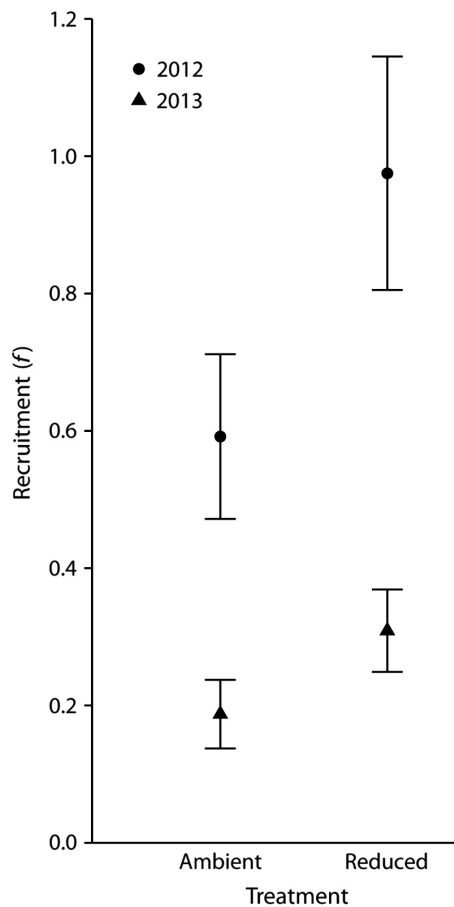
Fig. 1. Recruitment (f) of eastern fence lizards (*Sceloporus undulatus*) located within enclosures with ambient ($n = 4$) and reduced ($n = 4$) numbers of red imported fire ants (*Solenopsis invicta*; RIFA) in 2012 and 2013 on Ichauway, the research site of the Joseph W. Jones Ecological Research Center, in Newton, Georgia, United States.

that RIFAs can consume eggs pre-hatching (Newman et al. 2014, Thawley and Langkilde 2016). Moreover, there have been observations of RIFAs depredating hatchling reptiles within nests including gopher tortoises (*Gopherus polyphemus*; Landers et al. 1980, Dziadzio 2015), American alligators (*Alligator mississippiensis*; Allen et al. 1997*a*), broad-snouted Caiman (*Caiman latirostris*; Parachú Marcó et al. 2015), and loggerhead sea turtles (*Caretta caretta*; Parris et al. 2002). Additionally, Dziadzio (2015) monitored tortoises post-hatch using radiotelemetry and 31% of juvenile tortoises died from fire ant depredation within

24 d of hatching. Similarly, there may be a period post-hatching (<1 month) that fence lizards are still vulnerable to depredation by RIFAs due to their small size. Future studies should focus on elucidating which of these mechanisms caused the lower recruitment in fence lizard populations in ambient RIFA conditions in our study.

Our finding that RIFAs did not decrease fence lizard survival was unexpected. Studies show that consumption of as few as four RIFAs in 2 d may cause mortality of juvenile fence lizards (Langkilde and Freidenfelds 2010) and exposure to envenomation by 12 RIFAs for a period of 60 s can cause paralysis and subsequent mortality in adults (Langkilde 2009). However, these studies were completed under laboratory conditions and it may be that RIFA attacks of fence lizards in
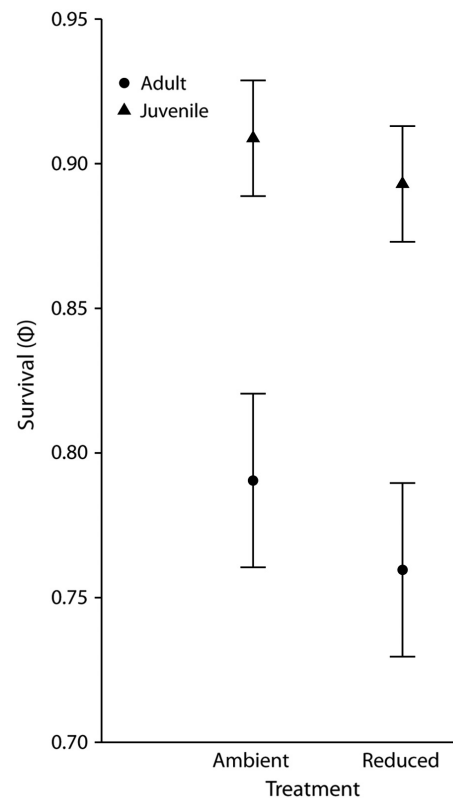

Fig. 2. Survival (Φ) of juvenile and adult eastern fence lizards (*Sceloporus undulatus*) located within enclosures with ambient ($n = 4$) and reduced ($n = 4$) numbers of red imported fire ants (*Solenopsis invicta*; RIFA) on Ichauway, the research site of the Joseph W. Jones Ecological Research Center, in Newton, Georgia, United States.

nature do not occur at the rate necessary to cause mortality. Moreover, there may be a size at which fence lizards are less vulnerable to depredation by or risk of injury from RIFAs. It is possible that RIFAs depredate adult or juvenile fence lizards opportunistically, which may have little influence on the overall survival of fence lizards.

There are numerous examples of native species rapidly adapting to novel predation pressures (e.g., Phillips and Shine 2004, 2006, Carroll et al. 2005), and fence lizards within the range of RIFAs have developed longer hind limb lengths and a body-twitching behavior to cope with RIFAs in under 40 generations (Langkilde 2009). Red imported fire ants have been present on our study site for at least 30 yr and are the dominant ant on site (Callcott and Collins 1996, Stuble et al. 2009). Thus, it is possible that the fence lizards on our study site, which have experienced RIFAs for nearly 30 generations (Callcott and Collins 1996), have developed similar adaptations. An additional explanation for our finding that RIFAs did not influence fence lizard survival is that Amdro, although largely targeted to control RIFAs, can reduce native ant and orthoptera populations (Plentovich et al. 2010). Ants comprise a large proportion of the fence lizard diet (approximately 80% in juveniles), though other invertebrates (e.g., Orthoptera) make a considerable contribution (Hamilton and Pollack 1961, DeMarco et al. 1985). We found that treatment for RIFAs reduced the overall abundance of invertebrate orders and ant genera, largely due to decreases in RIFA abundance (Appendix S1: Table S2; Figs. 1, 2). This reduction in food resources may have lowered the survival of lizards within the enclosures with reduced RIFAs to levels similar to the enclosures with ambient RIFAs.

Globally, reptiles are declining and the southeastern United States is no exception (Gibbons et al. 2000). Specifically, 57% of the reptile species listed as federally endangered or threatened are found in the continental United States and 14% of globally listed species are found in the southeastern United States (USFWS 2014). Moreover, several reptile species not listed federally are listed as state threatened (e.g., southern hognose snake [Mississippi, Georgia], Texas horned lizard [Texas]). Interestingly, most of the listed species are oviparous and many lay thin-shelled eggs similar to

the eastern fence lizard (e.g., Texas horned lizard, blue-tailed mole skink [*Eumeces egregius lividus*], sank skink [*Neoseps reynoldsi*], southern hognose snake, eastern indigo snake [*Drymarchon corais couperi*]), and laboratory and field studies indicate that RIFAs can consume the thin-shelled eggs of several other reptile species including yellow rat snakes (*Pantherophis alleghaniensis*), burmese pythons (*Python molurus bivittatus*), loggerhead sea turtles (Diffie et al. 2010), and six-lined racerunners (*Aspidoscelis sexlineatus*; Mount et al. 1981). It is likely that reptiles with life history characteristics comparable to those of eastern fence lizards experience decreases in recruitment similar to what we documented in our study in the presence of RIFAs. Thus, RIFAs may play a role in the population declines of currently rare or endangered, as well as common, reptiles and could have undesirable consequences for the biodiversity of reptiles within the southeastern United States and other countries where RIFAs have been introduced.

It may be important for the conservation of reptile biodiversity to consider management for RIFAs, particularly in areas with rare species with similar life history characteristics as fence lizards. Specifically, areas with relatively new introductions of RIFAs should plan and implement a long-term management strategy immediately to reduce negative impacts of RIFAs on native reptiles (e.g., Australia; Wylie et al. 2016). However, the effects of management strategies (e.g., broadcast application of insecticide) should be further studied, particularly relative to species that are ant specialists, to assure that the benefits of management (e.g., increased recruitment) for RIFAs exceed the potential costs (e.g., decreased survival), if they do exist.

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