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Effects of an invasive ant and native predators on cotton rat recruitment and survival

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We used the imported red-fire ant (*Solenopsis invicta*; hereafter fire ant) and hispid cotton rat (*Sigmodon hispidus*) as model species to address the population-level effects of an invasive ant on a semiprecocial small mammal. We stocked cotton rats into 8 enclosures, implementing a 2-way factorial design with predator (ambient or excluded) and fire ant (ambient or reduced) treatments as factors. We trapped monthly from June 2012 to June 2013 and calculated monthly recruitment and survival. Rats in enclosures with ambient predators had a risk of mortality approximately 2 times greater than rats in enclosures with predators excluded. The risk of mortality was 3 and 4.5 times greater for female and male cotton rats, respectively, in enclosures with ambient fire ants and predators compared to enclosures with reduced fire ants and excluded predators. We found no effects on recruitment. Our results indicate that native predators had the greatest influence on cotton rat populations. Nevertheless, in the absence of other predators, the effects of fire ants on cotton rat survival are compensatory.

Key words: competition, invasive species, population parameters, predation, *Sigmodon hispidus*, *Solenopsis invicta*

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The introduction of invasive species to an ecosystem can disrupt processes occurring at multiple levels of biological organization (McNeely et al. 2009; Pyšek and Richardson 2010), including altering predator–prey and competitive interactions. Native species often lack behavioral, morphological, and/or physiological mechanisms to cope with invasive predators or competitors (Preisser et al. 2005; Salo et al. 2007; Sih et al. 2010). Accordingly, changes in predator–prey dynamics and competitive interactions may affect the abundance and/or composition of native populations (e.g., Dick and Platvoet 2000; Gurnell et al. 2004) and populations of other native species via indirect effects (e.g., prey switching, reduced prey abundances—Doody et al. 2006; Nelson et al. 2010). Ultimately, introduced predators and competitors may lead to extinction of species (Clavero and Garcia-Berthou 2005) and affect ecosystem functioning (e.g., Strecker and Arnott 2008; Wardle et al. 2009).

Invasive ants, which may compete with and/or depredate native species (Lach and Hooper-Bui 2010), are an increasing problem worldwide (Suarez et al. 2010), yet few studies have addressed the population-level impacts of invasive ants on native vertebrates. Imported red-fire ants (*Solenopsis invicta*; also referred to as red-imported fire ants, hereafter fire ants), native to South America, currently inhabit North America,

Australia, and portions of Asia (Tschinkel 2006). They are generalists that consume seeds, carrion, and live vertebrates and invertebrates (Tschinkel 2006). In the southeastern United States, native fire ants (*S. geminata* and *S. xyloni*) have been largely extirpated in areas where imported red-fire ants have become established (Vinson 1997). Compared with native fire ants in the southeastern United States, imported red-fire ants are able to overwhelm large vertebrates due to their greater aggression, large population sizes, and differences in venom composition (MacConnell et al. 1971; Brand et al. 1972; Vinson 1997). Consequently, imported red-fire ants have been implicated in the decline of several native vertebrates via direct (e.g., competition and predation) and indirect (e.g., increased stress and reduced growth) mechanisms (Mount 1981; Allen et al. 2004).

There are large gaps in our understanding of the influence of fire ants on native mammal populations (Allen et al. 2004). Specifically, there has been minimal effort to quantify the effects of fire ants on small mammal (< 5 kg—Merritt 2010) populations. With their ability to disperse seeds and shape vegetative communities, small mammals play a critical role in most ecosystems (Sieg 1987). Small mammals that bear altricial or semiprecocial young should be most vulnerable to direct predation by fire ants (Lach and Hooper-Bui 2010). Additionally, small mammals with an omnivorous diet similar to fire ants

likely are vulnerable to risk of injury through interference or exploitive competition while foraging or when attending young (Lach and Hooper-Bui 2010).

Studies have established that prey may respond to perceived predation risk by reducing mobility (e.g., Skelly 1994; Martel and Dill 1995; Norrdahl and Korpimäki 1998), but research has demonstrated that fire ants indirectly influence the recruitment of white-tailed deer (*Odocoileus virginianus*) by stinging fawns and causing them to move frequently to limit envenomation (Allen et al. 1997a; Mueller et al. 2001). Although increased mobility is an advantageous response to fire ants, it leads to greater fawn mortality by increasing the opportunity of predation by other predators (Allen et al. 1997a; Mueller et al. 2001). Consequently, small mammals, which likely interact with fire ants more frequently due to their small size, may increase their movement in response to the perceived risk of injury associated with fire ants and experience increased mortality from other predators.

We used the hispid cotton rat (*Sigmodon hispidus*) as a model species to address the influence of fire ants on a semiprecocial, omnivorous small mammal. Our specific objectives were to 1) quantify the effects of fire ants on cotton rat recruitment and survival and 2) determine if fire ants indirectly influence cotton rat population demographics by increasing mortality from other predators. Studies indicate that cotton rats and other species of small mammal alter their foraging patterns (A. K. Long, pers. obs.; Holtcamp et al. 1997; Orrock and Danielson 2004), remove fire ants from their young to protect them from envenomation, and move their nests in response to fire ants (Ferris 1994). This suggests that fire ants do impose a risk of injury and/or predation to cotton rats. Consequently, we predicted that fire ants would reduce survival and recruitment of cotton rats and would negatively affect cotton rat populations by increasing mortality from other predators.

MATERIALS AND METHODS

Study site.—Our study site was located on the southwestern portion of Ichauway (latitude 31°11'32.8734", longitude -84°29'14.766"), the 12,000 ha research site of the Joseph W. Jones Ecological Research Center in Newton, Georgia. We established eight 0.2-ha enclosures in a stand of 10-year-old longleaf pine (*Pinus palustris*) regeneration. Prescribed burns are used to maintain the longleaf pine on Ichauway and the stand outside the enclosures was burned biannually, whereas the herbaceous vegetation within the enclosures was managed by mowing. The dominant plants in the enclosures included blackberry sp. (*Rubus* sp.), giant ironweed (*Vernonia gigantea*), and common ragweed (*Ambrosia artemisiifolia*).

Study species and stocking.—Cotton rats have a bimodal breeding season with a peak in late spring and late summer to early autumn (Cameron and Spencer 2001), which coincides with greatest fire ant activity (Tschinkel 2006). Cotton rats bear semiprecocial young above ground in ball or cup-shaped nests composed of woven grass (Cameron and Spencer 2001). Newborns are mobile within a few hours following birth which

may allow them to escape some predators (Meyer and Meyer 1944).

We stocked 8 adult cotton rats (weight > 50 g, range: 53–161 g), 3 males and 5 nonpregnant females (39.5 individuals/ha), into the enclosures from 2 May to 5 June 2012. We chose the stocking density to correspond with natural cotton rat densities in Georgia, which range from 8 to 69 individuals/ha (Odum 1955). We captured cotton rats elsewhere on Ichauway and marked them with a unique ear tag (National Band and Tag Co., Newport, Kentucky) in each ear. When mortality occurred (an individual was not captured during ≥ 1 session), we replaced the individual either with a recruit from another enclosure or a new individual of the same sex captured from outside the enclosures.

Treatments.—Our experiment consisted of a 2-way factorial design with predator and fire ant treatments as factors. We included a predator exclusion treatment to evaluate our second objective, assessing if fire ants indirectly increased predation by other predators. Irrespective of the predator treatment applied to the enclosures, the enclosures did not exclude semiarboreal and highly mobile predatory snake species (e.g., coachwhip [*Masticophis flagellum*], black racer [*Coluber constrictor*], corn snake [*Pantherophis guttatus*], and gray rat snake [*Elaphe obsoleta*]) and likely excluded smaller mesopredators (e.g., striped skunk [*Mephitis mephitis*], nine-banded armadillo [*Dasyus novemcinctus*], and opossum [*Didelphis virginiana*]—Smith et al. 2006). Consequently, our predator exclusion treatment was limited to assessing the effects of larger mammalian (e.g., coyote [*Canis latrans*], bobcat [*Lynx rufus*], raccoon [*Procyon lotor*], red fox [*Vulpes vulpes*], and gray fox [*Urocyon cinereoargenteus*]) and avian predators (e.g., red-shouldered hawk [*Buteo lineatus*], red-tailed hawk [*Buteo jamaicensis*], Cooper's hawk [*Accipiter cooperii*], northern harrier [*Circus cyaneus*], and barred owl [*Strix varia*]—Smith et al. 2006). We had 4 treatments, with 2 replicates of each, including a control with ambient numbers of fire ants and predators (RIFA [+]/PRED [+]), fire ants reduced and predators excluded (RIFA [-]/PRED [-]), ambient numbers of fire ants and predators excluded (RIFA [+]/PRED [-]), and fire ants reduced and ambient numbers of predators (RIFA [-]/PRED [+]; Fig. 1).

Enclosures.—We constructed eight 45×45-m enclosures from Galvalume (BIEC International Inc., Kalama, Washington) metal siding buried in a 1-m-deep trench, to prevent rats from digging out, and the aboveground portion of the siding was 1 m high. To discourage attempts at cotton rat emigration or immigration into the enclosures, we maintained a 1-m mowed buffer on the inner and outer perimeter of each enclosure (Fig. 1). During mark-recapture sampling, our capture probability was nearly 100%, indicating that the enclosures were able to contain the cotton rats. In addition to vegetation present in the enclosures, we provided cover for the cotton rats by placing 24 piles of 1–1.25-m long live oak (*Quercus virginiana*) logs with 10–20-cm diameter between grid intersections on a 4×4 grid with 10-m spacing centered in each enclosure in 2012 (Fig. 1).

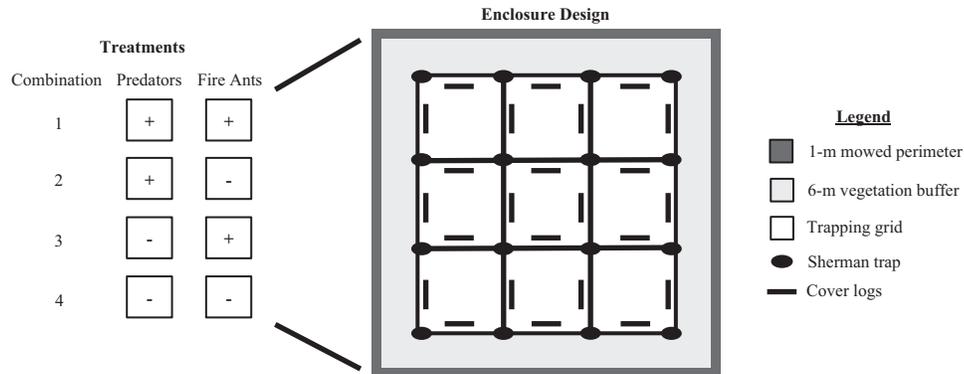


Fig. 1.—A schematic of the experimental design, including treatment combinations and enclosure design, used to assess the influence of predators (PRED) and imported red-fire ants (*Solenopsis invicta*) on the survival and recruitment of hispid cotton rats (*Sigmodon hispidus*) located in 8 enclosures on Ichauway, Newton, Georgia: ambient predators and ambient red-imported fire ants ([RIFA (+) × PRED (+)]; $n = 2$); excluded predators and ambient fire ants ([RIFA (+) × PRED (-)]; $n = 2$); excluded predators and reduced fire ants ([RIFA (-) × PRED (-)]; $n = 2$); and ambient predators and reduced fire ants ([RIFA (-) × PRED (-)]; $n = 2$).

To exclude mammalian predators from half of the enclosures, we attached game farm netting (Promounds Inc., Brockton, Massachusetts) to the top of the metal barrier and extended it 2 m above the entire enclosure (Desy and Batzli 1989). We tied strands of UV-stabilized twine across the top of the enclosures every 0.3 m to exclude predatory birds (Desy and Batzli 1989). The twine was held in position horizontally by placing it over and perpendicular to two 45-m pieces of 3.18-mm galvanized metal wire that we attached 15 m from each end of each enclosure. Occasionally raccoon sign (e.g., tracks) was found in the PRED (-) enclosures and entry points were located and repaired immediately. These modifications were applied only to the 4 predator exclusion plots. Mammalian and avian predators had free access to enter the other 4 enclosures.

We used Amdro (Ambrands, Atlanta, Georgia), a conventional bait formula, to reduce fire ant 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; Parker 1994). We applied Amdro in the morning before 1100 h 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 fire ants were present at 30–40% of the bait stations used to sample fire ant foraging pressure (see “Ant monitoring”).

Ant monitoring.—We quantified fire ant foraging activity using bait sampling (Collins et al. 1992) to monitor the effectiveness of the Amdro treatment and to determine the necessary timing for reapplication of Amdro in treated plots. We sampled monthly from May 2012 to October 2013 within enclosures by using bait traps comprised of 20 ml scintillation vials and 3 g of hot dog. We located traps at each intersection of the 4 × 4-m sampling grid described previously (16 total bait traps/enclosure per session; Fig. 1). For the first 4 sessions, we placed the vials on the ground with no cover. However, because other animals often consumed the hotdogs prior to collection, for the remaining sessions, we constructed 12.7 × 12.7-cm enclosures from 1.27 × 1.27-cm hardware cloth and placed them over the top of the vials. This allowed ants to forage on the hot

dogs but excluded other animals. We attached the containers to the ground with 3.81-cm fence staples and removed them between sessions. We placed traps during peak fire ant foraging times (Tschinkel 2006) in the morning before 1100 h and collected them after 1 h. We counted and identified fire ants within each trap. All other ants captured were identified to genus and counted.

Mark-recapture.—We sampled for cotton rats every 4 weeks for 13 months from June 2012 to June 2013 (14 sessions). Each mark-recapture session consisted of 4 nights of trapping. We placed 2 Sherman live traps (H.B. Sherman Traps, Inc., Tallahassee, Florida) at each grid intersection (32 traps/enclosure; Fig. 1) and baited them with a mixture of oats and birdseed. Upon capture, we recorded the cotton rat’s identification number, weight, sex, hind foot length, and reproductive condition. For new recruits, we recorded their weight, sex, and hind foot length and then removed them from the enclosure to maintain consistent densities of cotton rats across enclosures. All trapping methods followed recommendations of the American Society of Mammalogists’ Guidelines for the use of wild mammals in research (Sikes et al. 2011) and were approved by the University of Florida Institutional Animal Care and Use Committee (Approval number 201207414).

Statistical analyses.—We completed all analyses in Program R (R Core Team 2014). To compare fire ant foraging pressure between enclosures with ambient (RIFA [+]) and reduced (RIFA [-]) fire ants, we used the fire ant counts at each trap as our dependent variable and fit generalized linear mixed models (GLMMs) with a Poisson distribution (count data) with the package lme4 (Bates et al. 2014). We only included sampling periods of peak fire ant (Tschinkel 2006) activity in the analysis, which included May–September 2012 (5 sessions; $n = 579$) and April–September 2013 (6 sessions; $n = 865$). To determine if foraging pressure was comparable across years, we included the variable Year as a fixed effect in the model with Trap nested within Enclosure as a random effect. We subsequently completed the analysis for 2012 and 2013 separately and fit a GLMM with the variable fire ant treatment (RIFA) as a fixed effect and Trap nested within Enclosure as a random effect to

determine if the RIFA (–) enclosures had lower numbers of fire ants than the RIFA (+) enclosures in 2012 and 2013. We considered $P \leq 0.05$ to indicate a significant difference.

To evaluate the effects of RIFA, predator treatment (PRED), and their interaction (RIFA \times PRED) on the survival time in months (T) of cotton rats, we fit Cox-proportional hazard models using the package “Survival” (Therneau 2014). We first assessed differences in T by sex and subsequently fit models for males and females independently. We used the control (RIFA [+]/PRED [+]) populations as our reference when assessing the variable RIFA \times PRED and considered variables with a P value < 0.05 to be significant. When variables were significant, we used the hazard ratio (HR) to determine differences in the relative risk of mortality between groups (RIFA [+]/PRED [+]; RIFA [–]/PRED [–]; RIFA [+]/PRED [–]; RIFA [–]/PRED [+]).

To assess the effects of RIFA, PRED, and RIFA \times PRED on cotton rat recruitment (f), we fit a GLMM with a Poisson distribution using package “lme4” (Bates et al. 2014). We used the number of young captured in each enclosure per month as our dependent variable and included a random variable to account for multiple measures from the same enclosure. We also included the number of adult females in each enclosure as an offset term in the model. Inclusion of the offset term permitted use of a Poisson distribution and allowed us to calculate f by adjusting the raw count of juveniles by the number of females available to reproduce in each enclosure. We considered parameter estimates with a P value ≤ 0.05 to be significant.

RESULTS

We found that fire ant abundance was 38% greater in 2012 ($\bar{X} = 161.6$, $SE = 12.2$) than 2013 ($\bar{X} = 117.1$, $SE = 8.6$; GLMM: $\beta = -0.28$, $SE = 0.01$, $Z = -60.74$, $P < 0.0001$). In 2012, mean fire ant abundance was approximately 14 times greater in the RIFA (+) enclosures ($\bar{X} = 290.2$, $SE = 19.8$) compared to RIFA (–) enclosures ($\bar{X} = 20.5$, $SE = 6.5$; GLMM: $\beta = -7.63$, $SE = 0.80$, $Z = -9.59$, $P < 0.0001$). Fire ant abundance within RIFA (+) enclosures ($\bar{X} = 200.6$, $SE = 15.4$) was approximately 6 times greater than the RIFA (–) enclosures ($\bar{X} = 31.8$, $SE = 4.9$; GLMM: $\beta = -5.07$, $SE = 1.45$, $Z = -3.50$, $P = 0.0005$) in 2013.

The relative risk of mortality (HR) for female cotton rats was 1.65 times greater than the relative risk for males ($\beta = 0.50$, $SE = 0.23$, $HR = 1.65$, $Z = 2.199$, $P = 0.0279$). We found that the variable PRED affected the survival of male and female cotton rats. Specifically, the enclosures with PRED (+) had an HR approximately 2 times greater than rats in the enclosures with PRED (–) (Table 1; Fig. 2).

The variable RIFA did not affect survival of male or female cotton rats (Table 1; Fig. 2). Analyses of the PRED \times RIFA interaction indicated that the HR was 3 and 4.5 times greater for female and male cotton rats, respectively, in enclosures with RIFA (+)/PRED (+) compared to enclosures with RIFA (–)/PRED (–) (Table 1; Fig. 2). We found no difference for other treatment combinations ($P > 0.05$). The variables RIFA,

Table 1.—The beta (β) coefficients, SE s, hazard ratios (HRs), Z -statistic (Z), and P values associated with Cox-proportional hazard models fit to assess the effects of imported red-fire ants (*Solenopsis invicta*) treatment (RIFA), predator treatment (PRED), and their interaction (RIFA \times PRED) on the survival time in months (T) of male ($n = 72$) and female ($n = 98$) cotton rats (*Sigmodon hispidus*) from June 2012 to June 2014 stocked into 8 enclosures located on Ichauway, Newton, Georgia: ambient predators and ambient red-imported fire ants ([RIFA (+) \times PRED (–)]; $n = 2$); excluded predators and ambient fire ants ([RIFA (+) \times PRED (–)]; $n = 2$); excluded predators and reduced fire ants ([RIFA (–) \times PRED (–)]; $n = 2$); and ambient predators and reduced fire ants ([RIFA (–) \times PRED (–)]; $n = 2$). Parameter estimates with a P value ≤ 0.05 were considered significant.

Variables	β	SE	HR	Z	P value
Males					
RIFA	–0.48	0.38	1.62	–1.277	0.2020
PRED	–0.86	0.44	2.36	–1.965	0.0494
PRED (+) \times RIFA (–)	0.07	0.47	0.93	0.153	0.8788
PRED (–) \times RIFA (+)	–0.27	0.54	1.31	–0.502	0.6157
PRED (–) \times RIFA (–)	–1.52	0.69	4.59	–2.207	0.0273
Females					
RIFA	0.00	0.26	1.00	–0.013	0.9900
PRED	–0.81	0.29	2.24	–2.739	0.0062
PRED (+) \times RIFA (–)	0.11	0.33	0.89	0.331	0.7409
PRED (–) \times RIFA (+)	–0.58	0.37	1.78	–1.571	0.1162
PRED (–) \times RIFA (–)	–1.11	0.50	3.02	–2.229	0.0258

PRED, and the RIFA \times PRED interaction did not affect cotton rat recruitment (Table 2).

DISCUSSION

Our findings indicate that native predators (e.g., bobcat, red-shouldered hawks [*B. lineatus*]) had the greatest influence on cotton rat populations, although fire ants did affect their survival. When native predators are present, it is likely that cotton rat populations have high mortality rates and rapid population turnover. Consequently, the effects of fire ants on survival, which may manifest over relatively longer temporal scales, would not be apparent. Because we found that survival of cotton rats only increased in the RIFA (–)/PRED (–) treatment and that the RIFA (+)/PRED (–) treatment was not different from the RIFA (+)/PRED (+) treatment, the effects of fire ants on cotton rat mortality appeared to be compensatory (one cause of mortality replaced by another—Barbosa and Castellano 2005). In the absence of other predators, mortality caused by fire ants was equivalent to mortality associated with the major predators on our study site.

Neither fire ants nor other predators influenced cotton rat recruitment. One possible explanation for this finding is that fire ants may be unable to penetrate the finely woven plant material surrounding cotton rat nests (Hill 1969). An additional explanation is that because cotton rats have semiprecocial young (Johnson 1961), the rats can move to avoid predation. It is also possible that fire ants may depredate some cotton rat young prior to the rats exiting the nest, but that the amount of depredation of young may not be sufficient to affect recruitment. Additionally, cotton rat females will protect their young

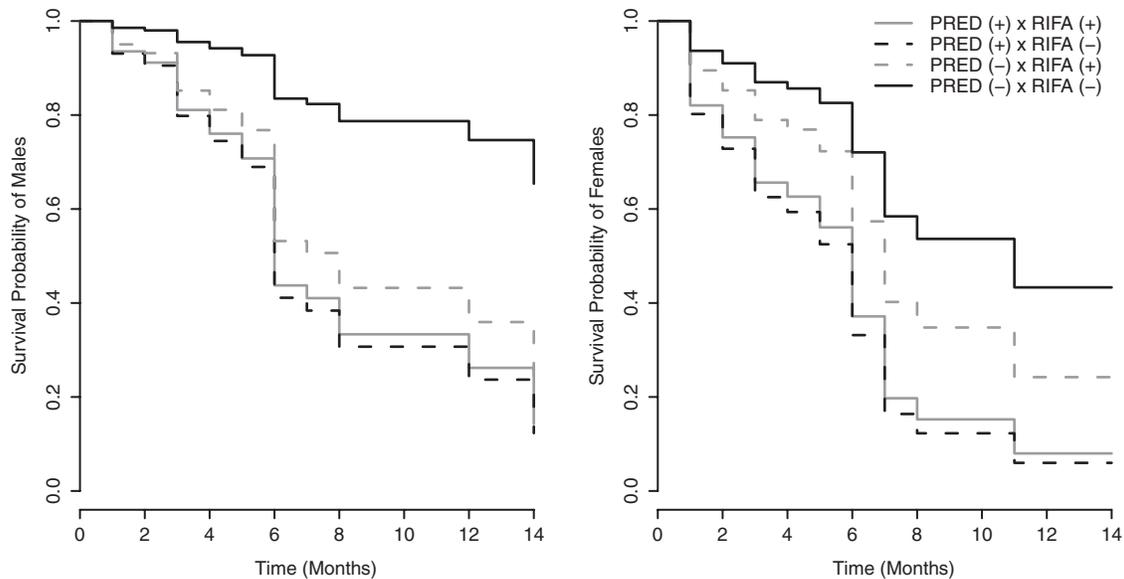


Fig. 2.—Monthly survival probabilities from June 2012 to June 2013 of hispid cotton rats (*Sigmodon hispidus*) located in 8 enclosures on Ichauway, Newton, Georgia: ambient predators and ambient imported red-fire ants ([RIFA (+) × PRED (+)]; $n = 2$); excluded predators and ambient fire ants ([RIFA (+) × PRED (-)]; $n = 2$); excluded predators and reduced fire ants ([RIFA (-) × PRED (-)]; $n = 2$); and ambient predators and reduced fire ants ([RIFA (-) × PRED (+)]; $n = 2$).

Table 2.—The beta (β) coefficients, *SEs*, *Z*-statistic (*Z*), and *P* values associated with generalized linear mixed models fit to assess the effects of imported red-fire ants (*Solenopsis invicta*) treatment (RIFA), predator treatment (PRED), and their interaction (RIFA × PRED) on the recruitment (number of young per female) of cotton rat (*Sigmodon hispidus*) populations from June 2012 to June 2014 stocked into 8 enclosures located on Ichauway, Newton, Georgia: ambient predators and ambient red-imported fire ants ([RIFA (+) × PRED (+)]; $n = 2$); excluded predators and ambient fire ants ([RIFA (+) × PRED (-)]; $n = 2$); excluded predators and reduced fire ants ([RIFA (-) × PRED (-)]; $n = 2$); and ambient predators and reduced fire ants ([RIFA (-) × PRED (+)]; $n = 2$).

Variables	β	<i>SE</i>	<i>Z</i>	<i>P</i> value
RIFA	-0.17	0.19	-0.899	0.3680
PRED	-0.08	0.19	-0.393	0.6940
PRED (+) × RIFA (-)	-0.19	0.27	-0.695	0.4870
PRED (-) × RIFA (+)	-0.09	0.26	-0.347	0.7290
PRED (-) × RIFA (-)	-0.23	0.26	-0.915	0.3600

from fire ants by moving them or removing stinging fire ants (Ferris 1994), which may reduce the negative influence of fire ants on cotton rat recruitment. Future studies should assess how fire ants affect species with altricial young, which may be more vulnerable to depredation by fire ants.

We found no evidence that the presence of fire ants increased predation of cotton rats by other predators. However, this may be due to the scale of our study as the area of our enclosures was smaller than the home range of the predators found on our study site including bobcats, red (*V. vulpes*) and gray fox (*U. cinereoargenteus*), coyotes, raccoons (*P. lotor*), and multiple predatory birds and snakes species. Thus, it is likely that after a predator entered an enclosure, they were able to locate cotton rats easily, regardless of changes in movement related to the presence of fire ants. Other studies demonstrate that

increased movement by small mammals reduces survival by increasing predation (Jędrzejewski et al. 1993; Norrdahl and Korpimäki 1998). Future studies should address the effects of fire ants on movement of small mammals and the potential impact of these changes in movement on predation at multiple scales.

We demonstrated that fire ants affect cotton rat survival in the absence of other predators, but the mechanisms driving this effect are still unknown. We propose that fire ants likely affect cotton rats via increased risk of injury, rather than direct predation. Studies have established that stings from fire ants can cause reduced weight gain and growth and eventually lead to mortality of vertebrates (e.g., Allen et al. 1997b; Langkilde and Freidenfelds 2010). Moreover, small mammals, including cotton rats, consume less food (measured via giving up densities—Brown 1988) when foraging in the presence of fire ants (A. K. Long, pers. obs.; Holtcamp et al. 1997; Orrock and Danielson 2004) indicating that they perceive a risk from fire ants, likely through exploitive and/or interference competition (Orrock and Danielson 2004). Studies also have established that prey alter foraging strategies in response to risk of injury (Brown et al. 1999, 2001) and vertebrates, in particular, may increase their movement in response to risk of injury from fire ants (e.g., Allen et al. 1997a; Langkilde 2009). Cotton rats in our study may respond to fire ants using these strategies leading to a decrease in the longevity of individuals by reducing caloric intake, particularly of protein-rich foods that are attractive to fire ants (Tschinkel 2006), increasing energy expenditure, and/or eliciting a stress response. Additionally, female cotton rats may invest more time in protecting their young from fire ants (e.g., nest relocation and fire ant removal—Ferris 1994), which may increase mortality via stress and reduced foraging effort.

The mechanisms by which native populations respond to invasive species may vary across spatial and temporal scales.

We suggest that studies on invasive predators need to control for more factors, such as other predators, to better understand how invasive species influence native populations. For instance, without the inclusion of a predator treatment in our study, we would not have demonstrated that fire ants could negatively influence cotton rat populations. Although cotton rats are not experiencing population declines, there are several small mammal species in the southeastern United States of primary conservation concern (e.g., Florida mouse [*Podomys floridanus*], Lower Keys marsh rabbit [*Sylvilagus palustris hefneri*], and Key Largo woodrat [*Neotoma floridana smalli*]). Fire ants may play a role in their declines (Frank et al. 1997; Forsys et al. 2002) and our results suggest that to conserve the biodiversity of native small mammals, and other vertebrates that may respond similarly in the southeastern United States, management of fire ants in combination with controlling other predators may be necessary.

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