Impacts of Red Imported Fire Ants (*Solenopsis invicta*) on Nestling and Hatchling Gopher Tortoises (*Gopherus polyphemus*) in Southwest Georgia, USA

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Abstract.—Invasive species, such as the Red Imported Fire Ant (*Solenopsis invicta*, hereafter, Fire Ant), impact native species via predation, competition for resources, and modifying prey behavior. However, relatively little is known about the effects of Fire Ants on oviparous reptiles. Therefore, we quantified nestling and hatchling survival and examined indirect effects of Fire Ants on growth rate and movement patterns of hatchling Gopher Tortoises (*Gopherus polyphemus*) using four 0.2-ha enclosures where we reduced Fire Ant abundance and four enclosures with ambient Fire Ant abundance. Both nestling and hatchling survival were greater in enclosures with reduced Fire Ants. Additionally, hatchlings exposed to ambient Fire Ant levels moved farther, used more locations, and had larger 6-mo home ranges than hatchlings exposed to reduced Fire Ant levels. Our study suggests Fire Ants may be a major source of Gopher Tortoise predation and have indirect effects on hatchling behavior, but further studies are needed to determine whether Fire Ants are having population-level impacts.

Key Words.—indirect effects; invasive species; oviparous reptiles; predation; survival

Introduction

Invasive species have been implicated in the decline of native species directly through predation (Vitousek et al. 1996; Pimentel et al. 2005), and indirectly through competition and behavioral modification (Wojcik et al. 2001; Langkilde 2009; Ligon et al. 2012). The invasive Red Imported Fire Ant (*Solenopsis invicta*; hereafter, Fire Ant) is known to negatively impact native birds (Giuliano et al. 1996; Campomizzi et al. 2009), lizards (Donaldson et al. 1994; Newman et al. 2014), mammals (Allen et al. 1997a), snakes (Tuberville et al. 2000), and turtles (Allen et al. 2001; Parris et al. 2002; Epperson and Heise 2003) in the southeastern U.S. However, less is known about indirect effects of Fire Ants on native fauna, which can include altered habitat use, activity patterns (e.g., foraging and resting behavior), and movements relative to the perceived risk of an individual to injury from predation or envenomization (Pedersen et al. 1996; Holtcamp et al. 1997; Langkilde 2009; Holtcamp et al. 2010). Sting and bite injuries delivered individually by Fire Ants may be non-lethal to prey, but could result in swelling, lesions, and infection, increasing the chance of mortality. Additionally, altered behavioral patterns including less time spent foraging can result in reduced fitness and growth rate (Giuliano et al. 1996; Allen et al. 1997b).

Fire Ants were introduced into the United States through the port of Mobile, Alabama in the 1930s (Wojcik et al. 2001). Since then, Fire Ants have spread rapidly through the southeastern USA and currently occupy more than 132 million ha in 15 U.S. states (Allen et al. 2004). Fire Ants are successful biological invaders due to their high reproductive and dispersal capabilities, lethal and non-lethal effects of stings, and aggressive foraging behavior (Parris et al. 2002; Allen et al. 2004). Foraging Fire Ants return small food items to the nest independently, but also recruit nestmates waiting in underground foraging tunnels to assist with the breakdown and transport of larger food items (Tschinkel 2006). This behavior allows for rapid forager recruitment to large food sources and the ability to immobilize large prey items (Tschinkel 2011).

In the Southeast U.S., Fire Ants occur in a range of habitats, including open canopy Longleaf Pine (*Pinus palustris*)-Wiregrass (*Aristida stricta*) savannas. In some Longleaf Pine stands, the Fire Ant is the dominant ant species (Stuble et al. 2009) and currently occupies the entire range of the Gopher Tortoise (*Gopherus polyphemus*), a species experiencing population declines and a candidate species for federal protection (U.S. Fish and Wildlife Service 2011). Longleaf Pine forests are primarily managed with frequent prescribed fire (Glitzenstein et al. 1995; Barnett 1999), potentially creat-

ing disturbance conducive to successful Fire Ant colonization. In Longleaf Pine forests, Fire Ants colonize patches of bare ground created by fire, or the bare soil at the entrance of Gopher Tortoise burrows, called aprons (Wetterer and Moore 2005), areas that coincide with Gopher Tortoise nesting habitat (Landers et al. 1980; Smith 1995). Consequently, Gopher Tortoise nestling and hatchling survival may be reduced in areas where Fire Ants are present, but little quantifiable evidence exists to document potential impacts.

Gopher Tortoises deposit their eggs from late April through July in below ground nests in sandy soils in full sunlight to facilitate incubation (Iverson 1980; Landers et al. 1980; Smith 1995). Mammals are the leading Gopher Tortoise nest predators, and nest predation may approach 90% within a given year in some populations (Landers et al. 1980; Marshall 1987). The majority of predation events occur within the first three weeks after nest deposition (Hamilton et al. 2002). Fire Ants cannot penetrate intact Gopher Tortoise eggs (Allen et al. 2004), but may build underground foraging trails to nests and attack nestlings while they are pipping from the egg (Allen et al. 2001, Buhlmann and Coffman 2001). This behavior in Fire Ants, coupled with the ability to envenomate prey, may act as an additive source of predation (Griswold and Lounibos 2006; Mills 2006) for species with immobile life stages including oviparous reptiles (Allen et al. 2004). Incubation of Gopher Tortoise eggs generally lasts 80–110 d and hatchlings emerge from nests between mid-August and October (Iverson 1980; Landers et al. 1980; Smith 1995). Nestlings commonly delay emergence from their nests for one or more days while absorbing residual yolk (Butler and Hull 1996; Buhlmann and Coffman 2001; Gibbons 2013). Immobile nestlings may be the most susceptible to Fire Ant predation as they cannot escape and may be fatally envenomated before emergence from the nest (Parris et al. 2002).

Fire Ants have been observed as predators of hatchling Gopher Tortoises in several studies (Landers et al. 1980; Smith 1995) including a study in Mississippi, USA, that found 26.8% of radio-tracked hatchling mortality was attributed to Fire Ant predation (Epperson and Heise 2003), indicating predation by Fire Ants may be considerable in some populations. However, to our knowledge, no study has experimentally examined the direct and indirect effects of Fire Ants on Gopher Tortoises before and after nest emergence. Therefore, we examined Fire Ant predation rates on Gopher Tortoise nestlings (i.e., Gopher Tortoises within the nest cavity) and hatchlings (i.e., Gopher Tortoises after nest emergence). We also examined indirect effects of Fire Ants and vertebrate predators (e.g., mammals, snakes, and raptors) on movement patterns, burrow use, and growth rates of hatchlings in their first six months of life.

Materials and Methods

Study site.—Our study was conducted at Ichauway, the 11,600–ha research site of the Joseph W. Jones Ecological Research Center, Baker County, Georgia, USA (31° 11′32.8734″ N, -84° 29′14.766″ W). The study site is comprised of 37% natural pine, 29% mixed pine-hardwood, 11% agricultural areas or food plots, 10% pine plantation, 6% wetland or open water, 4% scrub, 2% hardwood forest, and 1% urban area (Jean Brock, unpubl. data). Maximum daily air temperature at Ichauway averaged 31.9° C during the first month of the active season following Gopher Tortoise hatchling emergence (28 August to 28 September 2014), 25.6° C during the remainder of the active season (29 September to 14 November 2014), and 16.9° C during the dormant season (15 November to 3 March 2015; Georgia Automated Environmental Monitoring Network; http://georgiaweather.net). Fire Ants have been present in Baker County since the mid-1960s (Callcott and Collins 1996), though the exact date of arrival is unknown. The Fire Ant is the dominant ant species at Ichauway (Stuble et al. 2009).

We used eight existing enclosures originally designed to contain small mammals (see details below; Wolff et al. 1999) in a concurrent study (see Long et al. 2015). Enclosures were built in a 14-y old Longleaf Pine plantation where ground cover was primarily comprised of goldenrod (*Solidago* spp.), blackberry (*Rubus* spp.), Giant Ironweed (*Vernonia gigantea*), and Common Ragweed (*Ambrosia artemisiifolia*).

Field methods.—The perimeter of the eight 0.2 ha (45 × 45 m) enclosures consisted of galvanized metal siding (Galvalum®, BIEC International, Inc., Vancouver Washington, USA) extending approximately 1 m above and 1 m below ground and silt fence (Mutual Industries, Philadelphia, Pennsylvania, USA) extending 1 m above the metal siding to prevent small mammals from exiting. We used a two-way factorial design with Fire Ant and vertebrate predator treatments as factors; therefore, we had four treatments (ambient Fire Ant with ambient predator, reduced Fire Ant with ambient predator, ambient Fire Ant with reduced predator, and reduced Fire Ant with reduced predator) with two replicates of each treatment randomly assigned to enclosures. To exclude mammalian and avian predators in four enclosures, we attached game farm netting (Promounds Inc., Brockton, Massachusetts, USA) to the top of the metal siding that reached 2 m above the enclosure and ultraviolet (UV) resistant twine (Ambraco Inc., Orangeline TM, Dubuque, Iowa, USA) held in place with 3.18 mm galvanized metal wire secured with 12 wooden posts, and spaced twine 0.3 m apart across the top of the enclosures (Fig.
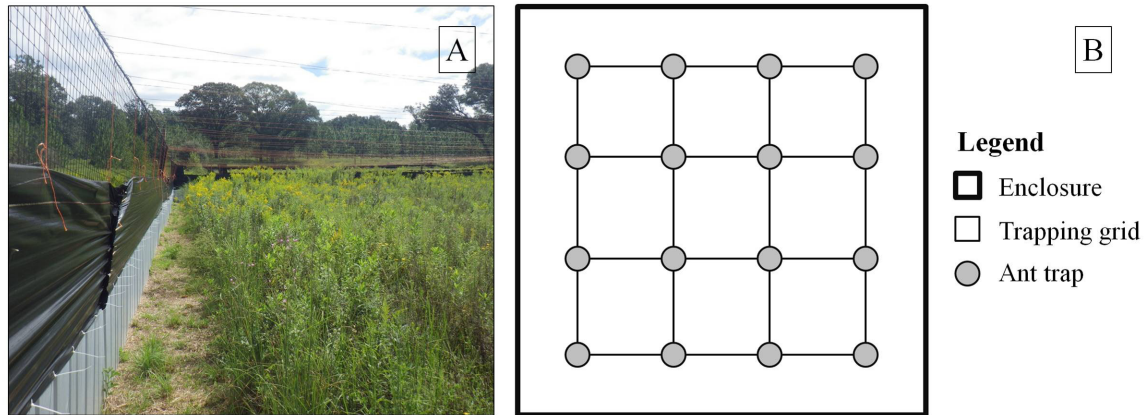
FIGURE 1. A) Enclosure with reduced vertebrate predator treatment (Photographed by Michelina Dziadzio). B) Diagram of the 10 × 10 m ant sampling grid used in enclosures to monitor abundance of Red Imported Fire Ants (*Solenopsis invicta*) in eight enclosures on Ichauway, Baker County, Georgia, USA.

1). Although we documented Raccoon (*Procyon lotor*) trespass in the ambient vertebrate enclosures, based on reduced predator sign (i.e., digs and tracks), enclosures with game farm netting and UV twine reduced the prevalence of vertebrate predators (e.g., meso-mammals, birds, and snakes) during the study.

We reduced Fire Ants in four of eight enclosures using Amdro® (Ambrands, Atlanta, Georgia, USA), a bait formula that can reduce Fire Ant populations for > 11 mo (Pedersen et al. 2003). We used a broadcast treatment of 1.7 kg/ha (Collins et al. 1992) and spot-treated new Fire Ant mounds throughout the study period, 25 May 2014 to 3 March 2015. The four remaining enclosures were not treated; we considered Fire Ant abundance to be ambient in these enclosures, or equal to abundances found in Gopher Tortoise habitats across Ichauway. We sampled ants on 18 September and 30 October 2014 in all eight enclosures by trapping foraging ants in 20-mL polyethylene screw-top scintillation vials (VWR®, 66022–241, Radnor, Pennsylvania, USA) on a 4 × 4 m sampling grid with 10 m spacing in each enclosure (16 samples per enclosure; Fig. 1). We placed vials horizontally on the soil surface and baited vials with approximately 4-g of processed slices of lunch meat (hot dog) following methods modified from Agosti et al. (2000). We set out baited vials between 0700 and 1100 during optimal Fire Ant foraging air temperatures (25–35° C; Drees et al. 2007). We collected vials after 1 h and preserved samples with 70% ethanol. We identified and counted *S. invicta* and identified all other ants to genus. We considered Fire Ant abundance to be the average number of Fire Ants per vial.

To obtain Gopher Tortoise eggs for this study, we located Gopher Tortoise nests laid on roads during the 2014 tortoise nesting season. If a female was observed nesting, we documented the location and returned to remove eggs once the female had completed deposition.

We also located road nests where females were not observed ovipositing by identifying physical evidence of nest deposition, i.e., a characteristic circle over the deposited nest resulting from the female covering the eggs. Although we were unable to determine when nests were deposited if a female was not observed, we relocated eggs within 24 h of nest discovery to minimize movement induced egg mortality (Limpus et al. 1979). We excavated, weighed, and numbered the tops of eggs with a pencil to assist in maintaining orientation of the eggs during transport (Limpus et al. 1979). We relocated Gopher Tortoise eggs to randomly selected nest sites with sparse vegetation in each enclosure (four nests in each of eight enclosures). We dug each nest 14 cm below ground and each nest contained two randomly assigned Gopher Tortoise eggs. To prevent vertebrate predation and to restrain hatchlings upon emergence, we covered nests with cages made from hardware cloth using a design modified from Smith (1995). Hardware cloth (Blue Hawk, L.G. Sourcing, Inc., North Wilkesboro, North Carolina, USA) nest cages in our study measured 30 × 30 × 12 cm with 10-cm hardware cloth flaps buried parallel with the ground to prevent predators from digging under the cage. To ensure an adequate sample size for the post-emergence experiment, we also caged nests in burrow aprons elsewhere on the site (Dziadzio et al. 2016) and collected Gopher Tortoise hatchlings as they emerged.

We monitored nests weekly until two weeks before hatchlings were expected to emerge (18 August 2014), when we began checking nests daily. We transported all hatchlings found in nest cages back to the lab for processing. If hatchlings did not emerge within 120 d of nest placement, we excavated nest sites to determine if animals had hatched and were subsequently depredated by Fire Ants before emerging, or if eggs were not viable. A nest was considered depredated by Fire Ants if

we discovered skeletonized nestling remains in the nest cavity upon excavation.

After transporting hatchlings back to the laboratory, we uniquely marked each animal using an alpha-numeric tag (VI Alpha Tags, Northwest Marine Technology, Inc., Shaw Island, Washington, USA) attached to the plastron with super glue (Liquid Professional, Loctite®, Henkel Corporation, Westlake, Ohio, USA). For each hatchling, we measured straight-line carapace length to the nearest 0.1 mm using digital calipers (Model 700–126, Mitutoyo Corporation, Aurora, Illinois, USA) and mass to the nearest 0.1 g with a digital scale (PB-500, Brecknell, Fairmont, Minnesota, USA). Additionally, we attached a 1.8 g radio transmitter (Model BD-2, Holohil Systems Ltd., Carp, Ontario, Canada) with an approximate 4-mo battery life to the fourth vertebral scute (Epperson and Heise 2003) of each individual with super glue and silicone aquarium sealant (Marineland®, Perfecto Mfg. Inc., Noblesville, Indiana, USA; Smith et al. 2013). Transmitter packs weighed approximately 1.8 g and ranged between 4.6–6.3% ($\bar{x}$ = 5.4%) of the day-old body mass of the tortoise ($\bar{x}$ = 33.9 g, range 29.9–38.1 g). Transmitter packs weighing up to 12.0% of a tortoise's body mass have no effect on hatchling survival (Epperson and Heise 2003). We returned hatchlings to their enclosure nest site within 36 h of capture.

We tracked 32 hatchlings (n = 16 per ant treatment) and recorded tortoise locations using a Trimble Nomad GPS unit (Trimble Navigation, Ltd., Sunnyvale, California, USA) with submeter accuracy. We tracked hatchlings 7 d per week during the active season, from 28 August to 14 November 2014, and 3 d per week during the dormant season, between 14 November and 2 March 2015. We did not track hatchlings at specific times, but primarily monitored hatchlings in the afternoon during the dormant season. If a hatchling was found dead, we inspected the remains to infer cause of death. We considered mortality of a tortoise with a transmitter still attached and no shell damage to be caused by Fire Ants. If the shell of the deceased tortoise was damaged and the transmitter removed, we inferred the hatchling was killed by a Raccoon because Raccoons were the only mammalian predators documented in enclosures (i.e., we observed Raccoon tracks scaling galvanized metal siding of the enclosures).

We excavated burrows and captured hatchlings between 3–8 March 2015 to remove radio transmitters as well as measure carapace length and body mass. While excavating burrows to recover hatchlings, we measured burrow depth (i.e., vertical distance from the soil surface to the bottom of the burrow) to the nearest cm. Upon completion of the study, we returned hatchlings to suitable habitat in the vicinity of the original nest locations.

Statistical analyses.—We used Program R (R Core Team 2013) to complete all statistical analyses. To compare Fire Ant foraging pressure between enclosures with ambient and reduced Fire Ants, we analyzed our two sampling occasions (September and October 2014) separately, and fit generalized linear mixed models (GLMM) with a Poisson distribution including the variable Fire Ant treatment (i.e., ambient or reduced) as a fixed effect, and Trap nested within Enclosure as a random effect. We completed analyses using the package lme4 (Bates et al. 2014). We analyzed nestling survival using a test of equal proportions to determine the effect of Fire Ant treatment. We considered a nest successful if at least one of the two nestlings emerged from the nest.

To examine only the effect of Fire Ant treatment on hatchling survival, we did not include hatchlings that were depredated by Raccoons (n = 6) in this analysis. Because hatchlings entered the study between 27 August and 14 September 2014, we used a staggered-entry Kaplan-Meier survival analysis (Pollock et al. 1989) to examine survival rates for radio-tagged hatchlings between ant treatments. We completed this analysis using the function survfit in the package Survival in R (Therneau and Grambsch 2000). We right-censored radio-telemetered Gopher Tortoises that survived to the completion of the study and we set alpha at 0.05.

We evaluated five hatchling movement metrics: (1) number of observed locations; (2) number of burrows used; (3) home range size, calculated using minimum convex polygon (MCP; Mohr 1947); (4) maximum dispersal, calculated as the straight-line distance between the nest location of the tortoise and the farthest radio-tracked location; and (5) total distance traveled, calculated as the sum of the straight-line distances between locations. We used Hawth's Analysis Tools in ArcGIS 9.3 (Esri, Inc., Redlands, California, USA) to calculate home range (m^2), maximum dispersal (m), and total distance traveled (m). We used generalized linear models (GLM) to test for an effect of ant treatment, predator treatment, and enclosure on the five movement metrics. To meet model assumptions, we log transformed home range area, maximum dispersal, and total distance measurements, and square root transformed the number of locations and burrow counts.

We tested for an effect of Fire Ant treatment, vertebrate predator treatment, initial morphological measurements, and number of locations on hatchling growth rate using GLM. We calculated growth rate per day (final measurement - initial measurement/days between measurements) using mass to the nearest 0.1 g and straight-line carapace length (i.e., the center of the nuchal scute to the center of the anal scute) to the nearest 0.1 mm. To compare generalized linear models for hatchling growth rate and movement patterns, we used Akaike's Information Criteria (AIC) corrected for small sample size (AIC_c; Burnham and Anderson 2002). We considered the model with the lowest AIC_c to be the best model, but all models with an AIC_c < 2 units from the best fit model

TABLE 1. Overall percentage of nest survival, mean number of nests that survived (at least one hatchling emerged from the nest; four nests per enclosure), mean number of nests depredated by Fire Ants, mean number of nests not viable, and mean number of nests with unknown cause of failure in four enclosures with ambient levels of Fire Ants (*Solenopsis invicta*) and four enclosures with reduced Fire Ants during the 2014 Gopher Tortoise hatching season on Ichauway, Baker County, Georgia, USA. SE represents the standard error.

Ant treatment	Survival (%)	Survived ± SE	Fire Ants ± SE	Not viable ± SE	Unknown ± SE
Ambient	31.25	1.25 ± 0.24	2.00 ± 0.00	0.75 ± 0.24	0.00 ± 0.00
Reduced	75.00	3.00 ± 0.20	0.00 ± 0.00	0.50 ± 0.14	0.50 ± 0.25

were considered supported. We model-averaged parameter estimates included in multiple supported models ($AIC_c < 2$) to calculate parameter estimates and unconditional standard errors, and considered parameters useful for prediction if their 95% confidence interval (CI) did not include zero (Burnham and Anderson 2002).

RESULTS

We found that Fire Ant abundance was greater in ambient Fire Ant enclosures than reduced Fire Ant enclosures during both sampling occasions. During the first sampling occasion on 18 September 2014, Fire Ant abundance was approximately 1,990 times greater in ambient Fire Ant enclosures ($\bar{x} = 537.18$, SE 62.15) compared to reduced Fire Ant enclosures ($\bar{x} = 0.27$, SE = 0.19; GLMM: Estimate = -9.396, SE = 1.069, $Z = -8.790$, $P < 0.001$). During the second sampling occasion on 30 October 2014, Fire Ant abundance was approximately 13 times greater in ambient Fire Ant enclosures ($\bar{x}$ = 121.84, SE = 20.57) compared to reduced Fire Ant enclosures ($\bar{x} = 9.64$, SE = 3.22; GLMM: Estimate = -3.138, SE = 0.550, $Z = -5.704$, $P < 0.001$).

We located 10 Gopher Tortoise nests along roads on Ichauway between 25 May and 19 June 2014, relocated eggs into enclosures, and monitored nests until hatching (four nests per enclosure, two eggs per nest, $n = 64$ eggs). Of the 16 Gopher Tortoise nests monitored in ambient Fire Ant Enclosures, eight nests (50.0%) were depredated by Fire Ants before emergence, whereas none of the 16 nests in reduced Fire Ant enclosures were depredated by Fire Ants (Table 1). All eggs depredated by Fire Ants contained fully, or near-fully developed nestling Gopher Tortoises still partly encased in shell fragments. Ant treatment (i.e., ambient or reduced Fire Ants) influenced overall nestling survival ($\chi^2 = 6.15$, df = 1, $P = 0.013$), with $75.0 \pm 5.1\%$ (SE; Table 1) survival in enclosures with reduced levels of Fire Ants and $31.3 \pm 6.0\%$ (SE) survival in enclosures with ambient Fire Ant levels.
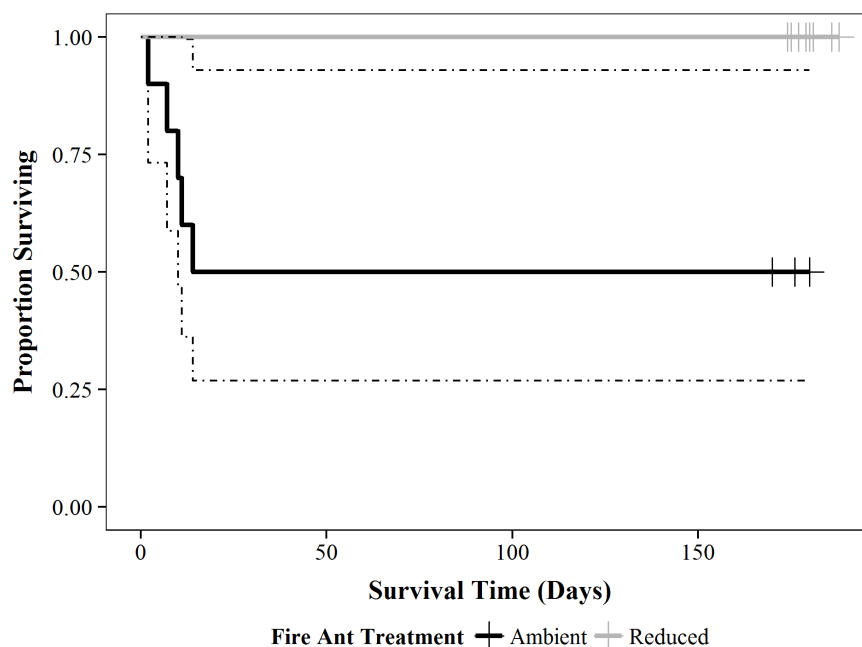

FIGURE 2. Kaplan-Meier survival curve of 26 hatchling Gopher Tortoises (*Gopherus polyphemus*). We excluded six of 32 monitored hatchlings that were killed by Raccoons (*Procyon lotor*) from this analysis. We monitored Gopher Tortoises with radio telemetry at four enclosures with ambient Fire Ant levels (*n* = 10) and four enclosures with reduced Fire Ants (*n* = 16) between 28 August 2014 and 2 March 2015 at Ichauway, Baker County, Georgia, USA. Dashed lines indicate 95% confidence intervals and vertical lines indicate right-censoring resulting from removal of tortoises at the end of the study period.

TABLE 2. Number of parameters (K), Akaike's Information Criterion corrected for small sample size (AIC_c), differences in AIC_c values from the top model (ΔAIC_c), and model weights (w_i) for models estimating daily movement patterns of radio-tracked Gopher Tortoise (*Gopherus polyphemus*) hatchlings from August 2014 through March 2015 on Ichauway, Baker County, Georgia, USA, ranked in order of support. Predictor variables include ant treatment, predator treatment, and enclosure ID.

Model	K	AIC_c	ΔAIC_c	w_i
Number of unique locations				
Ant treatment + Predator treatment	4	84.99	0	0.64
Ant treatment × Predator treatment	5	87.71	2.72	0.16
Ant treatment	3	88.41	3.42	0.12
Predator treatment	3	89.19	4.20	0.08
Enclosure ID	9	100.16	15.17	0
Home range (m²)				
Ant treatment + Predator treatment	4	116.12	0	0.62
Ant treatment × Predator treatment	5	117.72	1.60	0.28
Ant treatment	3	119.82	3.70	0.10
Enclosure ID	9	130.13	14.01	0
Predator treatment	3	133.73	17.61	0
Total distance moved (m)				
Ant treatment + Predator treatment	4	72.73	0	0.73
Ant treatment × Predator treatment	5	75.35	2.63	0.20
Ant treatment	3	77.39	4.67	0.07
Enclosure ID	9	86.69	13.96	0
Predator treatment	3	87.06	14.33	0
Maximum dispersal from nest site (m)				
Ant treatment + Predator treatment	4	66.97	0	0.73
Ant treatment × Predator treatment	5	69.6	2.63	0.20
Ant treatment	3	72.07	5.1	0.06
Predator treatment	3	74.68	7.71	0.02
Enclosure ID	9	81.23	14.26	0
Number of burrows used				
Ant treatment	3	57.21	0	0.46
Predator treatment	3	57.57	0.35	0.39
Ant treatment + Predator treatment	4	59.84	2.62	0.12
Ant treatment × Predator treatment	5	62.65	5.43	0.03
Enclosure ID	9	71.31	14.1	0

Because of timing and nest failure in enclosures, we added nine hatchlings to ambient Fire Ant enclosures and eight to reduced ant enclosures captured from Gopher Tortoise nests elsewhere on the site. In total, we monitored 16 hatchling Gopher Tortoises in enclosures with ambient Fire Ants and 16 in reduced Fire Ant enclosures. Of the 32 Gopher Tortoise hatchlings monitored, 11 (34.4%) did not survive the 6-mo study period. All mortality occurred within the first 60 d of the study, and all Fire Ant predation occurred within 24 d of release. Five individuals (15.6%) were depredated by Fire Ants in ambient Fire Ant enclosures; six (18.8%) were depredated by Raccoons, all of which were in enclosures with ambient Fire Ants, but in both vertebrate predator treatments (ambient = 3, reduced = 3). Of the five Fire Ant predation events, three occurred when the tortoise was above ground, whereas two hatchling Gopher Tortoises were killed by Fire Ants inside their burrows. Because we did not include hatchlings depredated by Raccoons ($n = 6$) in the hatchling survival analysis, hatchling survival was 50% in ambient ant enclosures compared to 100% at reduced ant enclosures (Fig. 2); survival differed between ant treatments ($\chi^2 = 11.28$, df = 1, $P < 0.001$), but not between vertebrate predator treatments ($\chi^2 = 0.18$, df = 1, $P = 0.668$).

For all movement metrics, the top model included ant treatment and predator treatment (Table 2) with the exception of number of burrows used in which the top
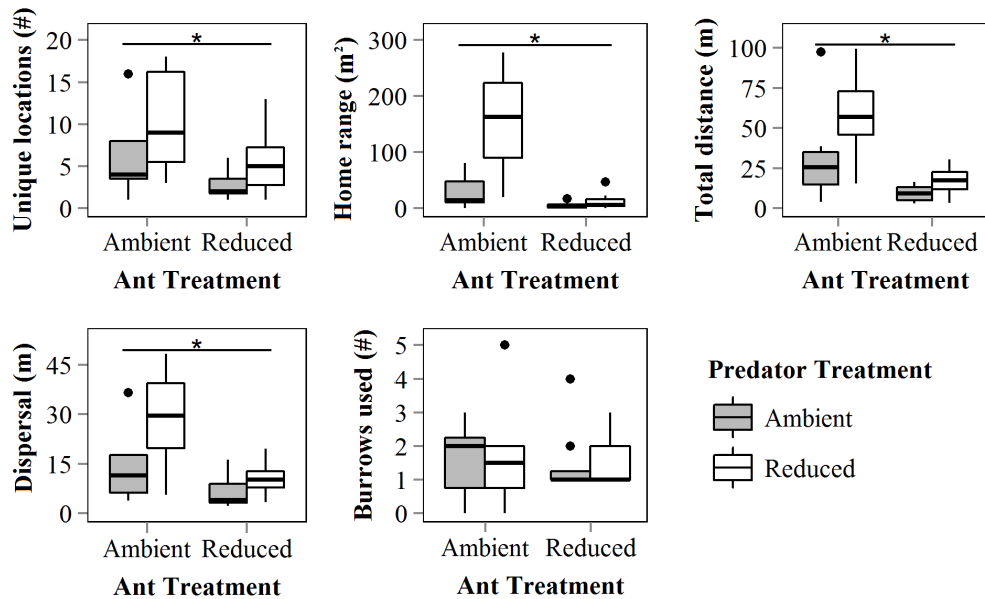
FIGURE 3. Movement summaries for hatchling Gopher Tortoises (*Gopherus polyphemus*) on Ichauway, Baker County, Georgia, USA monitored with radio telemetry between 27 August 2014 through 2 March 2015. Box boundaries extend from the 25th to 75th percentile, the horizontal line within boxes represent the median, and whiskers indicate 10th and 90th percentiles; outliers beyond this measurement are shown as points. Significant differences between ant treatments are indicated with an asterisk (*).

model contained only ant treatment, but the effect was not significant (Estimate = 0.112, SE = 0.194, 95% CI = -0.269 to 0.492). Parameter estimates examining the effect of ant treatment across the metrics of number of locations, home range, distance moved, and maximum dispersal contain negative parameter estimates, indicating hatchlings moved less frequently and shorter distances when exposed to reduced levels of Fire Ants than ambient Fire Ant levels (Fig. 3, Table 3). Additionally, two individuals abandoned burrows that contained foraging Fire Ants. These two individuals moved 11.2 and 33.8 m from their burrows within a 24-h period and did not return, but rather dug a new burrow in a different location. Furthermore, these straight-line distance movements were the greatest observed for these individuals during the study period. Parameter estimates examining the effect of vertebrate predator treatment on number of locations, home range, distance moved, and maximum dispersal were positive, indicating hatchlings moved more frequently and farther distances in enclosures with reduced vertebrate predators than hatchlings in ambient vertebrate predator enclosures (Fig. 3, Table 3). Hatchling burrows averaged 16 cm (range = 6–28 cm) in depth.

When first captured, hatchling Gopher Tortoises had an average carapace length of 51.5 mm (range = 48.2–53.9 mm) and weighed 33.9 g (range = 29.9–38.1 g). Hatchlings that survived the 6-mo study period had an average growth rate of 0.011 mm/day (range = 0.004–0.015 mm/day) and 0.006 g/day (range = -0.002–0.014 g/day) in ambient Fire Ant enclosures ($n = 8$) and 0.014

mm/day (range = 0.003–0.021 mm/day) and 0.014 g/day (range = 0.001–0.031 g/day) in reduced Fire Ant enclosures ($n = 13$). Model selection tables describing carapace length and weight gain contained multiple supported models (Table 4). Model-averaged parameter estimates for variables describing carapace length indicated no parameters were useful for predicting carapace length growth. Model-averaged parameter estimates indicated ant treatment was useful for predicting weight gain per day (Estimate = 0.004, SE < 0.001, 95% CI = 0.000 to 0.008), but contained a small effect size.

DISCUSSION

Although Gopher Tortoise nestling predation by the invasive Red Imported Fire Ant has been observed in previous studies (Landers et al. 1980; Epperson and Heise 2003), ours is the first to experimentally manipulate Fire Ant abundance to examine their effects on nestling survival. Epperson and Heise (2003) found four of 127 nestlings (3.1%) were killed by fire ants before emergence, whereas we documented a 50% depredation rate for nestlings exposed to Fire Ants. It is possible this disparity is related to variation in Fire Ant densities due to differences in environmental factors (e.g., soil type, precipitation), Fire Ant foraging behavior (e.g., in response to naturally versus artificially constructed nests), or some other difference between study sites. Therefore, future studies should examine depredation rates of Gopher Tortoise nestlings in relation to environmental factors and Fire Ant abundance. Fire Ants cannot pen-

TABLE 3. Parameter estimates (Estimate), their unconditional standard errors (SE), and 95% confidence intervals (CI) for parameters affecting movement patterns of hatchling Gopher Tortoises (*Gopherus polyphemus*) on Ichauway in Baker County, Georgia, USA. For home range and the number of burrows used, model averaged parameter estimates of models with $\Delta AIC_c < 2$. An asterisk (*) indicates that the 95% CI does not include zero.

Parameter	Estimate	SE	95% CI
Number of unique locations			
Intercept	2.305	0.253	1.808 to 2.801*
Ant treatment (reduced)	-0.768	0.292	-1.341 to −0.195*
Predator treatment (reduced)	0.718	0.292	0.145 to 1.291*
Home range (m²)			
Intercept	3.390	0.466	2.477 to 4.302*
Ant treatment (reduced)	-2.251	0.613	-3.452 to −1.051*
Predator treatment (reduced)	1.351	0.613	0.150 to 2.552*
Ant treatment (reduced) × Predator treatment (reduced)	-0.308	0.719	-2.938 to 0.952
Total distance moved (m)			
Intercept	3.220	0.209	2.811 to 3.630*
Ant treatment (reduced)	-1.087	0.241	-1.560 to −0.614*
Predator treatment (reduced)	0.658	0.241	0.185 to 1.131*
Maximum dispersal from nest site (m)			
Intercept	2.516	0.191	2.141 to 2.890*
Ant treatment (reduced)	-0.734	0.221	-1.166 to −0.301*
Predator treatment (reduced)	0.621	0.221	0.188 to 1.053*
Number of burrows used			
Intercept	1.101	0.146	0.814 to 1.387*
Ant treatment (reduced)	0.061	0.159	-0.285 to 0.510
Predator treatment (reduced)	-0.002	0.137	-0.404 to 0.393

etrate intact Gopher Tortoise eggs (Allen et al. 2004), but may monitor nests using underground foraging trails and attack when nestlings have breached their eggshells (Buhlmann and Coffman 2001). In our study, all eggs depredated by Fire Ants contained skeletonized remains of fully developed nestlings, supporting the supposition that Fire Ants cannot penetrate intact Gopher Tortoise eggs, but are successful in locating nests before hatchling emergence.

Hatchling Gopher Tortoises that survived nest emergence in our study were also susceptible to predation by Fire Ants; 31% of hatchlings that were exposed to Fire Ants emerged from nests, and 50% of hatchlings that emerged from nests and survived native predators (Raccoons), were depredated by Fire Ants in the first 6-mo of life. Previous studies on Gopher Tortoises indicate Fire Ant predation may exceed 25% during the first two years of life (Epperson and Heise 2003; Matthew Hinderliter, pers. comm.). It is possible that, because vertebrate predators were greatly reduced in enclosures, either through exclusion with game netting and UV twine or by galvanized metal fences, the Fire Ant acted as a compensatory predator in our study. However, because of our limited sample size and experimental design, we cannot verify compensatory predation

was occurring. Additionally, our high predation rate for hatchlings could be partially attributed to misidentification of cause-specific mortality. For example, opportunistic feeding events by Fire Ants (i.e., if a hatchling died from another cause) may have been misidentified as an ant predation event. However, because we documented no mortality events for hatchlings in reduced Fire Ant enclosures, any observer misidentifications of mortality would likely not have influenced our findings.

Our findings of increased hatchling movements (i.e., increased number of locations, home range size, dispersal from nest location, and total distance traveled) are consistent with previous accounts of indirect effects of Fire Ants on chelonians and other taxa (Pedersen et al. 1996; Parris et al. 2002; Long et al. 2015). Interestingly, the opposite effect was observed for enclosures with ambient vertebrate predator levels, in that Gopher Tortoises moved less frequently in these plots. Gopher Tortoises use burrows for protection from predators and likely stay in close proximity to their burrows when under risk of predation by vertebrates; however, the mechanism by which hatchlings in our study altered their behavior (i.e., more frequent movements in the reduced vertebrate predator enclosures) is not known. Burrows do not necessarily confer protection, particularly for hatch-

TABLE 4. Number of parameters (*K*), Akaike's Information Criterion corrected for small sample size (AIC$_c$), differences in AIC$_c$ values from the top model (ΔAIC$_c$), and model weights (*w*$_i$) for models estimating daily growth rates (carapace length, CL, in mm/day and mass in g/day) of radio-tracked Gopher Tortoise (*Gopherus polyphemus*) hatchlings from August 2014 through March 2015 on Ichauway, Baker County, Georgia, USA, ranked in order of support. Predictor variables include initial measurement (initial CL or initial mass), number of locations (locations), ant treatment, predator treatment, and enclosure ID.

Model	*K*	AIC$_c$	ΔAIC$_c$	*w*$_i$
Carapace length (mm/day)				
Initial CL	3	-157.68	0.00	0.34
1 (null model)	2	-156.81	0.87	0.22
Ant treatment + Initial CL	4	-156.24	1.44	0.17
Ant treatment	3	-155.29	2.39	0.10
Predator treatment	3	-154.62	3.06	0.07
Locations	3	-154.07	3.61	0.06
Ant treatment + Predator treatment	4	-152.95	4.73	0.03
Enclosure ID	7	-142.11	15.57	0.00
Ant treatment + Enclosure ID + Locations + Predator treatment + Initial CL	9	-134.90	22.79	0.00
Weight (g/day)				
Ant treatment	3	-136.45	0.00	0.22
Locations	3	-136.17	0.28	0.19
Ant treatment + Initial mass	4	-135.73	0.72	0.16
1 (null model)	2	-135.46	0.99	0.14
Ant treatment + Predator treatment	4	-135.31	1.14	0.13
Predator treatment	3	-134.78	1.67	0.10
Initial mass	3	-133.95	2.49	0.06
Enclosure ID	7	-128.96	7.49	0.01
Ant treatment + Enclosure ID + Locations + Predator treatment + Initial mass	9	-120.94	15.51	0.00

lings, whose burrows may be within the 10 cm depth of foraging Fire Ants (Markin et al. 1975; Gravish et al. 2012). In fact, in natural situations where vertebrate predators are present, hatchlings that spend more time in their burrows to reduce predation risk by vertebrate predators may increase their risk of predation by Fire Ants. Therefore, hatchlings exposed to Fire Ants may move more frequently as a mechanism to reduce risk of predation. However, increased movement may increase risk of vertebrate predator predation because hatchlings spend less time in the relative safety of their burrows. Furthermore, if hatchlings abandon their burrows to avoid Fire Ants, they may be particularly vulnerable to predation by vertebrates until they construct a new burrow.

Because of the level of Gopher Tortoise hatchling mortality in our study, our sample size to examine the indirect effect of Fire Ants on Gopher Tortoise hatchling growth rates was small. However, the reduction in weight gain observed in this study would likely result in a decrease in survivorship for individuals exposed to Fire Ants, as has been observed in other species including Northern Bobwhite (*Colinus virginianus*, Giuliano et al. 1996) chicks and American Alligator (*Alligator mississippiensis*) hatchlings (Allen et al. 1997b). Bob-

white chicks and alligator hatchlings showed reduced weight gain for > 1 week after Fire Ant exposure, but long-term effects were not documented as the studies lasted 9 d and 3 weeks, respectively (Giuliano et al. 1996; Allen et al. 1997b).

In our study, all hatchling predation by Fire Ants occurred soon after emergence, but it is unclear if this was a result of predation risk relative to time since hatchling emergence, optimal Fire Ant foraging temperature, seasonality of Fire Ant resource preference, or some combination of these factors. Hatchling Gopher Tortoise predation is highest during the first month after emergence, and the majority of hatchlings are depredated by mammalian predators (Epperson and Heise 2003; Pike and Seigel 2006). However, environmental conditions also may have an impact on hatchling predation risk by Fire Ants. Optimal Fire Ant foraging temperatures occur between 25–35° C (Drees et al. 2007), a temperature range that occurred frequently at the onset of this study (Ichauway; Georgia Automated Environmental Monitoring Network; http://georgiaweather.net) when most predation occurred. Additionally, during the warm season, coinciding with larval ant production, Fire Ants have a preference for protein-rich food sources such as hatchling tortoises, but in cooler seasons primarily rely

on sugar-rich resources for worker maintenance (Stein et al. 1990; Tschinkel 2006). Future research should examine the long-term impacts of Fire Ant exposure on Gopher Tortoise nest and hatchling survival, as well as the effects of Fire Ants on other Gopher Tortoise age classes to determine potential population-level impacts.

Nest and hatchling predation is a significant source of mortality in Gopher Tortoises (Landers et al. 1980; Epperson and Heise 2003; Pike and Seigel 2006), and predation rates are likely inflated due to the introduction of non-native predators, such as the Red Imported Fire Ant (Allen et al. 2004). We found that Fire Ants had a negative effect on Gopher Tortoise nestling survival and in hatchlings following emergence. Therefore, an understanding of the direct and indirect effects of Fire Ants is necessary to form management strategies to mitigate these effects. Reduction of Fire Ant populations may be necessary to increase nestling and hatchling Gopher Tortoise survival in some populations. We found that broadcast Fire Ant bait treatments successfully reduced Fire Ants and increased Gopher Tortoise nestling and hatchling survival in small-scale enclosures, but this method may not be feasible to implement at a large scale. However, because most hatchling predation occurs shortly after hatching, land managers may only need to treat for Fire Ants during Gopher Tortoise hatching season (August-October).

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