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Southern toads alter their behavior in response to red-imported fire ants

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Abstract We used the southern toad (*Anaxyrus terrestris*) as a model species to explore how an invasive species, the red-imported fire ant (*Solenopsis invicta*; hereafter RIFA), influences amphibian predator avoidance and movement behaviors. Our objective was to determine if toads spent less time near and moved more frequently in the presence of RIFAs compared to pyramid ants by comparing behavioral reactions of toads to RIFAs versus a control and pyramid ants versus a control. Laboratory experiments involved three treatments including no ants, RIFAs, and native pyramid ants (*Dorymyrmex bureni*) within an experimental arena. We randomly placed ants into one of two containers located at each end of the arena. For each trial we placed a toad into the experimental arena, allowed the toad to acclimate and then recorded its behavior. We calculated the proportion of time the toad spent near ants and the number of movements completed by each toad. Comparing the RIFA treatment to the pyramid ant treatment, toads spent 35 % less time on the half of the experimental arena near RIFAs ($P = 0.0304$). Toad movements were 1.5 times more frequent in trials with RIFAs than pyramid ants ($P = 0.0488$). We propose that southern toads associate RIFAs either with increased predation risk or risk of injury compared to pyramid ants. Although the behaviors we observed might lessen the direct effects of RIFAs on southern toads via predation and injury, the indirect effects of increased movement and avoidance of RIFAs could also influence toad fitness by decreasing reproductive and foraging success.

Keywords Invasive species · *Anaxyrus terrestris* · *Solenopsis invicta* · Red-imported fire ant · Predator avoidance

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Introduction

Predation exerts strong selective pressures on prey species, driving evolutionary adaptations including cryptic coloration and chemical defenses (Cott 1940; Edmunds 1974; Endler 1984; Merilaita 1998). To increase their fitness while faced with a considerable risk of predation, prey organisms must integrate morphological adaptations with anti-predator behaviors (Lima and Dill 1990). Increased anti-predator behaviors benefit the fitness of a prey organism by reducing the risk of depredation and subsequent mortality (Lima 1998). Anti-predator behaviors that have been linked to fitness benefits include altered movement and/or activity patterns (e.g. Godin and Smith 1988; Skelly and Werner 1990; Ordiz et al.

2012), foraging behaviors (e.g. Lima and Valone 1986; Brown et al. 1988; Orrock et al. 2004; Sorato et al. 2012), and habitat use (e.g. Werner et al. 1983; Dickman 1992; Grovenburg et al. 2012).

Prey that have not co-evolved with a recently introduced predator may lack behavioral traits to detect and avoid predation (Van Damme et al. 1995; Polo-Cavia et al. 2010; Wanger et al. 2011). Without these behavioral traits it is likely that naïve prey will see a reduction in fitness associated with novel predators (Schlaepfer et al. 2005). Still, some prey species have developed the behavioral traits to detect and avoid relatively novel predators via natural selection and/or behavioral plasticity (e.g. Kiesecker and Blaustein 1997; Chivers et al. 2001; Freidenfelds et al. 2012).

The red-imported fire ant (*Solepnosis invicta*; hereafter RIFA) is an invasive species that was introduced to the southeastern United States in the late 1930s, which has caused significant economic and ecological impacts (Allen et al. 1994). The venom of RIFAs is composed of various alkaloids, which can negatively affect the cardiovascular and central nervous system of vertebrates (Howell et al. 2005). Although RIFA venom is similar to that of native fire ants [e.g. *S. xyloni* (MacConnell et al. 1971; Brand et al. 1972)], RIFAs are more aggressive than native fire ants and other native lipid-eating ants (e.g. *Dorymyrmex* sp.), which allows RIFAs to overwhelm larger vertebrate species (MacConnell et al. 1971; Wojcik et al. 2001). Moreover, RIFAs reach high population densities compared to native fire ants and often are the dominant ant in infested areas (Porter et al. 1988; Porter and Savignano 1990; Morrison 2003).

RIFAs have been implicated in the decline of several amphibians [e.g. *Bufo houstonensis* (Brown et al. 2012) and *Ambystoma opacum* (Todd et al. 2007)]. Amphibians may be particularly susceptible to predation by RIFAs following metamorphosis because of their small size. Moreover, RIFAs may act as both a predator and prey to amphibians (Deyrup et al. 2013; A. Long, Unpublished data) and a toxic prey item for some vertebrates [e.g. *Sceloporus undulatus* (Robbins and Langkilde 2012); *Colinus virginianus* (Myers et al. 2014)]. As the diet of many amphibians is largely comprised of ants (Duellman and Trueb 1994), over-ingestion of RIFAs may pose a risk of injury or mortality to individuals similar to other vertebrate

species that consume ants (Robbins and Langkilde 2012; Myers et al. 2014). Nonetheless, little research has been completed on behavioral responses of amphibians to RIFAs.

We used the southern toad (*Anaxyrus terrestris*) as a model species to explore how an introduced predator influences the behavior of amphibians. We selected southern toads as a model species because ants, including RIFAs (10 % of the diet of juvenile southern toads; A. Long, Unpublished data), are a regular part of their diet (Moseley et al. 2004). Moreover, southern toads likely interact with RIFAs because they frequently inhabit disturbed areas [e.g. residential areas, agricultural fields (Jensen 2005; Jensen et al. 2008)] that are also the preferred habitat of RIFAs (Tschinkel 1987). The objective of our study was to determine if individual southern toads altered their behavior in response to RIFAs compared to a native ant, *Dorymyrmex bureni* (hereafter pyramid ant). We chose the pyramid ant because it coexists with RIFAs (Carroll and Hoffman 2000) and is a component of the diet of some amphibians [e.g. *Gastrophryne carolinensis* (Deyrup et al. 2013)]. Additionally, although pyramid ants will scavenge on vertebrate carcasses and are predators of live arthropods, they have not been documented to depredate live vertebrates (D. Oi, USDA, personal communication, 10 March 2014). Based on these differing characteristics between RIFAs and pyramid ants, we predicted that southern toads would avoid RIFAs, but not pyramid ants. Moreover, we predicted that toads would exhibit increased movements when presented with RIFAs because changes in these behavioral traits would minimize risk of injury or mortality from RIFA envenomation.

Materials and methods

Study species and collection

We hand collected 18 juvenile [$\leq$40 mm snout-to-urostyle length (SUL); Jensen 2005; Jensen et al. 2008] southern toads in July 2013 on Ichauway, the 12,000 ha research site of the Joseph W. Jones Ecological Center located approximately 20 km south of Newton, in Baker County, GA (Georgia Department of Natural Resources Scientific Collecting Permit # 29-WJH-13-164). We limited collection to juvenile toads because juveniles would likely be

most affected by RIFAs due to their small body size and a diet that is comprised of a greater proportion of ants (Moseley et al. 2004). Records indicate that RIFAs arrived in Baker County, GA in 1966 (Callcott and Collins 1996) and RIFAs are the dominant ant species on Ichauway (Carroll and Hoffman 2000). Based on ant sampling efforts completed from 1991 to 1992 (Carroll and Hoffman 2000) and present sampling efforts from 2012 to 2014 (A. K. Long, Unpublished data) on Ichauway, it is likely that the native fire ant species, *S. geminata* and *S. xyloni*, do not occur on site. The prevalence of RIFAs, concurrent with their presence on site for at least 48 years, may have allowed time for southern toads to adapt to RIFAs.

After capture, we housed each toad within a laboratory on Ichuaway in a 1892.7 ml plastic container with moistened terrarium moss. We fed each individual one cricket (*Acheta domesticus*, Fluker Farms®, Port Allen, LA) every other day. We maintained the room at approximately 22 °C, and light was provided naturally from an uncovered window. We maintained toads in captivity for <1 week and released them at their initial capture location following behavioral trials. We housed toads for 48 h prior to trials to allow them time to acclimate to artificial darkness. Prior to each behavioral trial, we collected 25–30 live RIFAs and pyramid ants from mounds using a hand-made aspirator.

Experimental design

The experimental arena was comprised of a 46 × 32 cm plastic container with a piece of paper placed on the bottom (Fig. 1). The paper was divided in half by a centered line and changed for each trial. To minimize the potential for injury to the toads via ant stings, we enclosed the ants within a round tea strainer (Mainstays®) positioned on one end of the experimental arena and placed an empty tea strainer on the opposite end of the arena. No ants escaped from the tea strainers during trials. To document toad behavior, we centered a webcam (Logitech® HD Pro Webcam C920) over the experimental arena and recorded the video onto a laptop (HP® dv6-6100). We executed all trials in artificial darkness and attached a red light next to the camera to allow for recording in the dark. We placed an acclimation chamber, comprised of a 60 ml
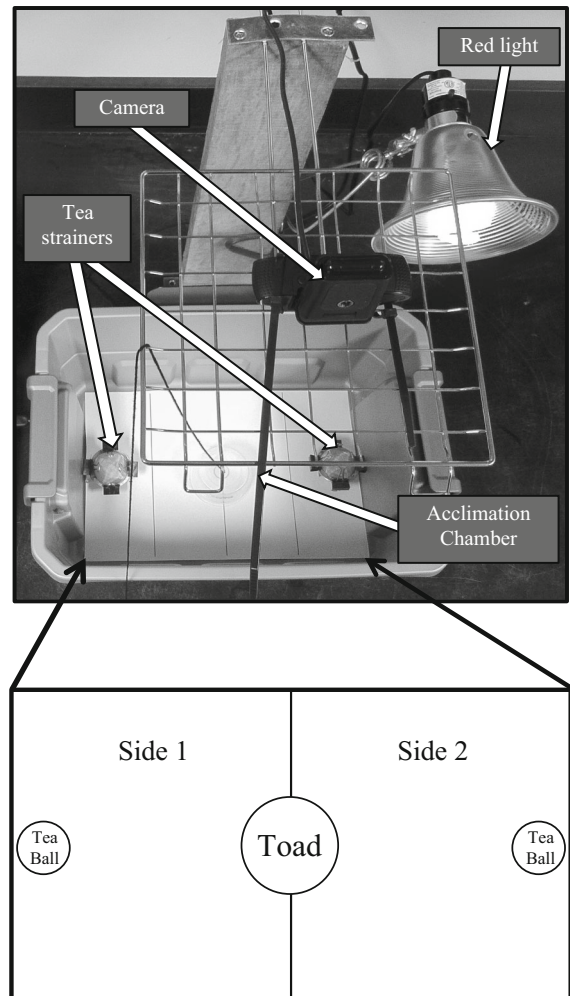
Fig. 1 The experimental arena used to test the effects of red-imported fire ants (*S. invicta*) and pyramid ants (*D. bureni*) on juvenile southern toad (*A. terrestris*) behaviors

clear plastic container, upside down within the center of the experimental arena. To minimize initial stress-induced movement, we attached a string to the acclimation chamber that allowed us to remove it from the arena remotely.

We had three treatments including a control with no ants, RIFAs, and pyramid ants. We subjected each individual toad to all treatments and randomly selected the order in which treatments were performed. We exposed each individual to one treatment per day to avoid memory retention of the experimental arena design and to limit stress. During ant treatments, one tea strainer was randomly selected to contain ants and the other was left empty, while both strainers were left

empty for the control trials. We rinsed the strainers with 90 % ethyl alcohol between trials.

We commenced trials by placing a single toad in the middle of the experimental arena within the acclimation chamber. After 2 min, we removed the acclimation chamber from the arena and recorded each individual's behavior for 15 min. We reviewed the videos and recorded how much time a toad spent on each half of the arena in seconds and the total number of movements made across the surface of the arena (postural adjustments were not counted).

Data analysis

To confirm that toads did not show a preference for either side of the experimental arena, we completed a one-sample, two-tailed t test comparing the time toads spent on the left side of the arena to 450 s (the amount of time toads should spend on each side of the arena if they showed no preference). Specifically, the alternative hypothesis was that the true mean was not equal to 450 s. To determine if toads spent differing amounts of time proximal to RIFAs compared with pyramid ants, we used the time (in seconds) each individual spent on the half of the arena nearest ants during trials with RIFAs and pyramid ants as our response variable. We used the total number of movements made by each toad during each trial as our response variable to determine if the number of movements made by toads differed between the control, RIFA, and pyramid ant treatments.

We used a linear mixed model (LMM) to determine if the time toads spent near ants differed between pyramid ant and RIFA treatments. We assessed differences in the number of movements completed by toads between the control, RIFA, and pyramid ant treatments using a generalized linear mixed model (GLMM) with a Poisson distribution. We initially included the following factors in the models: (1) 'Period', which indicated whether the recording was from the first, second, or third trial and showed the effect of passing time on toad response to ants; (2) 'Ant Treatment (pyramid ant or RIFA)' during recording (the control was also included as a treatment in models considering effects on the number of movements); (3) 'Toad ID', a random variable to account for individuals undergoing each treatment condition, (4) 'Time of Day' divided into two

categories based on if trials were completed between 1200 and 1530 h (category 1) or 1530 and 1900 h (category 2), and (5) 'SUL', which was included as a covariate to account for variability in response due to size. The variables Period and Time of Day were only included in the final models assessing the effects of treatment (RIFA or pyramid ant) if they were significant ($P < 0.05$). Because treatment order was selected randomly, we did not include it as a variable in our models. We used Program R Version 2.15.3 (R Development Core Team 2005) for all statistical analyses and ran the LMMs using package 'nlme' Version 3.1-117 (Pinheiro et al. 2014) and the GLMMs in package 'mass' version 7.3-33 (Venables and Ripley 2002).

Results

We completed behavioral trials including three treatments; control, RIFA, and pyramid ant (N = 18 for each treatment) from 13 July to 4 September 2013 between 1245 h and 1900 h. The average SUL of the toads used in the trials was 30.4 mm (range 14–40 mm). Toads showed no preference for the left ($\bar{X} = 346.2 \pm 63.9$) or right ($\bar{X} = 553.8 \pm 63.9$) side of the arena during control trials (One-way, two-tailed t test: $t_{16} = -1.6233$, $P = 0.1241$). The variables Period and Time of Day were not included in the final models as our initial assessment indicated that they did not affect the time toads spent near ants or the number of movements toads completed ($P > 0.05$). SUL did not affect the time toads spent near ants (LMM: $b = 5.63 \pm 5.27$, $t_{15} = 1.07$, $P = 0.3021$) or the number of movements completed by toads (GLMM: $b = -0.01 \pm 0.02$, $t_{15} = -0.72$, $P = 0.4820$; Fig. 2). Compared with pyramid ants, toads spent 35 % less time on the half of the experimental arena nearest ants during trials with RIFAs (LMM: $b = -173.29 \pm 72.99$, $t_{16} = 2.37$, $P = 0.0304$; Fig. 2). Compared with the control trials, toads did not move more or less during trials with RIFAs (GLMM: $b = 0.22 \pm 0.19$, $t_{32} = 1.11$, $P = 0.2753$) or pyramid ants (GLMM: $b = -0.21 \pm 0.22$, $t_{32} = -0.96$, $P = 0.0.3452$; Fig. 2). Toads completed approximately 1.5 times more movements during trials with RIFAs compared to pyramid ants (GLMM: $b = 0.42 \pm 0.21$, $t_{32} = 2.05$, $P = 0.0488$; Fig. 2).

Fig. 2 Mean and standard errors of the time spent nearer ants (*left*; the *dotted horizontal line* indicates no preference for being nearer or further from ants) and the number of movements completed (*right*) by juvenile southern toads (*A. terrestris*) within an experimental arena for control* (N = 18), red-imported fire ant [*S. invicta* (RIFA); N = 18], and pyramid ant (*D. bureni*; N = 18) treatments in behavioral trials. *Data for the control are only presented for the mean number of movements completed
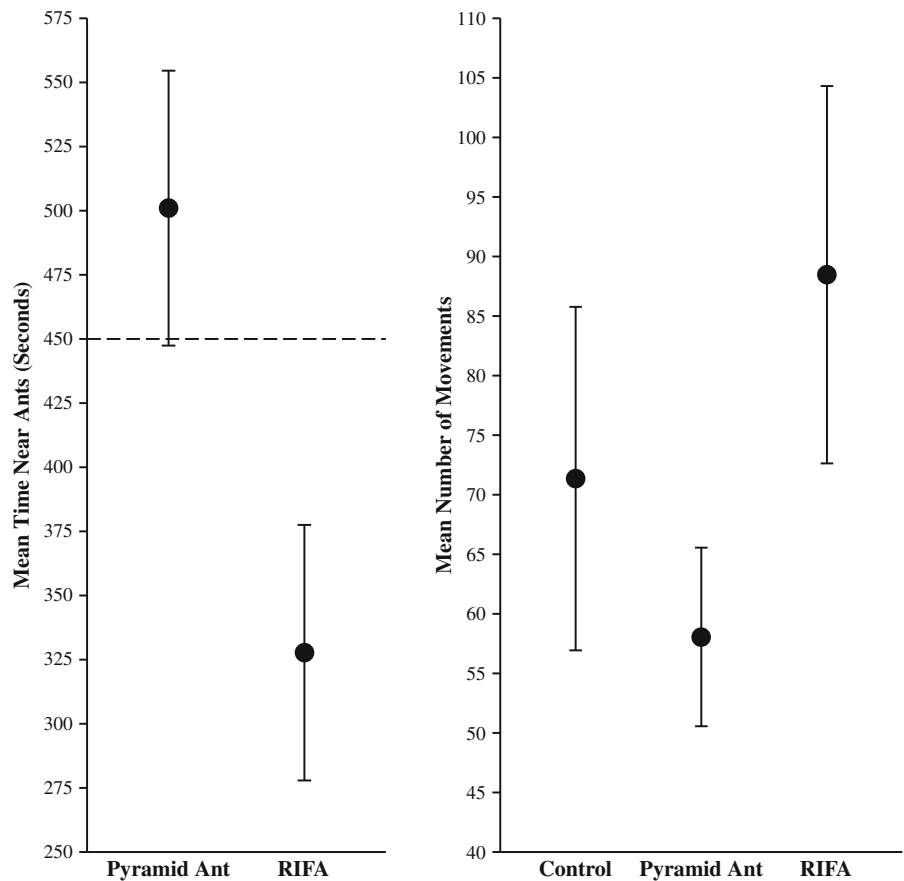
Discussion

Ants comprise a large portion of many amphibian diets (Duellman and Trueb 1994), and distinguishing between a non-lethal native ant and a lethal invasive ant has clear advantages (e.g. increased survival and reproductive output). Due to the risk of predation, injury, and mortality from ingestion of RIFAs, differentiating between RIFAs and pyramid ants may play a role in toad survival. Our study indicated that southern toads behaved differently when presented with RIFAs and the native pyramid ant.

Southern toads utilize a variety of anti-predator behaviors including crouching, fleeing, and body inflation in response to native predators (Marchisin and Anderson 1978). Many vertebrate predators find toads unpalatable because of the bufo toxins they secrete from their paratoid gland (Hayes 1989). When confronted by these predators, toads remain motionless and rely on their toxins to protect them (Hayes 1989). However, when threatened by a species that is

undeterred by bufo toxins [e.g. southern hognose (*Heterodon simus*) and common garter snake (*Thamnophis sirtalis*)] toads respond by fleeing (Hayes 1989). Although we did not find that toads moved more during trials with RIFAs compared with the control, our observations of increased number and variability of movements and avoidance behavior of southern toads in the presence of RIFAs compared to pyramid ants suggests that southern toads flee, rather than remain motionless, when in the presence of RIFAs. Based on these behaviors, we propose that southern toads may identify RIFAs as a predator.

Similar to eastern fence lizards that have developed behavioral [e.g. body twitching (Freidenfelds et al. 2012); change in behavioral response to stress (Trompeter and Langkilde 2011)] and morphological (e.g. longer hind limb length; Langkilde 2009) mechanisms to cope with RIFAs, the behavioral differences we observed in southern toads may be learned or formed over time via phenotypic plasticity and/or evolutionary adaptations. Conversely, the

behaviors we observed may be in response to similar stimuli they evolved to prior to the introduction of RIFAs (e.g. similar ant venoms). For instance, southern toads have co-occurred with *S. xyloni* and *S. geminata*, both native fire ants that occurred throughout the southeastern United States prior to the introduction of RIFAs (Trager 1991). Both species have a similar, but less toxic, venom to RIFAs (Blum et al. 1961; Brand et al. 1972), and this similarity may allow southern toads to generalize predator recognition and avoidance behaviors to RIFAs. However, weaker toxins found in the venom of *S. xyloni* and *S. geminata* (Blum et al. 1961), in combination with lower population densities (Porter et al. 1988), makes it unlikely that either species imparted strong selective pressures on southern toads relative to predator recognition and avoidance behaviors. Nonetheless, the possibility that southern toads are generalizing predator recognition and avoidance behaviors from native fire ants to RIFAs cannot be discounted and future research should incorporate the use of native fire ants in behavioral trials.

The sensory mechanisms underlying the behavioral responses we observed could be visual, chemical, or a combination of the two. Previous research indicates that southern toads use vision to detect prey (Taylor 2001). However, it is unlikely that toads could distinguish between RIFAs and pyramid ants based on observable characteristics (e.g. size and color) through the mesh of the tea strainer. Alternatively, RIFAs contain an alkaloid venom (Tschinkel 2006), which is absent in pyramid ants, while pyramid ants emit defensive compounds from their anal glands that are not present in RIFAs (Blum and Hermann 1978). As past studies indicate that anurans sense chemical cues emitted by predators (Hews 1988; Flowers and Graves 1997), toads may distinguish between ant species via chemical cues. Future studies should consider what mechanisms, chemical or visual, cause toads to move more in the presence of and avoid RIFAs.

Although RIFAs likely affect toads directly via predation, as RIFAs have been observed depredating other amphibian metamorphs (Todd et al. 2007), changes in toad behavior due to perceived predation risk or risk of injury by RIFAs may indirectly influence fitness as well. Other studies have found that perceived predation risk leads to decreases in reproduction (e.g. Allen et al. 1997; Zanette et al. 2011) and affects foraging success of vertebrates (e.g. Holtcamp et al.

1997; Schmidt et al. 2008). The increased movements in the presence of RIFAs compared to pyramid ants that we observed in southern toads could reduce foraging efficiency, increase caloric requirements, and make toads more susceptible to other predators. Thus, although the behaviors we observed might lessen the direct effects of RIFAs on southern toads via predation and injury, the indirect effects of increased movement and avoidance of RIFAs could decrease reproductive and foraging success of toads.

The inability of prey to recognize and adjust their behaviors in response to an invasive predator may reduce their fitness through direct mortality or increased risk of injury. There are tradeoffs associated with avoiding invasive predators and behaviors that reduce the risk of predation by an invasive predator [e.g. fleeing behavior (Trompeter and Langkilde 2011)] may increase predation by native predators that use different cues to detect prey (e.g. visual, olfactory) and ultimately be maladaptive. However, if a native prey species perceives the risk of predation by an invasive to be equal to or greater than the risk of predation by a native predator, it would be advantageous for the native prey species to develop strategies to minimize predation by the invasive. Without developing anti-predator behaviors to cope with an invasive predator, native prey may experience greater population declines and some populations may go extinct (Clavero and García-Berthou 2005), ultimately reducing the biodiversity of native species (Clavero et al. 2009; Wilcove et al. 1998). Consequently, as species invasions increase globally, understanding how native species cope with novel pressures is increasingly important. Future studies should emphasize not only understanding the benefits of anti-predator behaviors native prey acquire in response to invasive predators, but also the potential deleterious effects of these behaviors.

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