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ORIGINAL PAPER

The influence of invasive fire ants on survival, space use, and patterns of natural selection in juvenile lizards

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Abstract Invasive species have altered natural communities and exposed native species to new selective pressures. These pressures are particularly acute when invasive species are predators of natives. The invasive red imported fire ant has expanded its range significantly in the southeast United States and has become an important predator of native species that share similar habitat preferences, like the prairie lizard, *Sceloporus consobrinus*. Recent studies indicate that lizards that have coexisted for a long period of time with fire ants have responded both plastically and adaptively to this invasion. However, despite considerable work, few "controlled" experiments have been conducted to explore the influence of fire ants on vertebrates in natural populations. In this study we released hatchling lizards on two experimental islands that differed in fire ant density to investigate the influence of fire ants on lizard survival, habitat/space use, and patterns of phenotypic selection. We demonstrate that fire ant presence significantly explains patterns of lizard survival among populations and over small spatial scales within populations. As a consequence of survival patterns or avoidance behavior, lizard habitat use was significantly altered in the presence of fire ants in high density. Finally, we found strong signatures of natural selection on lizard body size and body condition, but the patterns of selection did not appear to be influenced by variation in fire ant density. This study highlights the direct influence of predatory fire ants on hatchling lizard mortality and habitat use. These effects can have important demographic and population-level consequences.

Keywords Fire ants · Natural selection · Survival · Lizards · Predation

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Introduction

Establishment and spread of nonnative species have been associated with declines of biodiversity (Millennium Ecosystem Assessment 2005). Invasive species have altered biotic communities exposing native species to new selective pressures. The consequences of invasive species establishment on native species are variable and include direct evolutionary changes (adaptation, hybridization) and indirect responses (behavioral and trait shifts, competitive exclusion, and extinction; examples reviewed in Mooney and Cleland 2001).

A highly invasive insect is the red imported fire ant, *Solenopsis invicta*; a species that was accidentally introduced into the southern United States in the 1930s from South America (Fadamiro et al. 2009) and has now expanded its range to cover much of the southeastern USA. Despite their small size (2–6 mm in length), fire ants are aggressive and swarm prey, simultaneously stinging to subdue it. This swarming behavior and simultaneous attack allows fire ants to subdue and kill large animals (Barr et al. 1994; Holtcamp et al. 1997; Langkilde 2009). Historically it has been difficult to study the impact of fire ants on vertebrate populations generally due to the lack of baseline data (Allen et al. 2004). However, some recent work has taken advantage of the well-documented invasion history of this insect and, using a comparative approach, determined that some species appear to be undergoing rapid local adaptation to fire ants in a suite of morphological, physiological, and behavioral traits. For example, populations of the fence lizard, *Sceloporus undulatus* that have coexisted with fire ants for nearly 50–70 years have longer hind limbs than populations at locations that have a shorter history of coexistence with fire ants or those from uninvaded sites (Langkilde 2009). In addition, lizards from these long-invaded populations more frequently use body-twitch behaviors and fleeing to escape swarming fire ants. Invasion history is not associated with any change in lizard resistance to fire ant venom (Boronow and Langkilde 2010), therefore, these behaviors and associated morphological changes appear to allow lizards to more effectively remove ants from their bodies and limit the number of stinging ants (Langkilde 2009). In addition to these morphological and behavioral changes, long exposure to fire ants appears to alter physiological responses of lizards to stress as well (Graham et al. 2012). Finally, fire ant envenomation has delayed effects on survival of fence lizards regardless of invasion history (Langkilde and Freidenfelds 2010).

Despite demonstration of these comparative patterns, there have been few “controlled” experiments to date that explore the influence of fire ants on vertebrates in natural populations (Allen et al. 2004). In this study we take advantage of natural variation in fire ant density on experimental islands to examine the influence of fire ants on hatchling/juvenile lizard mortality, geographic space use, and patterns of natural selection. To this end we make several predictions about the impact of fire ants on native lizards. First, given published evidence that fire ants can cause vertebrate mortality (Allen et al. 2004; Langkilde and Freidenfelds 2010) we predict that the probability of hatchling lizard survival will be lower on an island with higher density of fire ants than on an island with lower fire ant density. Second, within islands lizard survival should vary inversely with local fire ant density. Third, a high rate of local mortality or behavioral avoidance should generate non-random patterns of space/habitat use by lizards. Finally, we predict that higher fire ant density should dampen (i.e., weaken) phenotypic selection on size-related traits in lizards. Here we assume that hatchling lizard mortality due to fire ants is not size-specific and all sizes of hatchlings should be equally susceptible to predation.

Methods

We obtained eggs from 31 gravid *Sceloporus consobrinus* females collected from sites around Pulaski County, Arkansas. Lizards were housed individually in enclosures (45 cm × 20 cm × 25 cm, L × W × H). Each enclosure contained a substrate of sand at approximately 2 cm in depth, a hide, and a rock as a perch site directly beneath a suspended 40 W incandescent bulb. The room lights and incandescent bulbs were maintained on a 13L:11D photoperiod. We provided vitamin-dusted crickets three times per week and watered, by spraying the walls of enclosures, daily. We monitored lizards frequently and gauged progression of gestation by gently palpating each lizard’s abdomen. Once oviposition seemed imminent (females refused food and appeared lethargic), we induced egg laying using an intracoelomic injection of 0.1–0.3 ml of oxytocin (2–6 USP units; VetOne, MWI, Meridian, ID). After injection each female was placed individually in a ventilated plastic container containing a moist sand substrate and the oviposition container was placed into a dark incubator at 30 °C (VL-36, Percival Scientific, Perry IA). We checked each female every hour post injection to collect eggs. All females began laying eggs within 5 h of injection. Females were left undisturbed for 24 h after they finished laying eggs. All females fully recovered from this procedure and were released back at the capture location. We weighed eggs (to the nearest 0.1 mg) and placed them individually into a small plastic cup (59 ml) filled with a mixture of 350 g fine silica sand and 3.5 g of distilled water. This combination results in a water potential of approximately −10 kPa (Oufiero and Angilletta 2006).

As part of a separate study we used a split-clutch design to assign individual eggs from the same female into different experimental conditions, either at a mean temperature of 27 °C (range 23–32 °C), which approximates average incubation conditions in nature (Warner and Andrews 2002), or at a mean temperature of 30 °C with a higher variance in daily temperature extremes (range 23–38 °C).

We assigned each hatchling lizard a unique identification by clipping three toes. We never clipped multiple toes on the same appendage, and always avoided clipping the longest toes on the hind limbs. We measured each lizard for snout-vent length (to the nearest 0.5 mm) and body mass (to the nearest 0.1 mg) within 24 h of hatching. Hatchling lizards were maintained in enclosures (in groups of 5 lizards) organized identically to those used for adult females. While in the laboratory, we fed hatchling lizards small vitamin dusted crickets daily. We maintained hatchlings in the laboratory for a maximum of seven days prior to release onto experimental islands (see below). Before releasing lizards, we determined sex of each by checking for the presence of enlarged post-anal scales (present in males), and measured and weighed them a second time.

We released hatchling lizards onto two islands in Lake Ouachita, a large reservoir in Garland and Montgomery Counties in Arkansas. Experimental islands were similar and characterized by dense undergrowth and open understory in similar proportions on both islands and each contained an expanse of bare rock between the water and vegetation that fluctuated in size based on lake level. One island had a vegetated area of approximately 3800 m^2 and is hereafter referred to as Big Island. The second island had a vegetated area of approximately 1900 m^2 and is referred to as Bone Island.

We released hatchlings in two groups as a consequence of hatching time asymmetry based on incubation temperature. The first group was released on 29 June 2015 (30 °C treatment) and the second on 16 July 2015 (27 °C treatment). Each time we released hatchlings in groups at four specific locations on each island. Groups of lizards were chosen randomly with respect to clutch of origin and we attempted to maintain an equal sex ratio on each island (Big Island sex ratio = 51% M:49% F; Bone Island sex ratio = 55% M:45% F). On Big Island we released 160 hatchlings (40 at each location), resulting in a density of 0.042 lizards m^{-2}. On Bone Island we released 84 hatchlings (21 at each location), resulting in a density of 0.044 lizards m^{-2}. We revisited islands during 12–15 and 21–25 September 2015 to census for surviving lizards. All habitats on each island were searched completely by two or three people every day, varying the time of day for each daily census of each island. This way each island was searched repeatedly at all times of day during each visit. Lizards that were not recaptured during these censuses were assumed to have perished. We continued each census until no new lizards were captured during that time period (August or September). All lizards were captured by hand or pole and noose for identification. Given the relatively small size of each island and intensity of survey efforts, we are confident all surviving lizards were recaptured by the end of the September census. We quantified fire ant density on each island based on counts of fire ant mounds. The geographic location of each fire ant mound and each lizard recapture location was recorded in UTM coordinates using a Trimble Juno 3B GPS unit (Trimble Navigation Limited, Sunnyvale, CA).

Statistical analyses

All statistical analyses were performed using R (version 3.1.1). Statistical significance was determined at $P < 0.05$. We tested for differences in hatchling survival between islands and among release locations within islands using a generalized linear model (GLM) with logit link. In all of these models incubation temperature was also included as a factor. We assessed whether spatial variation in hatchling survival within islands was associated with local fire ant density using linear regression. To calculate fire ant density for each release location on each island we counted the number of fire ant mounds within a 28 m buffer zone of the release point. Then we regressed the estimated survival probability for lizards at each release location extracted from the GLM on each island against the estimated fire ant density for that location. We chose this distance because 28 m is the average dispersal distance of hatchling lizards on each island (Gifford et al. in review), and therefore represents the average local conditions to which hatchling lizards would be exposed during natal dispersal from the release point.

A strong influence of fire ants on hatchling lizards also should be reflected in the spatial distribution of lizards at recapture either because of spatially structured patterns of mortality or active avoidance of fire ants by lizards. We tested the prediction that lizards use habitat non-randomly with respect to fire ant locations using spatially explicit Monte Carlo simulations. For each simulation we generated random geographic locations on a given island (equal to the number of recaptured lizards on each island, 36 for Big Island, 41 for Bone Island). We then calculated the mean distance between random locations and the locations of fire ant mounds. We repeated this process 5000 times to generate a null distribution of geographic distances. We then calculated the proportion of simulated data sets (out of 5000) with mean distances greater than or equal to the mean distance between recapture locations and fire ant mounds to represent a P value. A P-value less than 0.05 would indicate that the observed recapture locations are a greater distance from fire ant mounds than expected by chance.

We quantified natural selection on morphological traits at release (SVL, body mass, and body condition) using conventional selection gradient analyses. All traits were standardized to the population mean in units of standard deviations (Lande and Arnold 1983; Arnold and Wade 1984). We standardized morphological traits separately for each island. In selection analyses, body condition was represented by the residuals of regressions of log transformed body mass on log transformed snout-vent length calculated independently for each island population. We estimated linear (i.e., directional) and quadratic (i.e., stabilizing or disruptive) selection gradients from the regression coefficients ($\beta \pm$ 1SE and $\gamma \pm$ 1SE, respectively) of separate logistic regressions (Brodie et al. 1995). We followed Janzen and Stern (1998) and converted standardized (i.e., multiplied by the preselection standard deviation of the trait) logistic regression coefficients into selection coefficients, using the average gradient of the estimated selection surface. We multiplied quadratic regression coefficients and associated standard errors by 2 to estimate quadratic selection gradients (Phillips and Arnold 1989; Stinchcombe et al. 2008). Statistical significance of selection gradients was determined from GLM's with a logit link function accounting for binomial error variance (Janzen and Stern 1998). We used cubic spline analyses to visualize selection surfaces (Schluter 1988). We formally tested for differences in the pattern of linear selection by including trait by island interactions in the logistic regression models. Within each island, we initially tested for sex differences in the nature and strength of linear selection by including a sex × trait interaction term in the logistic regression with survival as the dependent variable. This interaction was not significant for either island, and was excluded from the models

Results

Fire ant density differed drastically between the two islands and was 8.6 times higher on Big Island than on Bone Island (Big = 91 mounds, 23.3 mounds/1000 m^2, Bone = 5 mounds, 2.7 mounds/1000 m^2). The mean distance between fire ant mounds was similar on both islands (mean ± SD, Big = 27.48 ± 19.09, Bone = 21.49 ± 14.80). The inter-mound distance on these islands is greater than, but comparable to those measured in natural habitats where interactions between fire ants and fence lizards have been studied (~12.37 m, Langkilde 2009). In addition, on Big Island fire ant mounds were not evenly distributed across the island and were clustered in very high density in the southeastern and southern portions of the island (Fig. 1).

Hatchling lizard survival differed significantly between islands ($\chi^2 = 7.64$, $df = 1$, $P = 0.006$) but did not differ among lizards incubated at different temperatures ($\chi^2 = 1.56$, $df = 1$, $P = 0.213$). The probability of survival on Bone Island (low density) exceeded that on Big Island (high density) by over 50% (Bone = 51.8%, Big = 25.1%). In addition, the probability of survival varied depending on release location on Big Island ($\chi^2 = 15.58$, $df = 3$, $P = 0.001$), but not on Bone Island ($\chi^2 = 6.34$, $df = 3$, $P = 0.09$). In neither case did incubation temperature have a significant effect (Big, $\chi^2 = 2.21$, $df = 1$, $P = 0.14$; Bone, $\chi^2 = 1.30$, $df = 1$, $P = 0.25$). Across islands, the probability of survival was negatively correlated with the density of fire ant mounds within 28 m of the release location ($R^2 = 0.838$, $P = 0.001$, Fig. 2). This result was similar when using a range of cut-off distances (20 m, $R^2 = 0.802$, $P = 0.003$; 35 m, $R^2 = 0.771$, $P = 0.004$). On Big Island (high density), lizard recapture locations were located a significantly greater distance from fire ant mounds than random locations (mean recapture distance = 60.73 m, mean random

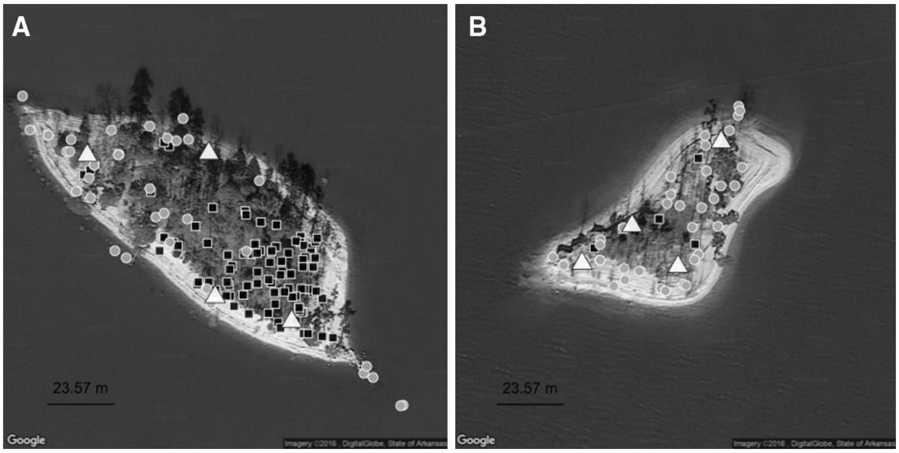

Fig. 1 Experimental islands (**a** Big Island, **b** Bone Island) illustrating the spatial distributions of hatchling lizard release locations (*large white triangles*), hatchling lizard recapture locations (*gray dots*), and the locations of active fire ant mounds (*black boxes*). Some of the lizard recapture locations appear outside the bounds of the emergent land in the figure. The amount of emergent land varies temporally as the water level of the reservoir fluctuates. A satellite image of the experimental islands for the time period coinciding with our recapture efforts was unavailable

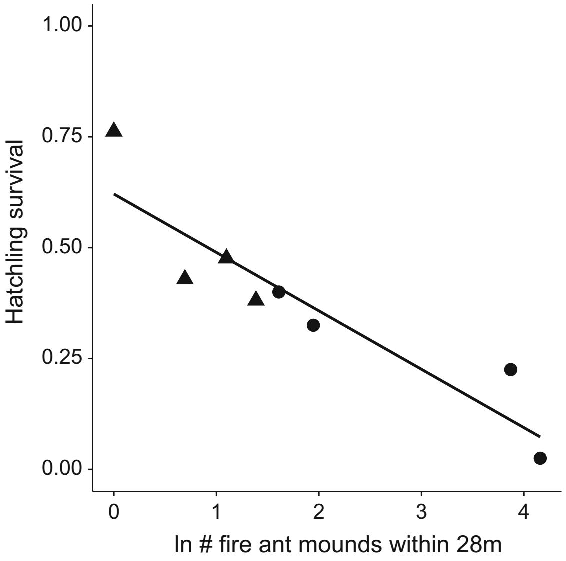

Fig. 2 The relationship between hatchling lizard survival (proportion of lizards recaptured from those released at each release location) and fire ant abundance (the number of fire ant mounds) within 28 m of each release location. *Symbols* represent experimental islands (*triangles* Bone Island (low density fire ants), *dots* Big Island (high density fire ants))

location distance = 44.73 m; $P = 0.00$). However, on Bone Island (low density), the distance of lizard recapture locations from fire ant mounds did not differ from random expectations (mean recapture distance = 29.35 m, mean random location distance = 28.33 m; $P = 0.216$).

We formally tested whether patterns of selection differed between islands by including an island by trait interaction in logistic regression models. In no case was this interaction statistically significant (SVL × Island, $\chi^2 = 0.040$, $df = 1$, $P = 0.841$; Mass × Island, $\chi^2 = 0.641$, $df = 1$, $P = 0.423$; Condition × Island, $\chi^2 = 2.58$, $df = 1$, $P = 0.108$). We detected a significant signature of linear selection on both measures of body size on Big Island (SVL, $\chi^2 = 6.74$, $df = 1$, $P = 0.009$; Mass, $\chi^2 = 5.76$, $df = 1$, $P = 0.016$) and Bone Island (SVL, $\chi^2 = 5.44$, $df = 1$, $P = 0.020$; Mass, $\chi^2 = 9.49$, $df = 1$, $P = 0.002$). In all cases, selection favored larger hatchling body size (Table 1). In addition, linear selection favored hatchlings with higher body condition on Bone Island (low density, $\chi^2 = 4.41$, $df = 1$, $P = 0.036$), but not on Big Island (high density, $\chi^2 = 0.064$, $df = 1$, $P = 0.801$). The pattern of quadratic (i.e., stabilizing) selection differed between islands and among traits (Table 1). Specifically, there was evidence of significant non-linear selection on hatchling SVL on Big Island (high density, $\chi^2 = 6.04$, $df = 1$, $P = 0.014$), but not on Bone Island (low density, $\chi^2 = 0.36$, $df = 1$, $P = 0.551$); whereas, hatchling body mass appeared to be influenced by stabilizing selection on Bone Island ($\chi^2 = 4.85$, $df = 1$, $P = 0.028$), but not on Big Island ($\chi^2 = 2.84$, $df = 1$, $P = 0.092$). There was no evidence of a quadratic component for body condition on

Table 1 Linear (β) and quadratic (γ) selection gradients (± 1 SE) for each trait on each island

Island	Trait	N	Linear selection β ± 1 SE	Quadratic selection γ ± 1 SE
Big	SVL	160	0.345 ± 0.137*	−0.668 ± 0.302*
	Mass	160	0.318 ± 0.136*	−0.420 ± 0.265
	Condition	160	0.034 ± 0.136	0.147 ± 0.163
Bone	SVL	84	0.244 ± 0.110*	−0.098 ± 0.160
	Mass	84	0.314 ± 0.110*	−0.392 ± 0.178*
	Condition	84	0.222 ± 0.109*	−0.127 ± 0.179

Significant selection gradients are indicated with asterisks. Big Island = high density fire ants, Bone Island = low density fire ants

either island (Table 1). Selection surfaces illustrating linear and nonlinear patterns are shown in Fig. 3.

Discussion

Since its introduction in the 1930s, the red imported fire ant has expanded its range to cover the entire southeastern USA and is predicted to eventually cover a significant portion of the earth's terrestrial surface (Morrison et al. 2004). Because fire ants seem to prefer relatively exposed, disturbed habitat (Porter and Tschinkel 1987; Tschinkel 2006) they frequently co-occur with native species sharing similar habitat preferences, like the prairie lizard, *Sceloporus consobrinus* (Trauth et al. 2004). Along a gradient of invasion history, *S. undulatus* (a species closely related to *S. consobrinus*) has responded plastically and adaptively in a suite of morphological, behavioral, and physiological traits (Langkilde 2009; Boronow and Langkilde 2010; Langkilde and Freidenfelds 2010; Graham et al. 2012). Despite these comparative results, no studies have examined the direct effects of fire ant density on patterns of lizard mortality and the strength of phenotypic selection in the field. In this study we demonstrated that fire ant density has a dramatic effect on hatchling lizard mortality at two different spatial scales (i.e., between isolated populations and locally within a population) and that the presence of fire ants influences local lizard distributions. Moreover, we showed that the pattern and nature of natural selection on morphological traits can differ depending on fire ant density.

Previous work showed that envenomation by fire ants can have delayed effects on survival in hatchling lizards in the laboratory (Langkilde and Freidenfelds 2010). Our study extends these results and suggests that a high density of fire ants in the field can reduce hatchling lizard survival by more than 50% among populations. Furthermore, within population survival scaled inversely with local fire ant density. In fact, the density of fire ant mounds in close proximity to the experimental release location explained ~84% of the variation in lizard survival. Therefore, it appears that fire ants had a direct impact on hatchling lizard survival both within and among populations. The fire ant associated mortality identified in this study is likely an underestimate given the high risk of lizards being predated while still in the nest, or during hatching. Female *S. undulatus* and *S. consobrinus* frequently dig shallow nests and lay eggs in open canopy habitat and along forest edges at sites with beneficial thermal properties for embryo development (Angilletta et al. 2009). Currently such habitats are often associated with human activities and are locations where fire ants can reach extremely high densities (Tschinkel and King 2013). Thus, at sites with high fire ant densities, developing embryos are at risk of predation while inside the nest (Newman et al. 2014; Thawley and Langkilde 2016) and hatchlings emerge from nests into extremely dangerous circumstances.

High rates of spatially structured predation and/or behavioral avoidance of predators should lead to nonrandom patterns of habitat/space use by prey (Power 1987; Mittlebach 1986). On Big Island (high density fire ants), fire ant mounds were non-randomly distributed across the island and were concentrated near the southeastern and southern portion of the island. On this island, lizard recapture locations were located a significantly greater distance from fire ant mounds than expected if the lizards used the habitat on

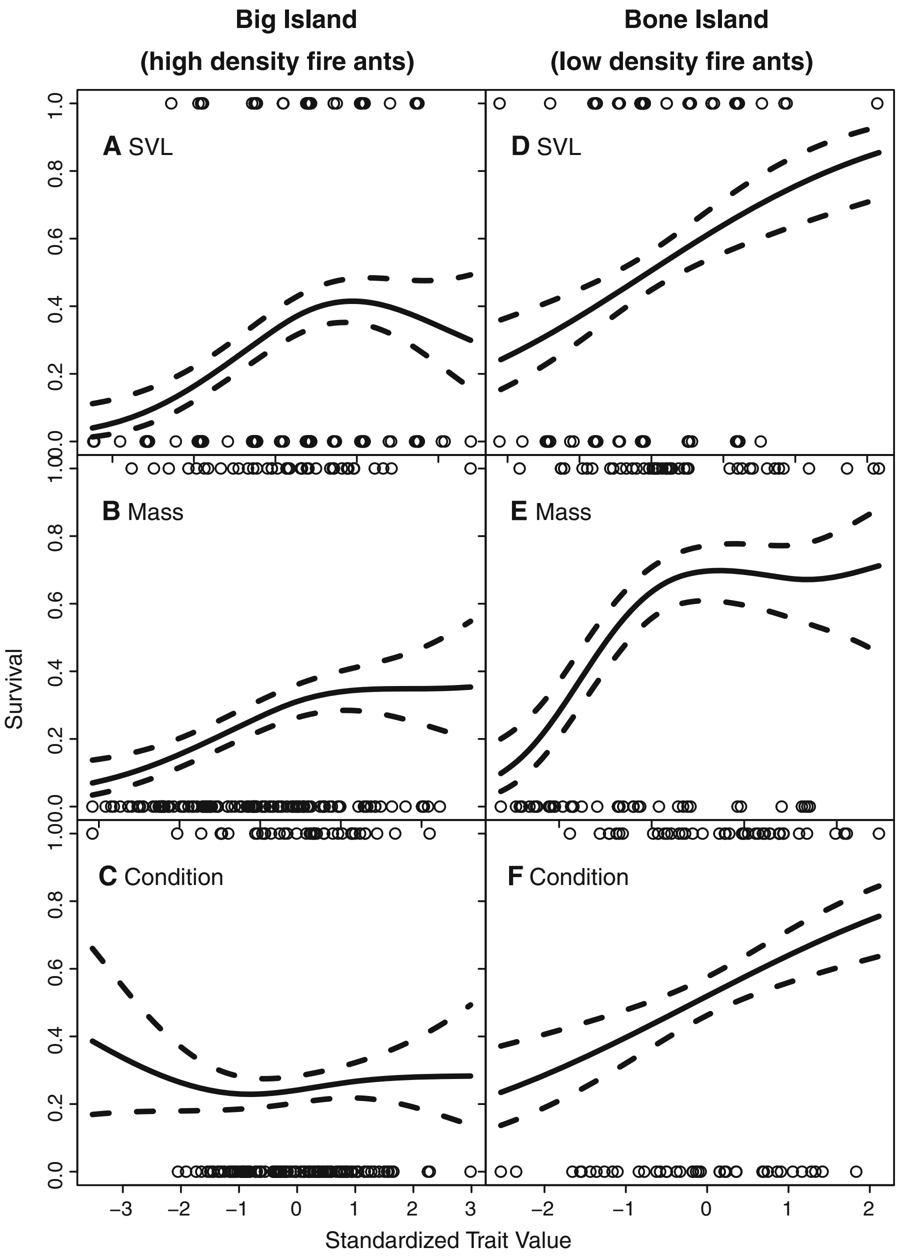

Fig. 3 Phenotypic selection surfaces estimated for each morphological trait on each island. *Dashed lines* denote 95% confidence intervals. Selection gradients and statistical significance are shown in Table 1

the island randomly. Lizard recaptures were concentrated on the opposite side of the island from the areas of high fire ant density (Fig. 1a). This pattern is at least partially a consequence of the high rate of mortality experienced by lizards released in locations with high fire ant density. In contrast, on Bone Island, where fire ants were found in substantially lower density, lizards appeared to use habitat randomly with resect to fire ants (Fig. 1b).

Because juvenile animals are more vulnerable to predation by fire ants (Allen et al. 1997, 2001), we predicted that the nature and strength of phenotypic selection would be influenced by fire ant density on each island. More specifically, we hypothesized that the strength of phenotypic selection would be dampened on the island with a high density of fire ants (Big Island). This is based on the assumption that fire ant predation would not be size specific and the risk of mortality would be similar in lizards of all body sizes. Generally this was not the case. Linear selection gradients for both measures of body size (SVL and mass) were of similar magnitude and had broadly overlapping standard errors. In all cases selection favored larger hatchlings. We also detected a pattern of stabilizing selection for hatchling SVL and body mass. The specific trait that exhibited nonlinear selection was different on each island. The presence of stabilizing selection was somewhat surprising, but might indicate a threshold size below which survival drops precipitously. Selection on body condition (residuals of log-mass by log-SVL regressions) differed between islands. There was no evidence of phenotypic selection on body condition on Big Island (high fire ant density), whereas, on Bone Island (low fire ant density) body condition was under strong linear selection. The results presented in this study are based on comparison of two islands, and thus lack replication. Therefore, it is possible that the differential pattern of mortality between islands could be a consequence of some correlated factor other than fire ants. Two lines of evidence strongly implicate fire ants as the main driver of lizard mortality, however. First, within islands, local fire ant density near release locations explained nearly 85% of the variation in lizard survival. Second, evidence of spatial avoidance further corroborates these results and suggests that fire ants are driving the survival patterns.

High juvenile mortality can have important population-level effects and can affect the evolution of life history traits within populations. A high rate of external juvenile mortality (size selective predation) is expected to increase the age and size at maturity (Stearns and Koella 1986; Stearns 1992); however, an *overall* higher rate of external mortality is expected to select for the opposite suite of traits, younger age and smaller size at maturity (Reznick and Endler 1982; Abrams and Rowe 1996). Thus, specific population-level effects of predation on life history depend on whether predation is size-dependent. Our results suggest that juveniles can experience very high mortality rates in the presence of fire ants in high density, but data are lacking on mortality rates of other age/size classes in the field. Existing comparative data suggest that adult body size in *S. undulatus* is smaller at sites that have a long history of co-existence with fire ants relative to adult body size at uninvaded sites (Langkilde and Freidenfelds 2010). Furthermore, lizards from more recently invaded sites express intermediate adult body sizes. Therefore, these published data are consistent with the hypothesis that in areas with high densities of fire ants, or a long history of co-existence with fire ants, mortality is likely not to be size-dependent. Additional studies examining the potential consequences of fire ant invasion on the life history of native species are sorely needed. The source population for hatchlings used in this study has coexisted with fire ants for only a very short period of time (~5–10 years, personal observ.) and can therefore be characterized as naive. It would be particularly interesting to compare our results with those from hatchlings from populations with a long history of coexistence with fire ants. So far, data suggest that no behavioral or physiological mechanisms exist that enhances tolerance to fire ant venom across the invasion front (Boronow and Langkilde 2010). Thus, it appears that hatchling/juvenile mortality due to fire ants (both immediate [this study] and delayed [Langkilde and Freidenfelds 2010]) might have important demographic and life history consequences.

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