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BOTTOM-UP EFFECTS ON PERSISTENCE OF A SPECIALIST PREDATOR: ANT INVASIONS AND HORNED LIZARDS

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Abstract. Maintaining biodiversity within fragmented landscapes has become a primary focus of ecology. Despite many theoretical and comparative studies on species persistence following fragmentation, experimental studies investigating the mechanisms behind population declines remain rare. In recent years, coastal horned lizards (*Phrynosoma coronatum*) have disappeared throughout much of their range in coastal southern California. In addition to the direct impact of habitat loss due to urbanization, horned lizard populations continue to decline in the remaining fragmented landscape. One factor that may contribute to their decline is the invasion of exotic species from the surrounding urban matrix. Horned lizards are ant specialists, and they may be particularly vulnerable to changes in the native ant community resulting from the invasion of Argentine ants (*Linepithema humile*). In this study we examined how Argentine ants influence horned lizard growth rates by raising hatchlings on prey typical of invaded and uninvaded sites. Hatchling horned lizards maintained positive growth rates on a diet of just one native ant species (*Crematogaster californica*). However, on a diet of Argentine ants or arthropods typical of an invaded community, horned lizard growth rates were either negative or averaged near zero. In addition, when lizards were switched from a diet of Argentine ants to native ants, growth rates increased. One factor contributing to growth was foraging rate; capture success appears partly responsible for why horned lizards specialize on ants vs. other, harder to capture, arthropods. Moreover, a comparison of diets among age classes of coastal horned lizards suggests a diversity of ants is necessary to support lizard populations. While stochastic demographic and environmental processes are often invoked to explain the decline of populations following fragmentation, it appears that horned lizards are disappearing from habitat remnants in southern California at least in part due to the deterministic effects of a biological invasion.

Key words: Argentine ants; biodiversity; biological invasions; bottom-up effects; coastal horned lizards; foraging; growth rate; habitat fragmentation; indirect effects; Linepithema humile; Phrynosoma coronatum; *specialization.*

INTRODUCTION

Anthropogenic habitat loss is often considered the leading cause of species decline and imperilment (Czech and Krausman 1997, Wilcove et al. 1998). Identifying the mechanisms that underlie species decline following fragmentation is essential to minimize the detrimental effects of human land use and to prevent further extinction. Of particular concern are edge effects such as the penetration of exotic species into natural areas from the surrounding matrix. While most edge effects may extend a few hundred meters into natural areas (Murcia 1995, Laurance 2000), biological invasions can spread much farther into a reserve and greatly reduce its effective size (Laurance 1991, Peters 2001). The interaction between fragmentation and invasion may be particularly important in determining species persistence in fragmented landscapes as the in-

troduction and establishment of non-native species is frequently accompanied by numerous direct and indirect detrimental ecological effects (Vitousek et al. 1996, Parker et al. 1999). Experimental studies are necessary to measure indirect impacts of non-native species, and recent work has demonstrated that some invasions may have community-wide consequences (Vitousek et al. 1987, Blossey 1999, Parker et al. 1999).

Argentine ants (*Linepithema humile*) provide an example of a species that causes numerous direct and indirect impacts on communities when it invades. Native to South America, Argentine ants have been introduced nearly worldwide (Suarez et al. 2001). Most notably, Argentine ants eliminate nearly all epigeic ants when they invade new habitats (Majer 1994, Human and Gordon 1996, Holway 1998, Suarez et al. 1998). Because ants fill important ecological roles as predators, scavengers, herbivores, and seed dispersers (Hölldobler and Wilson 1990), this loss of an entire assemblage can have numerous direct and indirect effects. This is well illustrated in South Africa where the displacement of native seed-dispersing ants by Argentine ants has resulted in reduced seedling recruitment in at

least one species of myrmecochorous shrub (Bond and Slingsby 1984). In coastal California, the penetration of Argentine ants into scrub habitats is facilitated by fragmentation, as they are most abundant in disturbed and urban areas and invade adjoining natural communities from these sites (Knight and Rust 1990, Human et al. 1998, Suarez et al. 1998). In addition, the displacement of native ants by *L. humile* has been implicated in the decline of a sensitive vertebrate, the coastal horned lizard (*Phrynosoma coronatum*) (Suarez et al. 2000).

Coastal horned lizards have undergone severe declines in California in recent years and are a candidate species for state and federal listing (Jennings and Hays 1994). While habitat loss is considered the major factor in their decline (Jennings and Hays 1994), an ant-specific diet may make coastal horned lizards particularly sensitive to the invasion of Argentine ants (Pianka and Parker 1975, Montanucci 1989, Suarez et al. 2000). Moreover, horned lizards produce large clutches of relatively small eggs compared to other lizard genera (Pianka and Parker 1975, Vitt and Price 1982, Pianka 1986). The strong disparity in size between hatchlings and adults necessitates high initial growth in order to reach reproductive maturity by the second year. This combination of traits may make coastal horned lizards particularly vulnerable to bottom-up effects (Hunter and Price 1992, Polis and Winemiller 1995) such as changes in prey availability. Preliminary evidence that Argentine ants may indirectly displace horned lizards by eliminating their primary food source comes from two sources. First, in a study of reptile communities across 22 sites throughout coastal southern California (Case and Fisher 2001), horned lizard abundance was negatively correlated with the presence of Argentine ants even when controlling for other factors such as reserve size (Fisher et al., *in press*). Second, horned lizards persisting in invaded areas changed their diet from ants to non-ant arthropods as the native ant species they prefer had been displaced (Suarez et al. 2000). As resource specialization is generally thought to make species more vulnerable to extinction (Terborgh and Winter 1980), it is of interest to determine if Argentine ants can indirectly cause population-level declines in horned lizards by eliminating their preferred prey.

In this paper we experimentally investigated the indirect impacts of a fragmentation-mediated invasion on the growth rate of a native vertebrate. Specifically, we measured the bottom-up effect of Argentine ant invasions on coastal horned lizards and determined if these specialist lizards can persist in invaded areas by changing their diet to incorporate remaining non-ant arthropods. This was accomplished by (1) comparing the diet of different age classes of coastal horned lizards to examine how Argentine ants may impact horned lizards by reducing prey diversity, (2) estimating the impact of Argentine ant invasions on hatchling growth rates by raising lizards on prey typical of invaded and un-

invaded communities, and (3) measuring foraging rates of lizards on different diets to differentiate between nutritional and behavioral constraints on hatchling growth.

METHODS

We collected hatchling coastal horned lizards (lizards within 3 mo of emergence, 1–3 g in body mass) between 9 July and 13 August 1999 from the University of California (UC) Elliot Chaparral Reserve in San Diego County, California. The reserve is nested within a large (>9000 ha) area of natural scrub habitat that makes up the Miramar Marine Air Station. Lizards were weighed, measured (snout–vent length), and randomly assigned to one of four experimental treatments. We kept lizards in the laboratory for the course of the experiment (≤28 d) and then returned them to the site of capture.

We placed lizards in individual 25 × 50 cm terraria, each containing soil from the site of capture (5–6 cm deep), a water dish, and some sparse vegetation. A 75-W heat lamp and a 40-W Reptisun UVB light (ZooMed Laboratories, San Luis Obispo, California 93401 USA) were placed over each terrarium on a timer set from 0700 in the morning to 1900 in the evening. The temperature directly under the heat lamp was maintained at 36–40°C (after Pianka and Parker 1975, Jennings and Hays 1994). The outside of each terrarium was coated with limousine-grade window tinting. The tinting allows only 5% of light to pass through and is reflective from the lit side, allowing an observer to watch the lizard's behavior without being seen. The insides of the terraria were also coated with Fluon (a liquid that dries to create a slick surface; Northern Products, Woonsocket, Rhode Island 02895 USA) to prevent ants and other arthropods from escaping and entering other treatments.

We randomly assigned lizards to one of four feeding treatments. The first three treatments were used to examine how changes in resources due to Argentine ant invasions affect the growth rates of hatchling coastal horned lizards. These included a native ant treatment, an Argentine ant treatment, and an arthropod community treatment. In the native ant treatment, horned lizards were fed exclusively one species of native ant, *Crematogaster californica*. This treatment resembles a subset of the actual field diet of coastal horned lizards (Suarez et al. 2000). The second treatment consisted entirely of Argentine ants. This treatment was used to determine if Argentine ants could act as a replacement food source for the ants they are displacing. The third treatment consisted of non-ant arthropods collected from an area within the UC Elliot reserve that has been invaded by Argentine ants for at least 5 yr (Suarez et al. 1998, 2000). Prey included individuals from many orders (e.g., Coleoptera, Hemiptera, Homoptera, Orthoptera, and non-ant Hymenoptera) known to be consumed by coastal horned lizards in invaded areas (Suar-

ez et al. 2000). This treatment was used to investigate the possibility that horned lizards may be able to persist in invaded areas by switching their diet from ants to other arthropod species. In addition to the three aforementioned treatments, a fourth treatment was used to further investigate whether ants are a dietary necessity and if capture success may influence initial growth. This treatment consisted of feeding lizards domestic crickets (*Acheta domestica*, Rainbow Mealworms, Compton, California 90220 USA) that had one hind leg removed to facilitate capture by lizards.

For the first three treatments, we collected ants and other arthropods daily from the UC Elliot Reserve using pitfall traps (20-L buckets) and vegetation sweeps. Prey items were added to the terraria throughout the day to maintain constant food availability. If too many prey items were present in the terraria, the horned lizards would bury themselves to escape threat (Montanucci 1985; A. Suarez, *personal observation*). To minimize this response, we maintained between 10 and 20 prey items in the terraria at all times. Because prey items were continuously being eaten (and occasionally escaped in the case of flying insects), cages were monitored throughout the day to ensure that prey were always available to the lizards. In the non-ant arthropod treatment, prey items in the terraria were added haphazardly and reflected the relative abundance of available prey in the field. Moreover, because of the difficulty in collecting enough arthropods for all the replicates, we were unable to quantify the prey presented to the lizards, or replace consumed items with the same species (or order).

Lizards were weighed once a week and snout–vent length was measured at the end of the experiment. If a lizard ever lost 20% of its initial body mass, it was immediately switched to a diet of native ants or returned to the field. Lizard fecal pellets were collected daily from each terrarium and dissected under a microscope to determine the identity and number of prey items eaten. Daily foraging rates were estimated for each lizard by summing the number of prey items in all the scats collected over the length of the experiment and dividing the total by the number of days. Fecal pellets deposited by the lizards before the onset of the experiments were used to estimate the field diet of hatchlings prior to capture. We also compared the composition of fecal pellets from hatchling horned lizards to those of juveniles (lizards in their 1st yr, prebreeding, between 6 and 20 g in body mass) and adults (lizards after their 2nd yr, >30 g) previously collected at the UC Elliot Reserve (Suarez et al. 2000).

We compared mean prey sizes among age classes using an ANOVA. For this analysis, the average prey size (head width of ant prey items) was determined for each fecal pellet and used as a datum in the analysis. We investigated differences in growth rates among treatments with an ANOVA using percentage change in body mass (log transformed) at week 2 of the experiment as the dependent variable. Differences in foraging rates among treatments (as inferred from the scats) were examined using an ANOVA with mean number of prey consumed per day (log transformed) as the dependent variable. Following each ANOVA, we used Fisher's protected least squares difference (PLSD) to examine pairwise differences among groups. Variation in growth rates across treatments was investigated using multiple regression with percentage change in body mass from time of capture as the dependent variable and initial body mass, sex, and average number of prey items eaten per day (foraging rate) as the independent variables. Initial body mass and number of prey per day were log transformed for this analysis. Finally, we compared the growth rates of hatchlings in our experiments with other published and unpublished records of growth rates in hatchling *Phrynosoma*.

RESULTS

The field diet of hatchling horned lizards consisted almost entirely of ants. In 66 scats from 39 lizards, 96.4% (1311/1360) of the prey items were native ants (range 75–100% per scat). The most common ant species in hatchling diet were *Crematogaster californica* (>80% of all prey items), *Pheidole vistana*, *Formica* spp., *Myrmecocystus* spp., *Messor andrei*, *Forelius macooki*, *Camponotus* spp., and *Solenopsis xyloni* in decreasing order of abundance. The scat data also revealed that the mean size of prey items differed among lizard age classes (ANOVA: df = 2, 153; $F = 64.56$; $P < 0.001$). Average prey size for hatchling lizards (head width 1.108 ± 0.021 mm [mean ± 1 SE]) was smaller than that of juveniles (1.360 ± 0.081 mm) (Fisher's PLSD: $P < 0.001$), which was smaller than that of adults (1.601 ± 0.032 mm) (Fisher's PLSD: $P < 0.001$). Argentine ants are smaller than the prey commonly eaten by any age class of lizard (Fig. 1).

Initial body mass for the 39 hatchlings averaged 1.21 ± 0.1 g (mean ± 1 SE). By the second week of the experiment, growth rates varied significantly among treatments (ANOVA: df = 2, 27; $F = 9.95$; $P < 0.001$) (Fig. 2A). Differences in growth rates were significant across all pairwise comparisons of the treatments (Fisher's PLSD: native ant vs. Argentine ant, $P < 0.001$; native ant vs. arthropod community, $P < 0.025$; Argentine ant vs. arthropod community, $P < 0.045$). In the Argentine ant treatment, lizards never achieved positive growth rates, and six individuals were switched to native ants after the second week while the remainder were released. After the switch, growth rates were positive and similar to those for lizards in the native ant treatment (Fig. 2B).

Lizard foraging rates, measured as average number of prey consumed per day as inferred from dissection of the scats, also differed across treatment groups (ANOVA: df = 2, 25; $F = 38.769$; $P < 0.0001$). Differences in foraging rates were significant across all pairwise
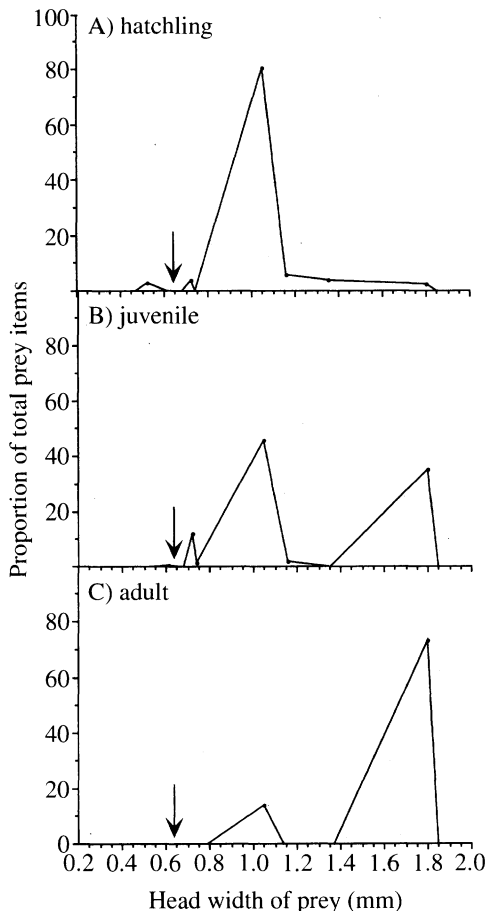
FIG. 1. Relative abundance vs. size of ant prey in fecal pellets from coastal horned lizards (*Phrynosoma coronatum*) at the UC Elliot Reserve: (A) adult (lizards after their 2nd yr, >30.0 g, *n* = 67 pellets), (B) juvenile (lizards in their 1st yr, prebreeding, 6–20 g, *n* = 21 pellets), and (C) hatchling (lizards within 3 mo of emergence, 1–3 g, *n* = 66 pellets). Values represent the overall proportion of each ant species pooled across all pellets within each age class. The prominent peaks in the distributions correspond to the ants *Cremato-gaster californica* (1.05 mm) and *Messor andrei* (1.80 mm). The arrows indicate the mean head width of the invasive Argentine ant (0.64 mm); Argentine ants are smaller than any ants regularly consumed by any age class of coastal horned lizards.

comparisons of the treatments (Fisher's PLSD: native ant vs. Argentine ant, $P < 0.0001$; native ant vs. arthropod community, $P < 0.0001$; Argentine ant vs. arthropod community, $P = 0.0022$) (Fig. 3). In addition, foraging rates of hatchlings in the Argentine ant treatment increased after the lizards were switched to a diet of native ants at week 2 (paired *t* test: df = 5, *t* = 7.794, *P* = 0.0006). Among treatments, foraging rate was positively related to growth rates in hatchling horned lizards (regression summary: $y = -0.295 + 0.256x$, $R^2 = 0.607$, $P < 0.001$) (Fig. 4). Multiple regression revealed that this relationship remained significant even when we controlled for initial body mass and sex (whole model: df = 3, 26, *F* = 13.585, *P* <

0.001; sex: *t* = −0.729, *P* > 0.4; initial body mass: *t* = 0.962, *P* > 0.3; foraging rate: *t* = 6.266, *P* < 0.001). Lizards that lost ≥20% of their body mass (and were subsequently released or switched to a diet of native ants) were excluded from these analyses. Including these lizards did not change the results.

The fourth treatment, consisting of wounded crickets, also suggests that capture success influences growth rate. Unlike the arthropod community treatment, where growth rates varied considerably and averaged near zero (Fig. 2A), hatchlings in the wounded cricket treatment maintained positive growth rates (Fig. 5).

An examination of published and unpublished data revealed that field growth rates (snout–vent length) for hatchling *P. coronatum* ranged from 0.08 to 0.37 mm/d (Table 1). Growth rates of hatchling horned lizards in other *Phrynosoma* species were similar to those of *P. coronatum* (0.06–0.41 mm/d) (Table 1). While the
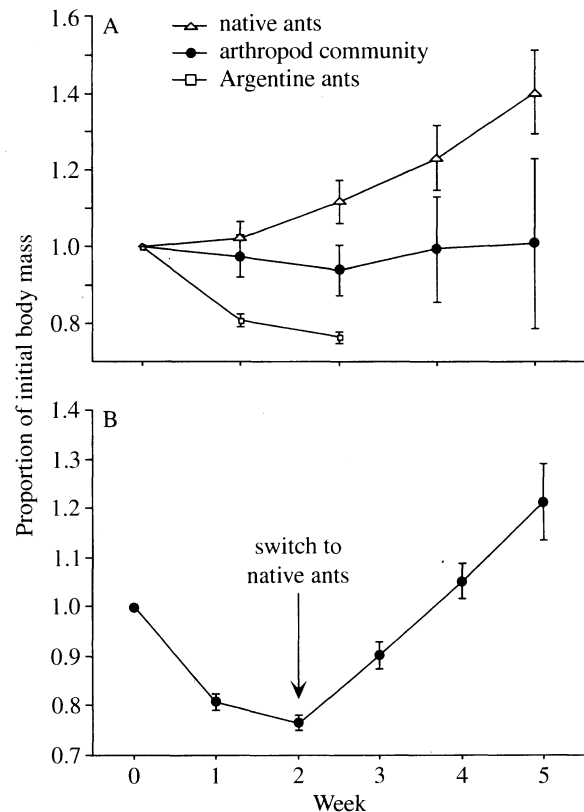

FIG. 2. (A) The effect of diet on growth rates of hatchling coastal horned lizards under three experimental treatments. By week 2, differences in growth rates were significant across all pairwise comparisons of the treatments (Fisher's PLSD: native ant vs. Argentine ant, *P* < 0.001; native ant vs. arthropod community, *P* < 0.025; Argentine ant vs. arthropod community, *P* < 0.045). Symbols represent mean percentage change in mass since the onset of the experiment. Error bars are ± 1 SE. (B) Growth rates of hatchling lizards in the Argentine ant treatment after being switched to a diet of native ants.
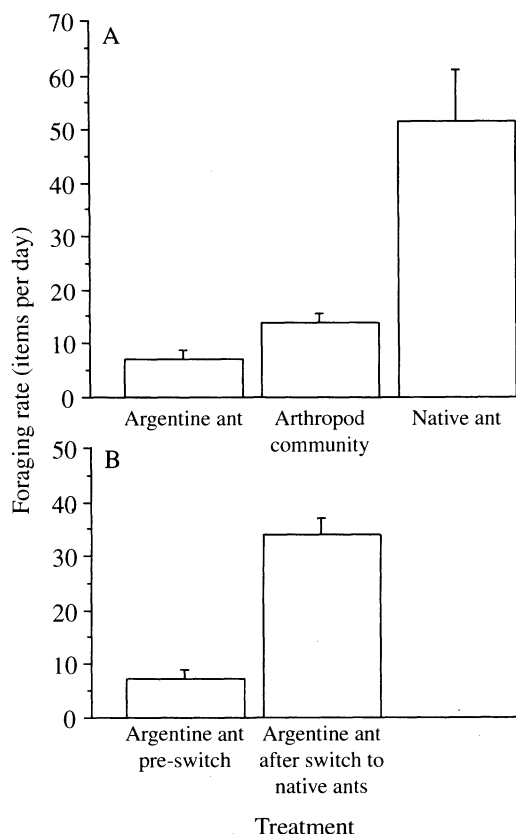
FIG. 3. (A) Foraging rate of hatchling coastal horned lizards in three treatments mimicking prey availability of invaded and uninvaded areas. Values are the number of prey items consumed per day (means and 1 SE) as estimated from the dissection of lizard fecal pellets. All three treatments were statistically different from one another (ANOVA, $P < 0.01$). (B) Foraging rates increased for six hatchlings that were switched from the Argentine ant treatment to native ants after the second week of the experiment ($P < 0.001$, paired t test).
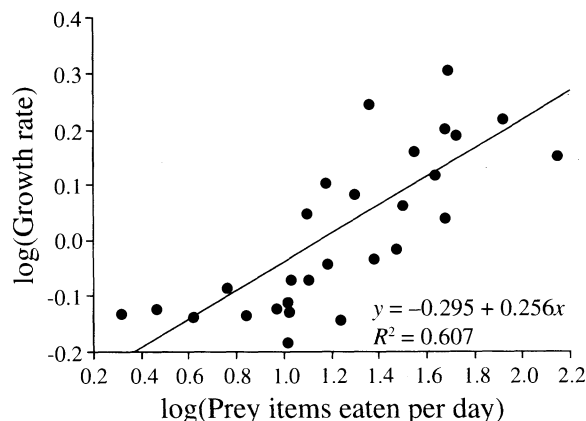

FIG. 4. Relationship between foraging rate (average number of prey consumed per day) and growth rate (mean percentage change in mass since the onset of the experiment) across the three treatments used to examine the effect of Argentine ant invasions on coastal horned lizard growth rates.

average growth rates of hatchlings in the native ant treatment (0.18 mm/d) were similar to field growth rates, lizards in the Argentine ant and arthropod community treatment averaged growth rates lower than field averages (0.05 mm/d and 0.07 mm/d, respectively). In contrast, average growth rates in the wounded cricket treatment were comparable to field rates (0.24 mm/d) (Table 1).

DISCUSSION

Our experiments indicate that resource specialization in horned lizards makes them vulnerable to the simplification of ant communities resulting from the invasion of Argentine ants. Growth rates of hatchling horned lizards raised on one species of native ant were similar to estimated growth rates of hatchlings in the field. However, both treatments emulating invaded communities resulted in growth rates that were either negative (Argentine ant treatment) or averaged near zero (arthropod community treatment). Furthermore,

hatchlings in the Argentine ant treatment that were switched to native ants after the second week resumed positive growth rates. Across treatments, the average number of prey consumed per day was positively related to growth rate. Compared to the native ant treatment, foraging rates were reduced on diets of Argentine ants or arthropods typical of an invaded community. While most hatchlings were unable to sustain positive growth rates in the treatment consisting of arthropods typical of an invaded community, in the treatment where crickets were wounded to facilitate capture, hatchlings did maintain positive growth rates. This suggests that capture success may largely influence postnatal growth in horned lizards, although the nutritional quality of these crickets may also be much higher than the field captured arthropods. Together, these results provide a mechanism for the reduced horned lizard abundance and lack of recruitment seen in areas invaded by Argentine ants in the field (Fisher et al., *in press*).
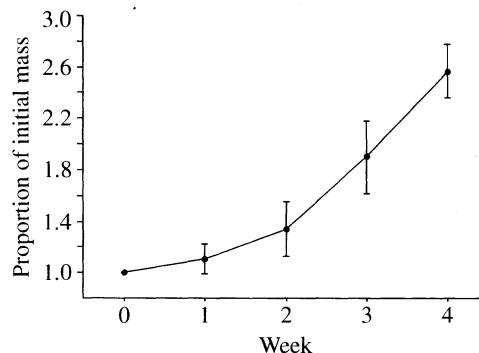

FIG. 5. Growth rates for hatchling horned lizards raised on crickets that had at least one leg removed to facilitate capture. Symbols represent mean proportional change in mass since the onset of the experiment. Error bars represent ± 1 SE.

TABLE 1. Growth rates (snout–vent length, mm/day) of hatchlings in field and laboratory studies of *Phrynosoma*.

Phrynosoma species	Study	Duration†	Growth		No. lizards‡	Treatment or field location
			Mean ± 1 SE	Range		
P. coronatum	this study	28 d	0.18 ± 0.03	0.01–0.25	9	captivity, native ants
P. coronatum	this study	28 d	0.07 ± 0.03	0.01–0.24	7	captivity, arthropod community
P. coronatum	this study	14 d	0.05 ± 0.02	0.00–0.13	6	captivity, argentine ants
P. coronatum	this study	28 d	0.24 ± 0.04	0.08–0.27	6	captivity, wounded crickets
P. coronatum	A. V. Suarez and T. J. Case (*unpublished data*)	34 d	0.19 ± 0.02	0.09–0.25	39	San Diego Co., California§
P. coronatum	R. N. Fisher and T. J. Case (*unpublished data*)	90 d	0.20 ± 0.03	0.14–0.24	40	Riverside and San Diego Co., California
P. coronatum	Hager (1995)	13–16 d	0.24 ± 0.07	0.08–0.37	4	Riverside Co., California
P. solare	Parker (1971)	90 d	0.19‖	0.16–0.22	3	Maricopa Co., Arizona
P. platyrhinos	Tanner and Krogh (1973)	29–51 d	0.23 ± 0.03	0.09–0.41	26	Mercury Co., Nevada
P. platyrhinos	Pianka and Parker (1975)	16 d–1 yr	0.25 ± 0.02	0.06–0.40	9	western Utah
P. douglassi	Pianka and Parker (1975)	13 d–9 mo	0.21 ± 0.06	0.12–0.39	4	western Utah
P. douglassi	Montanucci (1985)	1 yr	0.13‖	0.11–0.15	16	captivity

† Time period used to estimate growth rate starting within 1 mo of emergence.
‡ For captive lizards in this study, hatchlings that lost >20% of their mass were excluded from this table.
§ These values were extrapolated from the increases in snout–vent length of hatchlings lizards captured throughout the course of the study.
‖ Not enough data were provided to calculate standard error.

Resource specialization can increase extinction risk (Terborgh and Winter 1980). Horned lizards appear more vulnerable to Argentine ant invasions than other lizards with more general diets (Fisher et al., *in press*). While many of the arthropods remaining in invaded areas are suitable prey for other vertebrates, horned lizards are extreme ant specialists and do not appear to be behaviorally or physiologically suited for such a drastic change in diet. Horned lizards are sit-and-wait predators that exploit the clumped distribution of ants at colony entrances or foraging trails (Pianka and Parker 1975, Whitford and Bryant 1979, Munger 1984). These characteristics, along with physiological constraints specific to an ant diet (Montanucci 1989), may make it difficult for horned lizards to successfully change their diet away from ants.

Horned lizards do not appear to perceive Argentine ants as suitable prey. Argentine ant consumption by hatchling horned lizards was minimal, even when no other prey types were available. Moreover, it is likely that Argentine ants would not be profitable prey even if they were regularly consumed by horned lizards. The dry body mass of Argentine ant workers is only 1/4 that of *C. californica* workers and 1/27 that of *M. andrei* workers (A. Suarez, *unpublished data*). Assuming that energy values are similar among ants, hatchlings would have to forage four times and adults 27 times as much in invaded areas to maintain the energy intake of their preferred food. For a cryptic species that often remains motionless to avoid predation, an increase in foraging activity of this scale may be costly. In addition to being smaller than preferred ant species, Argentine ants may also be unpalatable due to defensive chemical compounds and may directly cause mortality in lizards because of their large colony sizes and aggressive mobbing behavior.

The variation in prey size seen across age classes of lizards (Fig. 1) suggests that a diversity of ant species may be necessary to maintain populations of coastal horned lizards. Differences in diet among age classes of horned lizards have been reported in other species (Rissing 1981) and may be an important factor in reducing intraspecific competition. Likewise, differences in prey selection relating to lizard size have also been reported between sexes of horned lizards (Powell and Russell 1984). Among species, a relationship between body size and prey size is common in lizards (Pianka 1973). In the genus *Phrynosoma*, different species rarely coexist in the same habitat, but when they do, they differ in size and feed on different ant species (Pianka and Parker 1975, Whitford and Bryant 1979, Shaffer and Whitford 1981).

The simplification of ant communities due to Argentine ant invasions may have other widespread impacts. Across plant taxa, seeds that vary in size are dispersed or eaten by different ant species (Davidson 1977, Brown et al. 1979). Argentine ants do not take many seeds (Markin 1970, Human et al. 1998) and therefore may not be effective seed predators or dispersers (Bond and Slingsby 1984). More studies are necessary to investigate how the replacement of ≥20 coexisting ant species by one invader affects plant communities. Argentine ants may also indirectly impact plants and animals by disrupting other components of arthropod communities (Cole et al. 1992, Human and Gordon 1997, Holway 1998, Bolger et al. 2000). Moreover, the results reported here are likely not unique to Argentine ants. Other invasive ants, such as the red imported fire ant (*Solenopsis invicta*) and the big-headed ant (*Pheidole megacephala*), are also known to disrupt arthropod communities (Porter and Savignano 1990, Hoffman et al. 1999) and even directly impact

a variety of vertebrates through predation (Allen et al. 1994).

Edge effects, such as the penetration of exotic species into natural areas, reduce the effective size of a reserve in proportion to the distance to which they penetrate. As Argentine ant abundance decreases as a function of distance to the nearest edge in many habitats (Fuentes 1991, Human et al. 1998, Suarez et al. 1998), it is the extent to which they penetrate into habitat fragments that determines the number of persisting native ant species. Similarly, while habitat destruction has reduced the total area suitable for populations of coastal horned lizards, much of the remaining habitat is unsuitable due to the penetration of Argentine ants and the subsequent displacement of native ant species. In addition, top-down edge effects, such as increased domestic cat abundance (Crooks and Soulé 1999), may also reduce horned lizard survivorship in these areas. While stochastic demographic and environmental processes have often been invoked for the local extinction of isolated populations, results such as ours implicate deterministic processes as major contributors to population declines. The growing body of evidence for a key role of deterministic factors in the decline and extinction of small populations indicated the critical need for more empirical research (Caughley 1994, Woodroffe and Ginsberg 1998).

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