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PREY SELECTION IN HORNED LIZARDS FOLLOWING THE INVASION OF ARGENTINE ANTS IN SOUTHERN CALIFORNIA

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Abstract. Biological invasions can have severe direct and indirect impacts on natural communities and are one of the leading reasons behind the loss of biodiversity. We investigated the indirect effects of Argentine ant (*Linepithema humile*) invasions on coastal horned lizards (*Phrynosoma coronatum*) through an examination of prey selection in the field and laboratory. In non-invaded areas, coastal horned lizard diet consists predominately of ants (>94% by prey item in three reserves examined), particularly harvester ants in the genera *Pogonomyrmex* and *Messor*. In invaded areas, most native ants were displaced, and remaining horned lizards incorporated more non-ant arthropods and smaller ants into their diet. In addition, Argentine ants were never detected in horned lizard fecal pellets, suggesting that they are not a suitable replacement food source for the native species they are displacing. Analysis of prey selection in uninvaded areas reveals that ant species consumption by adult lizards is correlated with ant body size rather than ant abundance, foraging behavior, or defensive method. Differences in diet between adult and juvenile lizards suggest that a diversity of ant species is necessary to support both age classes. Laboratory experiments, consisting of paired presentations of four native ant species and the Argentine ant, confirmed patterns found in the field. Both adult and juvenile horned lizards preferred native ants to Argentine ants. Patterns of preference suggest that, in addition to *L. humile*'s small size, other factors may contribute to the horned lizard's aversion to this species.

Populations of coastal horned lizards have undergone severe declines in recent years. While habitat loss has been the primary concern, the invasion of Argentine ants into their remaining suitable habitat needs to be monitored. Reserves need to be managed to prevent the penetration of Argentine ants in order to minimize their direct and indirect effects on natural communities.

Key words: Argentine ants; biological invasions; coastal horned lizards; conservation; edge effects; foraging; indirect effects of introduced species; Linepithema humile; Phrynosoma coronatum; *prey selection; southern California, USA.*

INTRODUCTION

Biological invasions pose a serious threat to the world's biota and, along with habitat loss to urbanization and agriculture, are the leading reason for decline of threatened and endangered species in the United States (Czech and Krausman 1997, Wilcove et al. 1998). Habitat loss and the spread of exotic species are not necessarily independent. One problem resulting from habitat loss is the subdivision of remaining habitat into small fragments that can lead to an increase in local edge effects (Soulé 1986). Among other problems, edges may facilitate the invasion of exotic species (Suarez et al. 1998) that negatively affect native species through predation, competition, parasitism, and disease.

Many studies have examined the impact of exotic or invasive species on natural communities (see Elton 1958, Mooney and Drake 1986, Drake et al. 1989). While most have focused on the direct impact of exotics on closely related taxa, few studies have investigated the impact of an introduced species, either directly or indirectly, on more distantly related taxa, or across entire communities (Diamond and Case 1986, Vitousek et al. 1987, Vitousek 1990). Indirect effects, when one species impacts another through a third (Wootton 1994*a*), can be particularly important in determining interactions among species (Paine 1966, Wootton 1994*b*). In addition, theoretical and experimental investigations highlight the importance of indirect effects in shaping communities (Case and Bender 1981, Wootton 1992). For example, defoliation by exotic insects has been correlated with higher predation rates on artificial avian nests (Thurber et al. 1994), and changes in avian communities (Rabenold et al. 1998).

Indirect effects of an invasion can be particularly devastating when an introduced species displaces many native species within the invaded community. For example, in the United States, the Argentine ant (*Linepithema humile*) has eliminated most native ant species in areas where it has invaded, including harvester ants (Erickson 1971, Human and Gordon 1996, Suarez et al. 1998). Harvester ants are important components of

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ecosystems in many aspects, particularly as seed dispersers (Holldobler and Wilson 1990) and as food for other animals, including horned lizards (*Phrynosoma* spp.). Declining throughout most of their range (Jennings and Hayes 1994), coastal horned lizards (*P. coronatum*) are ant specialists (Pianka and Parker 1975), making them vulnerable to changes in the native ant community. In addition, recent surveys have found little spatial overlap between coastal horned lizards and Argentine ants in reserves where Argentine ants have invaded (R. Fisher and T. Case, *unpublished data*).

In this paper we investigate the indirect impact of introduced Argentine ants on a declining vertebrate by examining resource selection of coastal horned lizards pre- and post-invasion. Resource-selection studies can be used to predict the effects of habitat change (Manly et al. 1993). Particularly, examination of an organism's diet prior to and after a disturbance can provide insight into the effect of disturbance on resource availability. When it is impossible to collect data prior to disturbance, undisturbed areas can be used as a reference to assess the impact of habitat change. Laboratory prey-preference experiments, in which animals are given a choice between prey items under controlled conditions, can be used to complement field data and provide insight into the mechanisms behind preference. This approach was employed by Rissing (1981), who examined prey selection in desert horned lizards (*P. platyrhinos*) to investigate why lizards ate one ant species disproportionately relative to its abundance in the field.

Here, we measured the impact of Argentine ants on coastal horned lizards by comparing prey selection in lizards from natural areas where Argentine ants have not invaded with paired areas in two reserves where Argentine ants have invaded. We also compared prey selection between adult and juvenile lizards in order to examine differences in diet between age classes of this declining vertebrate. We complement field data with a series of prey-preference experiments aimed at revealing the mechanisms behind prey selection in coastal horned lizards and determine the suitability of the exotic Argentine ant as a suitable replacement food source for the native ants they are displacing.

METHODS

Study organisms

The San Diego coastal horned lizard (*Phrynosoma coronatum blainvillei*) ranges from Santa Barbara and Ventura Counties, (California, USA), south into Baja California (Mexico) (Jennings and Hayes 1994). Like most *Phrynosoma* (Pianka and Parker 1975, Montanucci 1989), *P. c. blainvillei* specializes on ants, particularly harvester ants (*Messor* and *Pogonomyrmex*). 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). They rely on crypsis to escape detection by predators and likely make decisions regarding prey capture based on prey size and distance at the point of detection (Schoener 1969, Shafir and Roughgarden 1998). The San Diego coastal horned lizard is listed by the California Department of Fish and Game as a species of special concern and is also a candidate for listing by the U.S. Fish and Wildlife Service (Jennings and Hayes 1994). It has disappeared from up to 45% of its known range in the United States (Jennings and Hayes 1994), and much of what remains of its preferred scrub habitat (Jennings 1988) has been subject to massive fragmentation as a result urbanization over the past 100 years.

The invasive Argentine ant (*Linepithema humile*) was detected in California as early as 1907 (Woodworth 1908) and has since spread widely throughout coastal California (Smith 1936, Ward 1987). The life history of the Argentine ant is similar to other "tramp" species (Holldobler and Wilson 1990, Passera 1994). Argentine ants have generalized dietary and nesting requirements, maintain colonies with multiple queens, and reproduce by budding rather than by nuptial flights (Newell and Barber 1913). The success of Argentine ants at displacing native ant species likely stems from high worker densities, resulting from a lack of intraspecific aggression (Holway et al. 1998): numerical advantages underlie their high exploitative and interference ability (Human and Gordon 1996, Holway 1999). Argentine ants penetrate into natural scrub habitats in southern California through urban edges where they are more abundant (Suarez et al. 1998). The invasion of Argentine ants into natural areas has resulted in the decline and local extinction of many native ant species, including harvester ants (Suarez et al. 1998).

Study areas

We chose three study areas in southern California to investigate the foraging ecology of horned lizards (Fig. 1): the University of California's Elliot Chaparral Reserve (Elliot) and Torrey Pines State Reserve Extension (Torrey Pines) in San Diego County, and the Southwest Riverside County Multispecies Reserve (Riverside). All contain populations of San Diego coastal horned lizards and support diverse ant communities. Two of the sites (Elliot and Torrey Pines) are invaded by Argentine ants, allowing a direct comparison of ant communities and horned lizard diet in areas with and without Argentine ants. The area sampled adjacent to and including the Elliot reserve is ~205 ha in size but is nested within a much larger undeveloped area (the 9254.5-ha Miramar Naval Air Station). Torrey Pines is ~92 ha and is surrounded by urban development, effectively isolating it from other areas of natural vegetation. The area sampled at the Riverside site is ~700 ha (part of the 7850-ha reserve), and is surrounded primarily by suburban and agricultural development. All three sites consist of upland scrub habitat typical of Mediterranean-climate regions (Westman 1981). El-

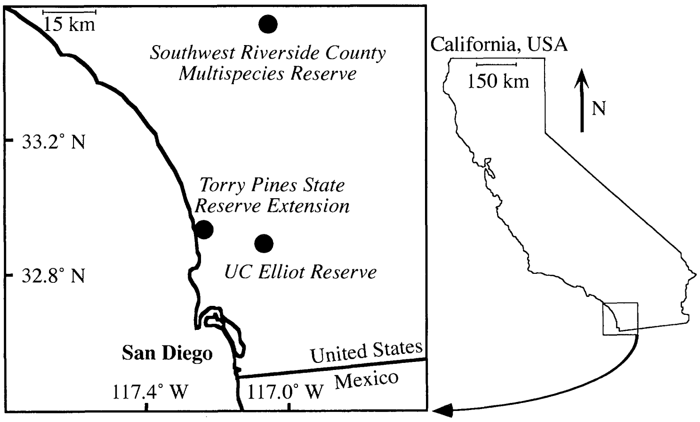

FIG. 1. Map of coastal southern California, USA, showing the three study areas where coastal horned lizard diet was examined.

liot and Torrey Pines consist predominantly of "chamise-chaparral," dominated by thick stands of chamise (*Adenostoma fasciculatum*), while the Riverside site also contains a successional mix of "coastal sage scrub," dominated by California sagebrush (*Artemisia californica*), black sage (*Salvia mellifera*), white sage (*Salvia apiana*), buckwheat (*Eriogonum fasciculatum*), and various exotic grasses.

Resource measurement and the effect of Argentine ants on the native ant community

Relative abundance of ants at each of the three study areas was assessed visually and with pitfall traps. Within Elliot and Torrey Pines, the extent of the Argentine ant invasion was determined by visual searching along transects, 50 m apart, extending into the reserves from edges where Argentine ants are established. Pitfall-trap arrays consisted of five glass jars (60-mm diameter), four placed 20 m apart in a square, and the fifth jar in the center. Traps contained a 50 : 50 mixture of water and non-toxic Sierra brand antifreeze. A total of 33 arrays were placed at the Riverside site, 14 arrays at Elliot, and 4 arrayss at Torrey Pines. These arrays were restricted to areas not occupied by Argentine ants, and were placed at least 100 m apart throughout the area surveyed for horned lizards. The purpose of these arrays was to measure patterns of ant species composition and abundance for comparison with horned lizard diet in uninvaded areas. In addition, another four arrays each were placed in paired areas matched for vegetation, topography, and the distance to the edge of the reserve, on either side of the Argentine ant front at Elliot for an independent estimate of the effect of Argentine ants on the native ant fauna. Four arrays also were placed in areas occupied by Argentine ants at Torrey Pines adjacent to the four arrays mentioned above. This design minimized differences in the ant community arising from factors other than the presence of the exotic Argentine ant. Pitfall trapping was restricted to late spring and summer months between August 1995 and August 1997, and coincided with activity periods for horned lizards. Ants were identified to species using published keys and a reference collection. Due to the difficulties of identifying some ant species from head capsules in fecal pellets (see *Field examination . . .*, below), species from a few genera (e.g., *Camponotus, Myrmecocystus, Formica*) were lumped for analyses in sites where a genus was represented by more than one species.

The abundance of ants found in pitfall traps is influenced by the distance from the pitfall trap to the colony entrance, the foraging method of the ant species, the size of the ant species, and its actual abundance at the site; therefore, the total number of workers per pitfall trap may be a biased estimate of activity. For this reason, we used the proportion of pitfall arrays in which a species occurred as a relative index of abundance for each species within each site. We also categorized ant foraging behavior (group vs. solitary), and defensive behavior (stinging vs. spray or smear chemical application) through direct observation and literature reviews. The size of each ant species was calculated by averaging the maximum head width (including the eyes) and the length of the thorax measured from 20 individuals of each species. Ants were measured with a micrometer under a dissecting microscope by one author (A.V. Suarez).

Field examination of horned lizard diet

The diet of coastal horned lizards was determined by dissecting fecal pellets. Study sites were searched for horned lizards in areas with and without Argentine ants. Lizards were collected, housed in 20 × 30 cm terraria, kept until they deposited a fecal pellet, and then returned to the field. The study areas also were visually searched for horned lizard fecal pellets, which are distinctive in shape and size, and easily distinguished from those of other lizard species (Rissing 1981; A. Alberts, *unpublished data*). Because fecal pellets of juvenile *Phrynosoma* (lizards in their first year, <13 g) resemble those of other lizard species, only pellets collected from captured juveniles were used to assess the diet of young horned lizards. Fecal pellets were dissected and all ants were identified to species

TABLE 1. Proportional abundance and characteristics of the Argentine ant (*Linepithema humile*) and of native ant species detected in pitfall arrays at the three study sites in southern California, USA.

	Abundance†				
	Riverside	UC Elliot Reserve		Torrey Pines	
Ant taxa	*L. humile* absent, n = 33 arrays	*L. humile* present, n = 4 arrays	*L. humile* absent, n = 12 arrays	*L. humile* present, n = 4 arrays	*L. humile* absent, n = 4 arrays
Pogonomyrmex rugosus	0.45	–	–	–	–
P. californicus	0.12	–	–	–	–
P. subnitidus	–	–	–	0	0.75
Messor andrei	0.12	0	0.71	–	–
M. pergandei	0§	–	–	–	–
Crematogaster californica	0.94	0	0.86	0	0.25
Solenopsis xyloni	0.36	0	0.43	0	0.5
S. molesta	0.21	0	0.28	1	0.5
Pheidole vistana	0.63	0	1	0	0.5
Pheidole spp.	0.48	–	–	–	–
Leptothorax andrei	0.54	0.5	0.64	0.5	1
Camponotus spp.	0.42	0.25	0.21	0	0.75
Myrmecocystus spp.	0.45	0	0	0	0.75
Formica spp.	0.18	0	0.36	–	–
Neivamyrmex californicus	0.06	0	0.14	0	0.25
Tapinoma sessile	0.03	0	0.64	0	0
Dorymyrmex insanus	0.03	0	0.14	1	0.5
D. bicolor	0§	–	–	0	0.25
Forelius maccooki	0.42	0	1	–	–
Linepithema humile	–	1	–	1	–

† The proportion of pitfall arrays with each ant species; n = the number of five-jar arrays used to estimate ant abundance; A dash (–) indicates that the species or genus does not occur at the site; an entry of 0 denotes that the species was present at the site but not detected in pitfall traps used to estimate abundance.

‡ Data are means with 1 SE in parentheses. NA = not appropriate to generate a single average to represent *Pheidole* spp. because this category refers to many small species, and in addition, these species have workers that are dimorphic in size.

§ Recorded in visual surveys, but not caught in pitfall traps.

based on head capsule morphology (R. R. Snelling and C. George, *unpublished report* [1979] to the Bureau of Land Management, U.S. Department of the Interior, Riverside, California, USA). Other insects present in fecal samples were identified to order. Fecal pellets were collected between March 1996 and August 1997.

For each age class and site we calculated mean abundance of each ant species across fecal pellets. Proportions rather than absolute numbers of prey items were used to control for variation in lizard size and hunger. We used multiple regression to estimate the relative importance of the ants' abundance, foraging method, defensive method, and size (independent variables) in affecting overall prevalence in diet (dependent variable). Foraging and defensive methods were entered as dummy variables (1 or 0). In addition, multicollinearity was not a problem as independent variables were weakly correlated to one another ($P > 0.05$). Mann-Whitney U tests were used to compare the composition of fecal pellets found in areas with and without Argentine ants at Elliot and Torrey Pines.

Laboratory prey-preference experiments

To further examine horned lizard prey preferences, we conducted laboratory experiments consisting of paired presentations of ant species to captive horned lizards, emulating those of Rissing (1981) for desert horned lizards (*Phrynosoma platyrhinos*). Lizards were placed in individual indoor 25 × 50 cm terraria, each containing sand, a water dish, and some sparse vegetation. A heat lamp was placed over each terrarium on a timer set from 0600 to 1800. The temperature was maintained at about 34–37°C during midday (after Pianka and Parker 1975). The lizards were kept only for the duration of the trials (~22 d) and then returned to the site of capture. Lizards were starved for 2 d at the onset of the experiments and 1 d between each prey-preference trial. For each trial, the lizard was placed into a different 25 × 50 cm terrarium that was coated with limousine-grade 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 lizard was allowed to adjust to the tank 5 min before each trial. Five individuals of each of two ant species were then placed into the tank with the lizard. Ants were replaced as they were eaten in order to maintain five individuals of each species of ant at all times during the trial. The trial lasted for 45 min or until the lizard buried itself in the sand.

To assess dietary preferences, we recorded how often the lizard fixed its attention on an ant, whether the ant was eaten, and how many steps the lizard took to reach the ant. We also recorded each time an ant made contact with a lizard along with the lizard's reaction to the ant. The percentage of total ants eaten was calculated for

TABLE 1. Extended.

Size (mm)‡			
Head width	Body length	Foraging method	Defense method
2.39 (0.03)	2.79 (0.03)	group	sting
1.69 (0.02)	2.16 (0.02)	solitary	sting
1.93 (0.02)	2.29 (0.02)	group	sting
1.80 (0.03)	2.54 (0.04)	group	chemical
1.62 (0.05)	2.05 (0.06)	group	chemical
1.05 (0.02)	1.16 (0.02)	group	chemical
0.68 (0.02)	0.92 (0.02)	group	sting
0.38 (0.01)	0.052 (0.01)	solitary	sting
0.72 (0.01)	1.23 (0.01)	group	chemical
NA	NA	group	chemical
0.46 (0.01)	0.67 (0.01)	solitary	sting
1.85 (0.18)	2.61 (0.20)	group	chemical
1.16 (0.03)	1.72 (0.03)	solitary	chemical
1.35 (0.05)	2.03 (0.06)	solitary	chemical
0.61 (0.04)	0.91 (0.04)	group	sting
0.65 (0.02)	0.89 (0.02)	group	chemical
0.74 (0.01)	1.11 (0.01)	group	chemical
0.83 (0.01)	1.19 (0.01)	group	chemical
0.52 (0.01)	0.75 (0.01)	group	chemical
0.64 (0.01)	0.99 (0.01)	group	chemical

each prey species after every trial to control for the effects of hunger and lizard size.

Each time a lizard turned its head and fixed its attention upon an ant we recorded a "fix." This behavior consists of a sudden motion where the lizard changes the direction of its head, and occasionally its body, to line up with a potential prey item. This is a common response of sit-and-wait predators to prey, particularly among horned lizards (Milne and Milne 1950, Whitford and Bryant 1979, Rissing 1981). After detecting an ant, lizards either ate it or ignored it. The ratio of fixed to eaten ants gives an approximation of how many ants were eaten that the lizard noticed and is thus a reflection of choice rather than detection. Differences between the percentage of ants eaten and the percentage of ants eaten after being fixed upon suggest that the ant's behavior influenced prey selection by the lizard. The number of steps taken by the lizard to reach the prey item is an estimate of the cost, in terms of energy expenditure or increased predation risk, that the lizard is willing to incur for that particular prey type.

Four native species and one exotic species, the Argentine ant, were presented to the lizards in 10 randomly ordered pairwise combinations. The four native ant species chosen, *Pogonomyrmex rugosus*, *P. californicus*, *Messor andrei*, and *Crematogaster californica*, are common prey items for coastal horned lizards in southern California that vary in size, foraging behavior, and defensive tactics (Table 1).

Twenty-seven lizards were collected from Elliot and Riverside. Two age classes of lizards were used in order to evaluate the role of experience and size on prey selection. Lizards under 13g and 60-mm snout–vent length were scored as juveniles after Pianka and Parker (1975) and Rissing (1981). Some of the smaller juvenile lizards (<8 g) were not subjected to all 10 trials in order to minimize stress. Instead, the 10 trials were split randomly between two juvenile lizards from the same location. A minimum of six lizards from each site and age class were tested in all 10 trials.

Mann-Whitney *U* tests were used to test for differences in preference for the percentage total eaten, eaten after fixed, and number of steps for each paired comparison. Two-way ANOVA was used to test for differences between sites and age classes in total percentage eaten and number of steps taken to reach prey items. Due to the inherent problem of independence when dealing with percentages in paired choice tests, the percentage total eaten was transformed using log ratio analysis (Elston et al. 1996). One value was calculated for each trial by dividing the percentage eaten of the larger sized ant species by the percentage eaten of the smaller ant species, giving a normally distributed range of values. The number of steps taken to reach a prey item also was transformed. One value for each trial was calculated by subtracting the number of steps taken to reach the smaller of the two ants from the number of steps taken to reach the larger. This value was also normally distributed and reflects the difference in steps taken to reach the two prey items. *P* values were adjusted using a sequential Bonferroni test (Rice 1989) to correct for multiple comparisons.

If the value of a prey item is proportional to its size, we expect preference, as measured by percentage eaten after fixed and the number of steps taken to reach the prey, to be correlated with the size of the ant. We tested this hypothesis with linear regressions. We also examined the degree to which Argentine ants deviate from a linear relationship. This was done by separating the experiments into four independent categories, divided by age class and site, because of differences in preference that may arise from these variables. The probability of the value for Argentine ants being an outlying point was then calculated for each category and an overall *P* value was determined using Fisher's combined-probability test.

To determine the influence of ant behavior on horned lizard preference, we used a relative score of aggression. For each trial, we recorded each time an ant made contact with a lizard and the lizard's reaction to the contact. A lizard responded to an ant either by remaining motionless with its eyes closed or reacting actively (i.e., shaking, running away, or burying itself). Data were pooled for each ant species across all trials, and an ANOVA was used to examine variation in contacts per minute and the lizards behavioral responses for each of the ant species.

All analyses were performed with Statview version 4.1 (Abacus Concepts, Berkeley, California, USA) for the Macintosh.

TABLE 2. Dietary differences between (A) adult and juvenile horned lizards, and (B) areas with and without Argentine ants (*Linepithema humile*).

		Diet (%) and comparisons				
Comparison	No. of fecal pellets	Harvester ants†	*Pogonomyrmex rugosus*	*Pogonomyrmex californius*	Other ants‡	Non-ants§
A) Adults vs. juveniles						
Riverside adults	40	56.4	51.5	2.1	36.4	5.1
Riverside juveniles	58	59.3	21.2	38.1	40.2	0.2
Mann-Whitney *U*		$U' = 1164.0$ $P = 0.9769$	$U' = 1543.5$ $P = 0.0056$*	$U' = 762.0$ $P = 0.0001$*	$U' = 1208.5$ $P = 0.7259$	$U' = 1380.5$ $P = 0.1110$
Elliot adults	67	69.8			23.7	5.4
Elliot juvenile	24	42.4			46.3	11.1
Mann-Whitney *U*		$U' = 1066.0$ $P = 0.0183$			$U' = 997.0$ $P = 0.0822$	$U' = 830.0$ $P = 0.8149$
B) Invaded vs. non-invaded areas						
Elliot, *L. humile* absent	91	62.6			29.6	6.9
Elliot, *L. humile* present	10	4.0			3.6	92.2
Mann-Whitney *U*		$U' = 782.0$ $P = 0.0002$*			$U' = 708.5$ $P = 0.0039$*	$U' = 893.0$ $P = 0.0001$*
Torrey Pines, *L. humile* absent	15	63.6			34.1	1.9
Torrey Pines *L. humile* present	5	0.0			66.0	12.0
Mann-Whitney *U*		$U' = 75.0$ $P = 0.0011$*			$U' = 56.0$ $P = 0.1064$	$U' = 64.0$ $P = 0.0207$*

Note: Values were calculated by averaging the percentage composition of each fecal pellet.

* $P < 0.05$; significant difference after correcting for multiple comparisons using the sequential Bonferroni test (Rice 1989) within each comparison (A or B).

† Harvester ants include *Pogonomyrmex rugosus, P. californicus,* and *Messor andrei* at Riverside; *M. andrei* at Elliot; and *P. subnitidus* at Torrey Pines.

‡ Other ants include all ants except the genera *Pogonomyrmex* and *Messor.*

§ Non-ants include prey items outside of the family Formicidae (Hymneoptera).

RESULTS

Prey communities

Riverside.—Twenty-seven species of ants were detected with our surveys (Table 1). Species recorded in visual surveys, but not caught in pitfall traps, included *Messor pergandei* and *Dorymyrmex bicolor.* These two species were seen infrequently and primarily along dirt roads. Two species (*Leptothorax nevadensis* and *Stenamma* sp.) detected with the pitfall traps were only represented by one worker each and forage primarily in leaf litter (Ward 1987) so were not included in the analysis.

Elliot.—Sixteen species of ants were collected in the pitfall-trap arrays in areas not invaded by Argentine ants (Table 1). *Leptothorax nevadensis* was represented by one worker and was again excluded from subsequent analyses. *Pseudomyrmex apache* was also excluded from subsequent analyses because it is an arboreal species that is inadequately detected with pitfall trapping.

Argentine ants are invading into the reserve from a landscaped facility and a large *Eucalyptus* grove that border the north edge of the reserve (Suarez and Case, *unpublished data*). Ant communities were reduced in areas occupied by Argentine ants (Table 1). Only two native ant species were found in the four arrays placed in areas dominated by Argentine ants. In contrast, eight native ant species were found in the four arrays placed in the paired area without Argentine ants. These species were a subset of the most common species found in the pitfall trapping throughout the reserve (Table 1).

Torrey Pines.—Argentine ants are penetrating into the reserve from the surrounding urban matrix (Suarez and Case, *unpublished data*). The four trap arrays in areas not occupied by Argentine ants yielded 11 species of ants, whereas four arrays in areas occupied by Argentine ants yielded only three species of native ants (Table 1). One species found in the uninvaded area, *Pseudomyrmex apache,* was not included in subsequent analyses for reasons mentioned above.

A summary of ant species variables including size, foraging method, defensive method, and relative abundance at each site can be found in Table 1.

Diet composition

Across age classes and study areas, we examined a total of 220 fecal pellets. In areas free of Argentine ants, native ants made up >98.5% of coastal horned lizard diet, and harvester ants (genera *Pogonomyrmex* and *Messor*) accounted for 65% of all prey items in fecal pellets. There were significant differences between adults and juveniles in diet (Table 2). While adult lizards predominately ate the largest ant species, juvenile lizards ate more smaller species (Fig. 2). Where Argentine ants have invaded, native ants only made up 55.5% of prey items, and harvester ants only 3% (Table 2, Fig. 2). Argentine ants were never found in horned

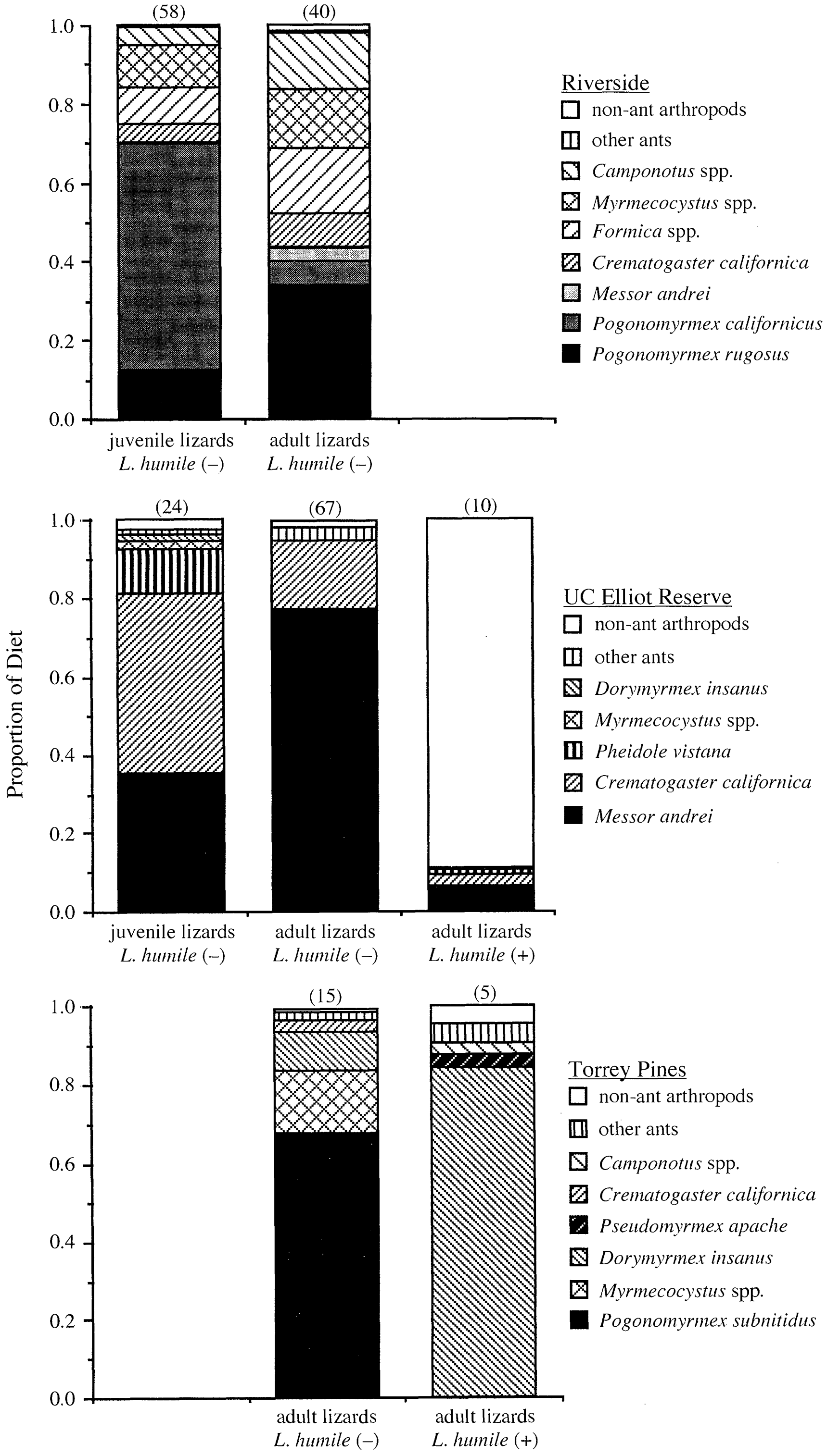

FIG. 2. Composition of fecal pellets of adult and juvenile coastal horned lizards in areas invaded (*L. humile* +) and not occupied (*L. humile* −) by the exotic Argentine ant (*Linepithema humile*) at all three southern California (USA) study areas. Sample sizes are reported in parentheses above the columns.

TABLE 3. Multiple-regression analyses, of ant size, abundance, foraging method, and defensive method as the independent variables and their prevalence in horned lizard diet as the dependent variable. Only Argentine ant-free areas at the three southern California (USA) sites were used.

Source of variation	df	R^2	Coefficient	1 SE	P
A) Adult diet					
Riverside, whole model	14	0.66			0.019
Intercept			−0.112	0.112	0.342
Size			0.109	0.029	0.003*
Abundance			0.133	0.066	0.072
Foraging method			0.03	0.038	0.441
Defense method			−0.029	0.041	0.494
Elliot, whole model	10	0.678			0.101
Intercept			−6.255	33.869	0.858
Size			37.69	11.628	0.017*
Abundance			22.023	20.426	0.322
Foraging method			−6.682	12.789	0.62
Defense method			−15.143	15.599	0.369
Torry Pines, whole model	10	0.871			0.007
Intercept			−3.371	16.439	0.844
Size			30.052	5.951	0.002*
Abundance			25.566	10.183	0.045
Foraging method			−8.486	6.093	0.213
Defense method			−11.69	6.569	0.125
B) Juvenile diet					
Riverside, whole model	14	0.515			0.095
Intercept			−0.043	0.205	0.838
Size			0.095	0.052	0.1
Abundance			−0.01	0.121	0.942
Foraging method			0.124	0.069	0.102
Defense method			−0.101	0.075	0.206
Elliot, whole model	10	0.506			0.303
Intercept			−5.245	29.282	0.863
Size			17.888	10.107	0.127
Abundance			20.264	17.754	0.297
Foraging method			−5.831	11.116	0.618
Defense method			−4.354	13.558	0.759

Notes: Ants in the genera *Camponotus* and *Neivamyrmex* are primarily nocturnal foragers and were excluded from the analyses. Inclusion of these groups does not change the observed patterns.

* $P < 0.05$ after correcting for multiple comparisons using the sequential Bonferroni test (Rice 1989) within each comparison (A or B).

lizard scat. Non-ant prey items in the fecal pellets predominately consisted of Coleoptera, Isoptera, and non-ant Hymenoptera. No juvenile lizards were found in areas dominated by Argentine ants at Elliot and only two juvenile horned lizards were found at Torrey Pines (both in areas without Argentine ants), so a comparison between adult and juvenile diet was not possible at these scales. However, both fecal pellets obtained from the juvenile lizards at Torrey Pines consisted entirely of native ants (*Pogonomyrmex subnitidus* and *Dorymyrmex insanus*).

Among possible factors influencing prey selection, we considered the ants' size, abundance, foraging, and defensive behavior. These four factors were weakly intercorrelated (correlation coefficient r varied from 0.01 to 0.5). When these factors are included in a multiple regression, only ant size influenced prey selection in adult horned lizards, and no factors were significant for juveniles (Table 3). The effect of ant size was consistent across all three sites (Table 3).

Laboratory prey preference experiments

In paired trials between native ants, adult horned lizards generally preferred the larger of the two species presented, regardless of foraging method or novelty. Juvenile lizards also tended to prefer larger ants, except for *Pogonomyrmex rugosus,* the largest ant presented. For all three measurements (total eaten, eaten after fixed [i.e., lizard turned its head and fixed its attention upon an ant], and number of steps taken to reach prey) all four native ant species were preferred over Argentine ants.

Percentage total eaten.—In paired comparisons between native ant species, adult lizards ate the larger of the two species more often than the smaller in all cases except between *P. rugosus* and *P. californicus.* In addition, Argentine ants were eaten less than all native ants except *Crematogaster californica* (Fig. 3). Juvenile lizards preferred the larger of the two native ant species presented except for comparisons with *P. ru-*

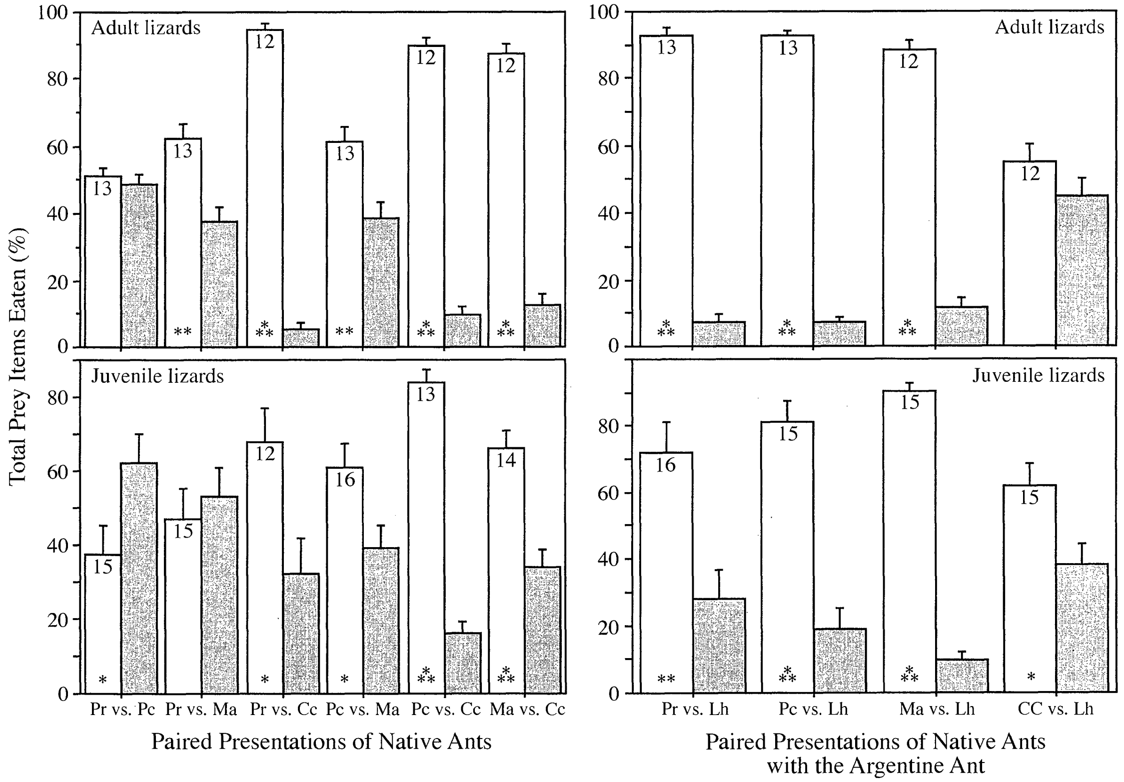

FIG. 3. Percentage of prey items consumed by adult and juvenile coastal horned lizards in paired laboratory prey-preference experiments. The white bar represents the larger of the two species in each pair. Sample sizes are presented for each paired comparison. The number of asterisks indicates the level of significance based upon a Mann-Whitney U test (none = not significant; $*P < 0.05$, $**P < 0.01$, $***P < 0.001$). Species abbreviations: Pr = *Pogonomyrmex rugosus,* Pc = *P. californicus,* Ma = *Messor andrei,* Cc = *Crematogaster californica,* and Lh = *Linepithema humile* (the Argentine ant).

gosus, which was eaten less frequently than either *Messor andrei* or *P. californicus.* Argentine ants were always eaten less frequently than native ants (Fig. 3). Log-ratio analysis revealed no significant variation in preference as a result of age class, location, or age × location interaction after correcting for multiple comparisons (Rice 1989).

Percentage eaten after fixed.—Based on ants that were fixed upon, adult lizards did not show preferences among the three harvester ants, but always preferred the harvester ants over the much smaller *C. californica* (Fig. 4). Juvenile lizards did not exhibit any preferences. In all comparisons between native ants and Argentine ants, native ants were eaten more often after detection than Argentine ants by both adults and juveniles (Fig. 4).

Number of steps taken to reach a prey item.—Among native ants, adult lizards took more steps to reach the three harvester ant species than the smaller *C. californica.* Adults also took more steps to reach *P. rugosus* than the smaller *P. californica* (Fig. 5). Juvenile lizards took more steps to reach *P. californicus* over *C. californica,* but no other significant differences were seen (Fig. 5). For all paired comparisons between native ant species and Argentine ants, lizards of both age classes took significantly more steps to reach the native ant species (Fig. 5). An ANOVA on the number of steps taken to reach a prey item revealed no significant differences between age class, site, or age × site interaction after correcting for multiple comparisons (Rice 1989).

The mean number of steps taken to reach a prey item, but not the percentage eaten after being fixed upon, was correlated with prey size for native ant species (Fig. 6). Argentine ants were eaten less frequently than expected based upon a linear relationship between preference and size of native ants (Fig. 6).

Ant aggressiveness.—The five ant species presented to the lizards in the laboratory varied with respect to how often they made contact with lizards. While the three harvester ants did not vary in the number of contacts with the lizards per minute of exposure, *Crematogaster californica* made fewer contacts than any other species, and Argentine ants made significantly more contacts per minute than any of the native ant species (Fig. 7). The frequency with which lizards closed their eyes per contact did not vary across ant species. However, lizards were more likely to shake, avoid, or bury themselves in the presence of the three harvester ant

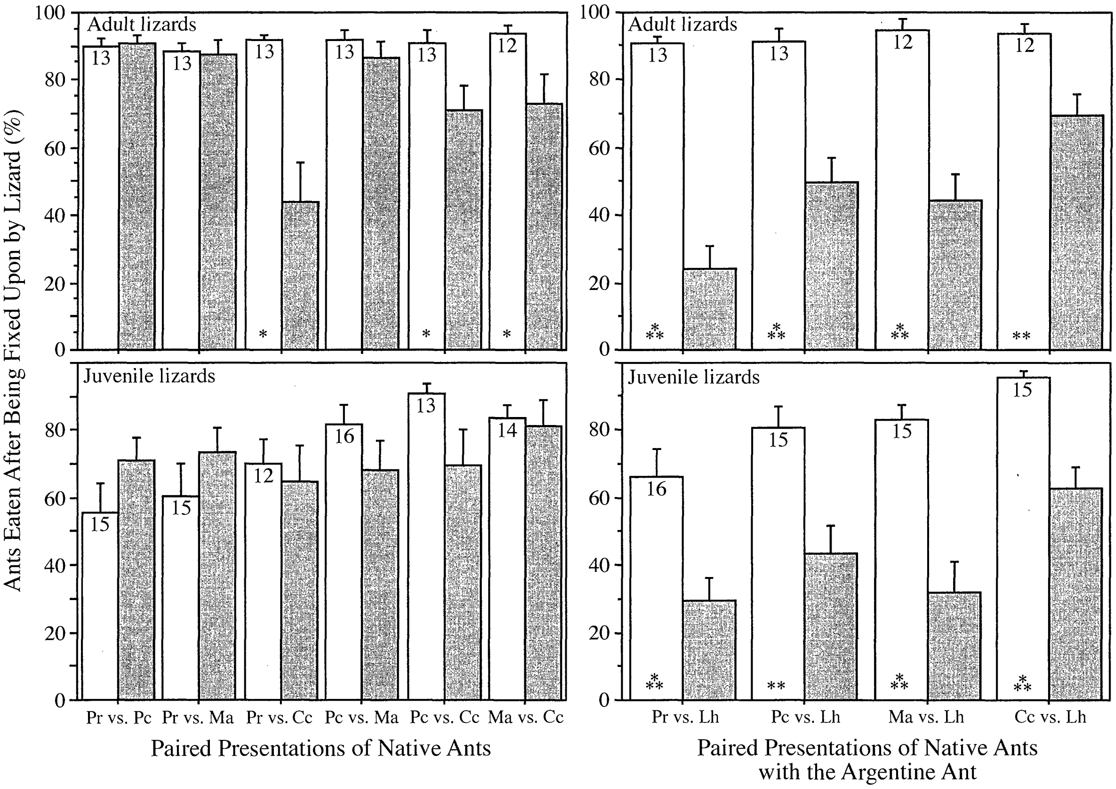

FIG. 4. The percentage of prey eaten after it was fixed upon by adult or juvenile coastal horned lizards in paired laboratory prey-preference experiments. The white bar represents the larger of the two species in each pair. Sample sizes are presented for each paired comparison. The number of asterisks indicates the level of significance based upon a Mann-Whitney *U* test (none = not significant; $*P < 0.05$, $**P < 0.01$, $***P < 0.001$). Species abbreviations: Pr = *Pogonomyrmex rugosus,* Pc = *P. californicus,* Ma = *Messor andrei,* Cc = *Crematogaster californica*, and Lh = *Linepithema humile* (the Argentine ant).

species than they were with either *C. californica* or Argentine ants (Fig. 7).

DISCUSSION

By investigating patterns of horned lizard prey preference in natural areas and in the laboratory, we demonstrate one mechanism by which Argentine ants may negatively affect horned lizards. Like their congeners, coastal horned lizards specialize on ants, specifically harvester ants. In areas where Argentine ants have invaded, these native ants are displaced, and horned lizards switch from eating predominately harvester ants to eating smaller ants (e.g., *Dorymyrmex insanus*) and non-ant arthropods. Horned lizards do not eat Argentine ants in the field, suggesting that *Linepithema humile* is not a suitable replacement food source for the ants they displace.

Based upon the preference of adult horned lizards for larger ants, Argentine ants may be too small to be perceived as profitable prey. Lack of detection by horned lizards due to the Argentine ant's small size may also influence the preference for native ants over Argentine ants, however, Argentine ants were rarely eaten even after being fixed upon by lizards in the laboratory. While the small size of Argentine ants clearly contributes to their unsuitability as a replacement food source for the native ants they are displacing, two lines of evidence suggest they may be unpalatable or avoided for other reasons as well. First, in invaded areas at Torrey Pines, Argentine ants were never eaten by horned lizards although they did eat *Dorymyrmex insanus*, an ant similar in size to *L. humile.* Second, in the laboratory prey-preference experiments, Argentine ants were significantly less preferred than would be expected based upon a linear relationship between percentage eaten after being fixed upon and ant size (Fig. 6). While this relationship might be nonlinear (and therefore include *L. humile*), it suggests that Argentine ants are below a threshold that horned lizards are using to select suitable prey. In addition, Argentine ants are aggressive group foragers (Human and Gordon 1996, Holway 1999) and made contact with lizards more often than did native ants during the laboratory experiments (Fig. 7). Together, the small size and aggressive mobbing behavior of Argentine ants may prevent them from replacing native ants in lizard's diets. Other factors such as unpalatability due to novel defensive chemical compounds also may deter horned lizards

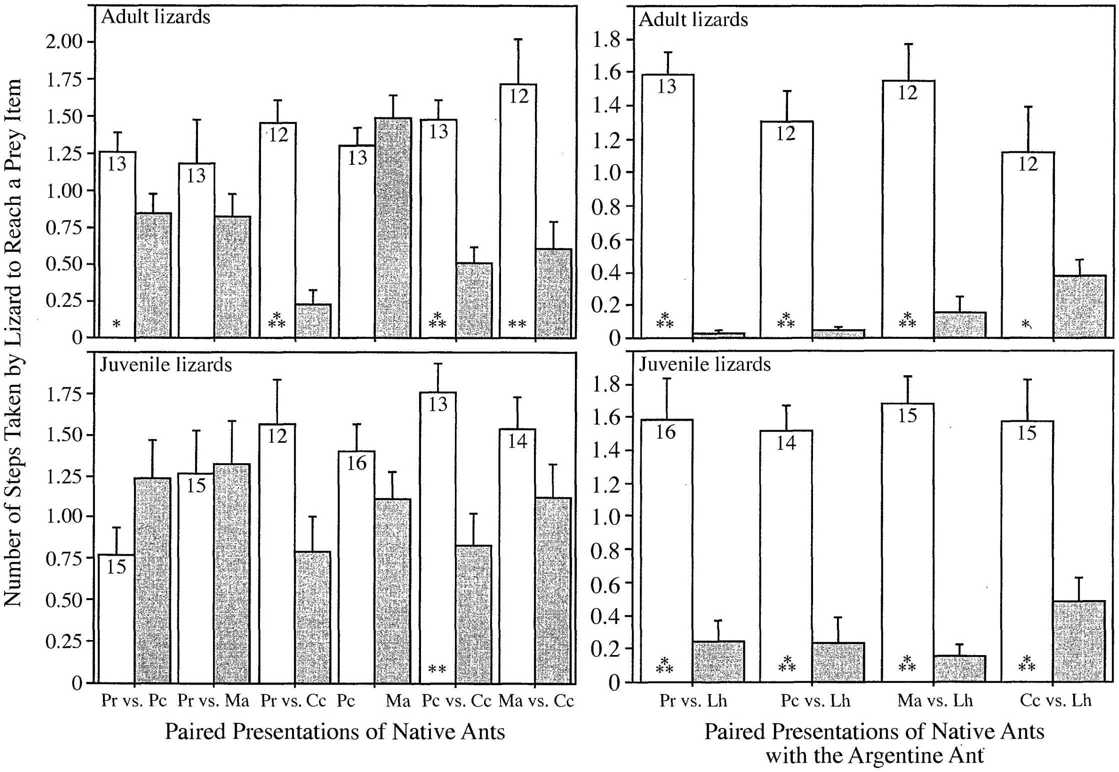

FIG. 5. Average number of steps taken to reach a particular prey item by adult and juvenile coastal horned lizards in paired laboratory prey-preference experiments. The white bar represents the larger of the two species in each pair. Sample sizes are presented for each paired comparison. The number of asterisks indicates the level of significance based upon a Mann-Whitney *U* test (none = not significant; $*P < 0.05$, $**P < 0.01$, $***P < 0.001$). Species abbreviations: Pr = *Pogonomyrmex rugosus,* Pc = *P. californicus,* Ma = *Messor andrei,* Cc = *Crematogaster californica,* and Lh = *Linepithema humile* (the Argentine ant).

from eating Argentine ants. Horned lizards are capable of detoxifying poisons of ants with which they share an evolutionary history. For example, *Phrynosoma douglassii* and *P. cornutum* have been shown to detoxify the venom of *Pogonomyrmex rugosus* and *P. maricopa*, respectively (Schmidt et al. 1989).

Unlike adults, juvenile lizards did not prefer the largest ants. Differences between age classes may arise from experience, physiological constraints related to body size, or higher success rates of foraging on small prey (Schmitt and Holbrook 1984, Juanes and Conover 1994). Differences in preference between juvenile and adult horned lizards may arise from gape limitations of young lizards: horned lizards seize their prey using their tongue and subsequently swallow it whole. This may prevent juvenile lizards from easily ingesting the largest prey items. Small lizards also may be more vulnerable to mobbing by group-foraging ant species, as suggested by Rissing (1981). Even though juvenile lizards ate smaller prey on average than adults, they still preferred all native ants to Argentine ants in the laboratory, and were absent from areas invaded by Argentine ants in the field. Differences in diet between adults and juveniles also suggest that a variety of ant species are necessary to support populations of horned lizards.

Differences between the percentage of each species among all ants eaten and percentage eaten after being fixed upon can help distinguish between true size preferences vs. differences in detectability of prey species (Zaret and Kerfoot 1975). Many of the significant differences between ant species disappear when we consider selection after detection. This suggests that the size and movement patterns of the ants may influence prey choice through enhanced initial detection of prey rather than preference for particular prey items. On average, however, more steps were taken to reach larger prey items than smaller ones. Because horned lizards are sit-and-wait predators and rely heavily on crypsis to escape detection by predators, the distance lizards travel towards a prey item provides an indication of its relative value (Petren and Case 1996, Shafir and Roughgarden 1998).

Rissing (1981) used a series of prey-preference experiments with three species of ants to confirm information gathered through analysis of fecal pellets and ant community composition for desert horned lizards (*Phrynosoma platyrhinos*). He found that horned liz-

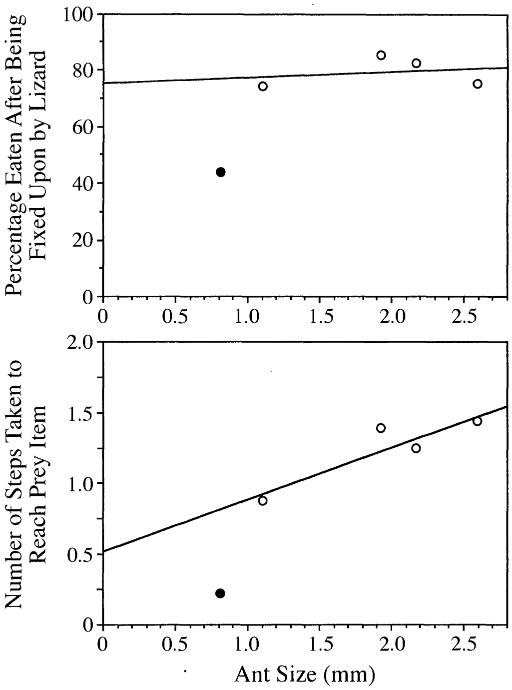

FIG. 6. Relationship between prey size and two measures of preference in the laboratory experiments. Prey size is the avarage of body length and head width (Table 1). Native ant size (○) was significantly correlated with the number of steps ($P = 0.04$) but not with percentage eaten after being fixed upon ($P = 0.75$). Trials were separated into four independent categories based upon lizard age class and site to investigate the degree to which the preference for the exotic Argentine ant deviated from these relationships. The value for Argentine ants (●) was significantly lower than the relationship between native ant size and the measurement of preference for "eaten after fixed" (df = 4, $\chi^2 = 9.4$; $P = 0.05$); but not for "number of steps" (df = 4, $\chi^2 = 5.5$; $P > 0.1$) (Fisher's combined-probability test for the four categories).

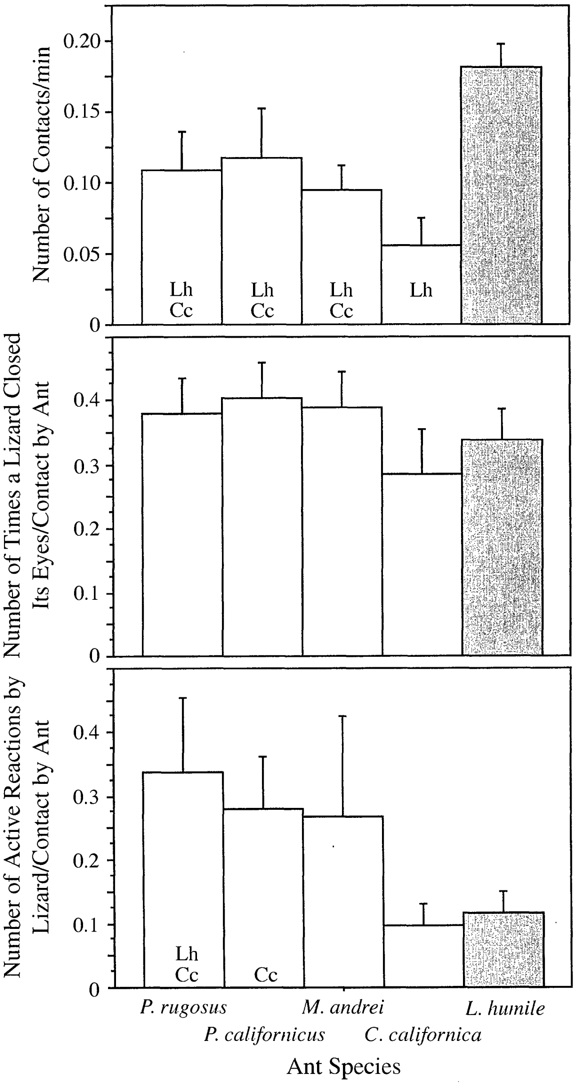

FIG. 7. The number of times ants made contact with coastal horned lizards, as well as the lizards' reaction to the contact (see *Methods: Prey-preference experiments* for complete description) in paired laboratory prey-preference experiments. Data were averaged across all pairwise comparisons to give one value per ant species. Significant differences between species were determined by Fisher's PLSD post hoc test of an ANOVA on the number of behaviors per minute. "Lh" denotes a significant difference ($P < 0.05$) between native ants and the *Linepithema humile*, exotic Argentine ant. "Cc" denotes significance ($P < 0.05$) between a species and *Crematogaster californica.*Vertical lines above the bars represent 1 SE.

ards consumed the harvester ant *Pogonomyrmex californicus* ten times more often than would be expected based on their densities at the study area, a pattern repeated in prey-preference experiments. He concluded that lizards avoided preying upon group-foraging species that are more likely to exhibit a mobbing response and instead preferred the solitary foraging ant species, *P. californicus.* However, it is also possible that lizard size (i.e., gape limitation) may have prevented the lizards from choosing the largest ant species, *Pogonomyrmex rugosus,* which happened to be a group forager. Desert horned lizards are smaller than coastal horned lizards (Pianka and Parker 1975) and may have gape limitations similar to the juveniles in our study. In the eastern short-horned lizard (*Phrynosoma douglassi*), Powell and Russell (1984) found a positive correlation between lizard snout–vent length and average prey size, indicating that prey selection may be influenced by body size in horned lizards.

The influence of ant foraging method on prey selection remains difficult to ascertain due to the relatively small number of individuals presented to the lizards in the laboratory experiments. However, evidence suggesting that ant foraging method may not determine preference among native ant species in horned lizards comes from personal observations in the field and from the literature. We frequently witnessed horned lizards foraging at colony entrances and adjacent to foraging columns of both *Pogonomyrmex rugosus* and *Messor andrei*, the two most prominent group-foraging ants at any of our sites. Although *Pogonomyrmex californicus* is a solitary forager, horned lizards tended to forage at or near colony entrances where the activity level of workers is often extremely high (De Vita 1979). It is therefore unlikely that the preferences for *P. californicus* by juvenile coastal horned lizards are entirely due to their solitary foraging method. Instead, the smaller juvenile coastal horned lizards may prefer *P. californicus* because it is the largest easily consumable ant available to the lizards during their peak foraging periods.

Defense mechanisms of the ants, either the use of stingers or spraying/smearing chemical defensive compounds, did not appear to influence prey selection by horned lizards (Table 3), as pointed out by Rissing (1981). This is supported in the laboratory experiments where horned lizards did not respond differently to contact with the three harvester ant that differed in their defense. However, it is still possible that species-specific chemical compounds may vary in their palatability.

Implications

In areas where Argentine ants have invaded, many native ant species are eliminated, and the few that remain are the same species reported in invaded areas throughout California (Ward 1987, Suarez et al. 1998). Horned lizards continued to eat ants in invaded areas at Torrey Pines only because of the presence of *Dorymyrmex insanus,* which continues to persist in some areas dominated by Argentine ants (Suarez et al. 1998). Since *D. insanus* is rare at Elliot, lizards are forced to incorporate non-ant arthropods into their diet. *Dorymyrmex insanus* is much smaller than the harvester ants preferred by horned lizards in non-invaded areas, and the increased foraging time required to capture enough of these ants may be costly. The long-term effects of such changes in diet need to be investigated through analysis of loss of mass or other indicators of physical condition. Extreme dietary specialization (Montanucci 1989) may make horned lizards vulnerable to dietary changes, particularly when lizards are forced to eat predominately non-ant arthropods. Unlike ants that occur in abundance at colony entrances and foraging trails, most other arthropods are not as abundant and predictable. The displacement of native ants by Argentine ants may cause horned lizards that persist in invaded areas to spend more time searching for food. In addition, there is evidence that Argentine ants can cause reductions in other groups of arthropods in southern California scrub habitats (Bolger et al. 2000), suggesting that resources may be reduced for many insectivores.

Although equal effort was spent searching invaded and uninvaded areas at Torrey Pines and Elliot, our sample sizes for fecal pellets are much smaller in invaded areas. Current monitoring of horned lizards with radiotelemetry also confirms that coastal horned lizards avoid areas occupied by Argentine ants (A. V. Suarez and T. J. Case, *unpublished data*). It is possible that Argentine ants influence habitat selection of horned lizards in addition to diet. At Torrey Pines, an area that is fragmented and heavily invaded by Argentine ants, horned lizards occur at low densities (R. Fisher and T. J. Case, *unpublished data*). Lizards with more general diets, such as *Sceloporous occidentalis* and *Uta stansburiana,* are less affected by Argentine ants (R. Fisher and T. J. Case, *unpublished data*).

The decline of coastal horned lizard abundance in California (Jennings 1988) is likely due to a combination of habitat loss and the elimination of native ants by Argentine ants in the remaining habitat. Argentine ants penetrate into natural areas through surrounding urban edges where they are more abundant (Suarez et al. 1998). This edge effect compounds detrimental effects associated with a reduction of habitat, including an increased vulnerability to stochastic processes of extinction. Without proper management to prevent the penetration of Argentine ants into natural areas, small reserves such as the Torrey Pines Extension may not support viable populations of horned lizards.

The negative effect of exotic ants on horned lizards is probably not unique to Argentine ants and coastal horned lizards in southern California. Horned lizards are common throughout the southwest and may be detrimentally affected by other exotic ant species such as the red imported fire ant (*Solenopsis invicta*) that is sympatric with *Phrynosoma cornutum* in eastern Texas and displaces many native ants, including harvester ants (Porter and Savignano 1990). It also disrupts patterns of arthropod diversity and abundance (Porter and Savignano 1990) and negatively impacts a variety of vertebrates (Allen et al. 1994).

The indirect effects of the Argentine ant invasion undoubtedly influence other aspects of community dynamics. For example, in addition to being the primary food source for horned lizards, harvester ants are important seed predators (Mares and Rosenzweig 1978, Brown et al. 1979) and seed dispersers (Davidson and Morton 1981, Bond and Slingsby 1983). In South African Cape fynbos shrublands, where Argentine ants have also been inadvertently introduced (De Kock and Giliomee 1989), at least one plant species has suffered reduced seedling emergence and dispersal (Bond and Slingsby 1994).

Our study examined ant community composition and horned lizard prey preference at a relatively coarse scale. While Torrey Pines and Elliot have relatively homogeneous vegetation (chamise–chaparral), Riverside is a heterogeneous mix of disturbed and undisturbed vegetation, including chamise–chaparral, coastal sage scrub, and exotic grasses. It is likely that both ant communities and horned lizards are sensitive to such microhabitat differences. Variability in habitat suitability related to vegetational differences also may be extremely important to management efforts and reserve design for the conservation of horned lizards (A. Alberts, *unpublished data*).

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