# Spatial Patterns in the Abundance of the Coastal Horned Lizard

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**Abstract:** *Coastal horned lizards (* Phrynosoma coronatum*) have undergone severe declines in southern California and are a candidate species for state and federal listing under the Endangered Species Act. Quantitative data on their habitat use, abundance, and distribution are lacking, however. We investigated the determinants of abundance for coastal horned lizards at multiple spatial scales throughout southern California. Specifically, we estimated lizard distribution and abundance by establishing 256 pitfall trap arrays clustered within 21 sites across four counties. These arrays were sampled bimonthly for 2–3 years. At each array we measured 26 "local" site descriptors and averaged these values with other "regional" measures to determine site characteristics. Our analyses were successful at identifying factors within and among sites correlated with the presence and abundance of coastal horned lizards. These factors included the absence of the invasive Argentine ant (* Linepithema humile*) (and presence of native ant species eaten by the lizards), the presence of chaparral community plants, and the presence of sandy substrates. At a regional scale the relative abundance of Argentine ants was correlated with the relative amount of developed edge around a site. There was no evidence for spatial autocorrelation, even at the scale of the arrays within sites, suggesting that the determinants of the presence or absence and abundance of horned lizard can vary over relatively small spatial scales (hundreds of meters). Our results suggest that a gap-type approach may miss some of the fine-scale determinants of species abundance in fragmented habitats.*

Patrones Espaciales en la Abundancia del Falso Camaleón Costeño

**Resumen:** *El falso camaleón (* Phrynosoma coronatum*) ha declinado severamente en el sur de California y es un candidato para ser incluido en la lista estatal y federal de especies amenazadas. Sin embargo, se carece de datos cuantitativos sobre la abundancia, distribución y utilización del hábitat. Investigamos los factores determinantes de la abundancia del falso camaleón en múltiples escalas espaciales en el sur de California. Específicamente, estimamos la distribución y abundancia por medio de 256 trampas de cerco colocadas en 21 sitios en cuatro condados. Estas trampas fueron muestreadas bimestralmente durante 2–3 años. En cada sitio medimos 26 descriptores "locales" y promediamos estos valores con otras medidas "regionales" para determinar las características del sitio. Nuestros análisis fueron exitosos para la identificación de factores dentro y entre sitios correlacionados con la presencia y abundancia de falsos camaleones. Estos factores incluyeron la ausencia de la hormiga argentina invasiva (* Linepithema humile*) (y la presencia de especies de hormigas nativas consumidas por los falsos camaleones), la presencia de una comunidad de plantas de chaparral y la presencia de sustratos arenosos. En una escala regional, la abundancia relativa de hormigas argentinas se correlacionó con la cantidad relativa de bordes en desarrollo alrededor del sitio. No hubo evidencia para autocorrelación espacial, aún en la escala de conjuntos dentro de los sitios, lo que sugiere que los factores determinantes de la presencia/ausencia y abundancia del falso camaleón pueden variar en pequeñas escalas espaciales (cientos de metros). Nuestros resultados sugieren que una aproximación de tipo espacial puede pasar por alto algunos de los determinantes de escala fina de la abundancia de especies en hábitats fragmentados.*

## Introduction

One goal in ecology is to understand and predict species abundance over space and time. The national Gap Analysis Program (1997; Scott et al. 1993) operates on the premise that, at least for common species and at broad spatial scales, a knowledge of land cover can be used to predict the distribution of vertebrate species, and that these predictions will be useful to land managers who must make decisions on where and how to protect these species. Many land-use decisions are made at the level of local government through the planning efforts of cities and counties. These municipalities sometimes band together into large cooperative entities to guide more regional decisions. It is an open question, however, the degree to which the gap approach—a habitat-based method for predicting species occurrences—will be successful when applied to finer spatial scales, to highly fragmented landscapes with much edge between cover types, and to species that have already become so rare that their present-day retracted ranges may reflect a large stochastic component.

Moreover, the type of vegetative cover at a particular point or area may be less revealing about a species' occurrence than the context of the area's position, the vegetation types of adjacent areas, or the area's degree of isolation from other patches. Empirical evidence shows that local animal populations persist longer in large patches of suitable habitat than in small patches and also in patches close to other suitable patches than in patches more isolated from neighbors (Lande 1987; Bolger et al. 1991; Stacy & Taper 1991). The importance of a single patch of a particular cover type in sustaining a species' population thus may depend on where that patch occurs with respect to the configuration of neighboring patches. Consequently, an analysis of spatial patterns in the abundance of a particular species should consider several hierarchical spatial levels.

An additional complication in deducing a habitat-affinity model for any particular species from spatial data is the problem of spatial autocorrelation (Cressie 1991; Legendre 1993; Roxburgh & Chesson 1998; Lennon 2000; Ver Hoef et al. 2001). Spatial autocorrelation is the tendency for random variables to covary as a function of their location in space, which violates the assumptions of classical linear regression. Therefore, it is imperative to determine the spatial range of autocorrelation in the data and factor this into the analysis.

We investigated the determinants of abundance for the coastal horned lizard (*Phrynosoma coronatum*) at two spatial scales in southern California. Coastal horned lizards have undergone severe declines in California in recent years and are a candidate species for state and federal listing under the Endangered Species Act (Jennings & Hayes 1994). Although habitat loss is considered the major factor in their decline (Jennings & Hayes 1994), a specialized diet may make coastal horned lizards particularly sensitive to in-

vasion by exotic ants (Pianka & Parker 1975; Montanucci 1989; Suarez et al. 2000). Introduced from South America earlier this century, Argentine ants (*Linepithema humile*) have spread throughout much of coastal California (Suarez et al. 2001) and displaced native ants that dominate the diets of coastal horned lizards (Suarez et al. 1998; Suarez et al. 2000). In addition, previous work suggests that Argentine ants are not a suitable replacement food for the native ants they displace (Suarez et al. 2000) and that hatchling horned lizards cannot persist on diets of arthropods typical of invaded communities (Suarez & Case 2002). We examined how local variables (slope, substrate, plant species composition, and ant species composition) versus landscape-level variables (latitude, area, isolation, and degree of urbanization) predict horned-lizard presence, abundance, and juvenile recruitment within and across 21 sites in southern California.

## Methods

### Spatial Sampling

We measured horned-lizard abundance at two scales. Our basic unit of sampling was an "array" clustered into "sites." We expected differences in scrub composition to be associated with a broad-scale north-south axis (latitudinal climate gradient), an east-west axis (elevational and rainfall gradient), and a natural land–urbanized land axis associated with differing degrees of fragmentation of natural lands (Westman 1981; Keeley & Swift 1995; Bolger et al. 1997). Thus, we selected sites to span these three dimensions with replication. Because arrays are potentially attractive to vandals and poachers, however, we also chose sites with restricted public access. The study sites ranged from sea level to elevations over 680 m (Table 1) and incorporated the diversity of natural habitat types present on the coastal slope of southern California. Locations of sites are shown in Fig. 1, and a complete description of each is provided by Fisher and Case (2000*a*). Sites that were physically close together (e.g., Torrey Pines 1 and 2 or Chula Vista 1 and 2) were typically separated by major highways.

Each array consisted of seven 18-L (5-gallon) buckets (pit-fall traps) connected by shade-cloth drift fences (15-m arms) positioned in the shape of a Y. When necessary, the arms of the array made gentle bends around trees, shrubs, and boulders (Fig. 1; Case & Fisher 2001). The arrays were efficient and effective at capturing small vertebrates (Gibbons & Semlitsch 1981; Fisher & Case 2000*a*,2000*b*), including horned lizards whose daily movement patterns would cause them to encounter the arrays regularly (A.V.S., unpublished data). We set up 256 arrays at 21 sites (Table 1). For 18 of these sites, sampling began in the spring of 1995. For 3 others (University of California Irvine, Santa Margarita, and Tijuana slough), sampling did not commence until the spring of 1996.

**Table 1. Study sites and regional-scale characteristics measured at each site of pitfall-trap arrays.**

| Site number and name[a] | No. of arrays | Mean elevation (m) | Landscape size (km²) | Edge index[b] | Total lizards |
|---|---|---|---|---|---|
| 1 Tijuana Slough | 15 | 27 | 11.40 | 0.48 | 74 |
| 2 Marron Valley | 9 | 409 | 243.00 | 0.00 | 0 |
| 3 Little Cedar Ridge | 9 | 403 | 243.00 | 0.00 | 76 |
| 4 Chula Vista 1 | 7 | 99 | 0.38 | 1.50 | 0 |
| 5 Chula Vista 2 | 9 | 126 | 2.16 | 1.50 | 0 |
| 6 Point Loma Reserve | 17 | 53 | 5.48 | 0.38 | 0 |
| 7 Sweetwater Reserve | 10 | 108 | 99.29 | 0.00 | 63 |
| 8 Elliot Reserve | 17 | 195 | 120.00 | 0.92 | 50 |
| 9 Torrey Pines State Park 1 | 10 | 99 | 1.47 | 0.83 | 4 |
| 10 Torrey Pines State Park 3 | 15 | 44 | 1.47 | 0.38 | 0 |
| 11 Torrey Pines State Park 2 | 10 | 83 | 0.79 | 2.00 | 29 |
| 12 Wild Animal Park | 20 | 219 | 397.00 | 0.75 | 92 |
| 13 Santa Margarita Reserve | 5 | 308 | 42.00 | 0.13 | 0 |
| 14 Lake Skinner | 17 | 479 | 103.00 | 0.10 | 47 |
| 15 Starr Ranch | 17 | 431 | 461.02 | 0.00 | 0 |
| 16 Rawson | 10 | 627 | 103.00 | 0.00 | 47 |
| 17 Irvine Reserve | 5 | 58 | 1.11 | 1.75 | 0 |
| 18 North Hills | 10 | 555 | 11.54 | 0.08 | 4 |
| 19 Limestone Canyon | 17 | 393 | 40.52 | 0.08 | 61 |
| 20 Motte Rimrock Reserve | 10 | 574 | 7.20 | 0.40 | 28 |
| 21 Lake Perris | 17 | 510 | 40.95 | 0.32 | 3 |

[a]Sites are listed from south to north; site numbers corresponds to those in Fig. 1.
[b]Range 0–2: 0, completely surrounded by native vegetation; 2, surrounded by urbanization (see methods, regional variables).

The placement of arrays within sites was haphazard, with a few constraints. The center points of arrays were at least 100 m apart. Results of a separate study of radiotracked horned lizards at two of our study sites (University of California Elliot Reserve and Torrey Pines 2) suggest that home-range sizes are about 0.1 km². Hence, a typical home range might span one or two arrays (A.V.S. et al., unpublished data). The number of arrays per site varied from 5 to 20. Small habitat fragments had fewer arrays than large sites in contiguous natural habitat, so sampling effort was adjusted to site area. It was logistically impossible to sample the largest core areas and the small areas on a per-unit-area measure. Although a few arrays were placed in habitat types bordering scrub (i.e., grassland, riparian habitats, oak woodland), these habitat types were not as effectively sampled as the scrub habitat types (coastal sage scrub and chaparral) that comprise the main focus of the study and are the dominant upland habitats of the study area.

Once established, a site was sampled each morning between 0700 and 1100 hours for 10 consecutive days. The traps were then closed and reopened about 6 weeks later. About one-third of the sites were sampled simultaneously and then closed when the next third were sampled, and so on, finally rotating back to the original one-third of the sites. This rotation schedule was repeated from 1995 to 1998. The average number of sample days for a site was 130 (range, 100–160).

Each animal falling into a trap was individually marked, weighed, measured to the nearest millimeter (snout to vent length), and sexed. Individuals under 59 mm were considered juveniles (Goldberg 1983; Fisher & Case 1997). Although we focused on the coastal horned lizard, the arrays proved effective in capturing a variety of reptiles and amphibians, with 17 families represented in over 30,000 captures (Case & Fisher 2001; Fisher & Case 2000a,2000b). The animals captured were individually marked (except for a few species for which there are no adequate marking techniques) either by toe or scale clipping (snakes) and then released. Individuals that died were preserved as vouchers and will be deposited in the California Academy of Sciences herpetological collection. Our protocols ensured that the majority of the animals captured remained alive when the traps were open, and we checked traps once every 24 hours in the morning.

**Explanatory Independent Variables**

For the purposes of measuring relevant habitat variables influencing species occurrence and abundance, we distinguished two spatial levels: within-site and among-site. Individuals will respond in terms of their local movements and probability of surviving to local variables at the scale of a few home-range sizes—the within-patch descriptors—which we measured at the scale of each array. At the among-site or regional spatial scale, sites were characterized by their overall area and mean latitude, longitude, elevation (at the centroid of the arrays),
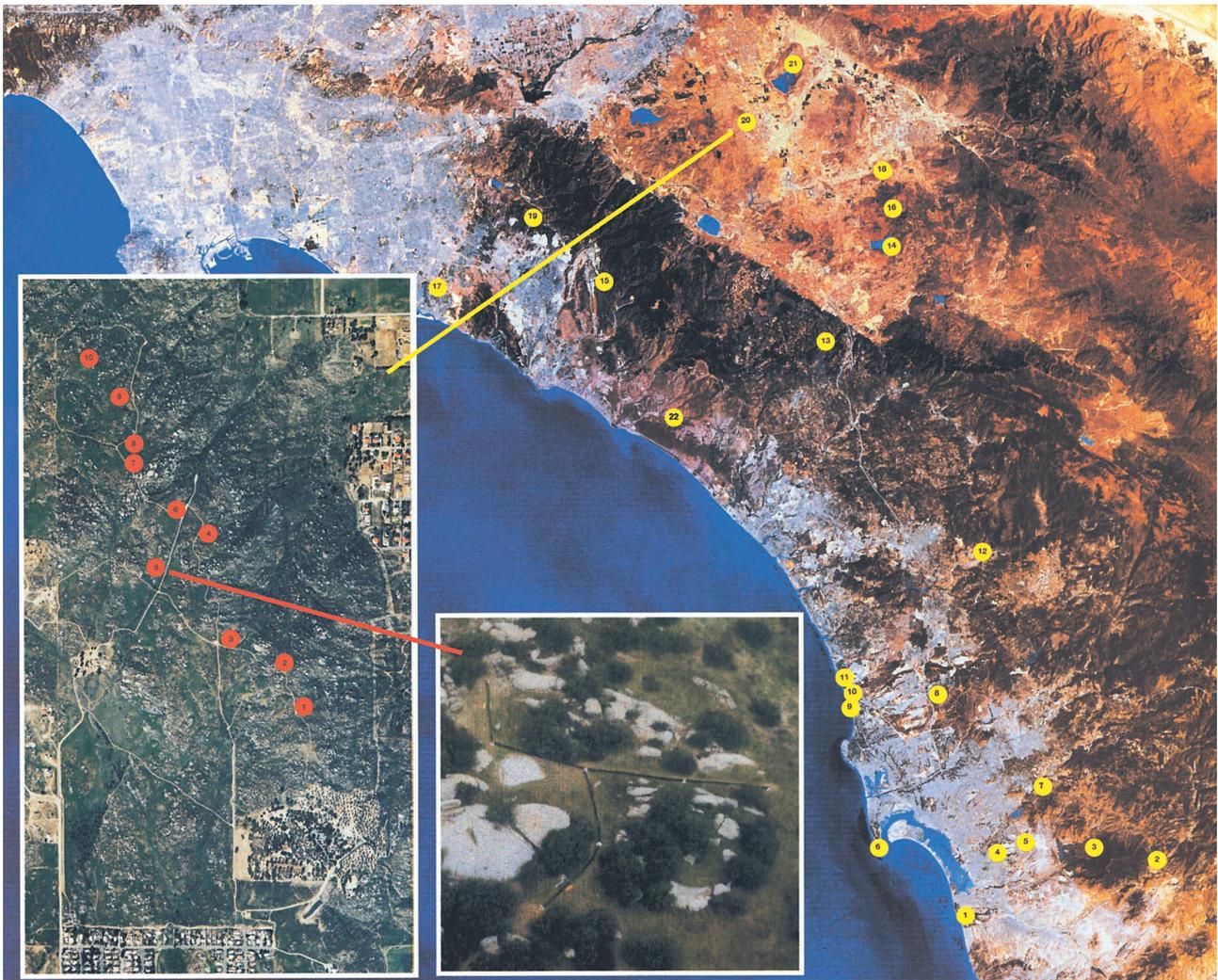
*Figure 1. Satellite photo of southern California showing the locations of each of the study sites (1 cm = 8 km); numbers refer to names in Table 1. Inset with 10 points is an aerial photo of one study site, Motte Rimrock Reserve, with dots showing the location of each array (1 cm = 200 m). The close-up is another aerial photo showing a single array, which consists of seven pitfall traps connected by drift fence (length of each arm is 15 m). Numbers refer to sites listed in Table 1.*

amount of urban edge, and predominant vegetation characteristics averaged across the arrays.

### LOCAL VARIABLES

At the local level we determined the latitude, longitude, and elevation with a global positioning system receiver (with real-time differential). We used a protractor and compass to determine slope and aspect. We measured the flora and vegetation at each array during the first year of sampling with two 25-m orthogonal line transects (Sawyer & Keeler-Wolf 1995). These transects were north and south of the center bucket of each array, and data were collected every 0.5 m along the transect for plant species, canopy height, soil type, and litter depth. Then we determined the proportion of coastal sage scrub and chaparral species based on the typical plant indicators of these two habitat types (Holland 1986). At each array we characterized the soil type into six categories: sandy soil, bare rock, organic soil, moss, leaf litter, and cryptogramic crust.

Finally, during April–June 1997, we determined the relative abundance (three categories: none; rare, 1–10 individuals observed; common, >10 individuals observed) of the invasive Argentine ant and three groups of native ants at each array by visual searches within the buckets. The native ants targeted for survey were harvester ants ( genera *Pogonomyrmex* and *Messor*, subfamily Myrmicinae, primarily seed predators), carpenter ants ( genus *Camponotus*, subfamily Formicinae, generalist predators, frequently nest in wood), and the genus *Crematogaster* (subfamily Myrmicinae). Harvester and carpenter ants are both conspicu-

ous aboveground foragers, whereas *Crematogaster* are typically more associated with vegetation. All three categories of ants are competitively displaced by Argentine ants (Ward 1987; Human & Gordon 1996; Holway 1998*a*; Suarez et al. 1998). The harvester and carpenter ants include the largest ant species in scrub communities, and both groups are commonly eaten by adult horned lizards (Suarez et al. 2000). One site, Tijuana Estuary, is unique in that a species of *Formica* (subfamily Formicinae) is the most abundant and dominant ant and is eaten by the lizards in place of harvester or carpenter ants (A.V.S., unpublished data). Subsequently, at this site this species was lumped into the carpenter ant category. *Crematogaster* are smaller and are the most common prey item in the diets of juvenile and hatchling horned lizards (Suarez & Case 2002). At 103 of the arrays (two-thirds of the sites), we also quantitatively measured ant abundance using pitfall traps (techniques described by Suarez et al. 1998). These more quantitative estimates of the ground-foraging ants were highly correlated ($p < 0.0001$ for Argentine ants and harvester ants and $p < 0.002$ for *Camponotus*) with our categorical measures based on visual searches. A summary of the local variables and their units is provided in Table 2.

### REGIONAL VARIABLES

We characterized each site by the average (across array) measures of the local variables. We also added three new variables: (1) area of the site sampled, (2) index of urban edge around the site, and (3) area of the undeveloped landscape around the site (Table 1). We determined the first two of these variables by drawing 500-m-diameter circles around each array and then connecting the arrays of a site into a convex polygon. We determined the area within this polygon that contained open space using the program Topo USA (DeLorme) and considered it the sampled area. The perimeter of this polygon was divided into 500-m segments, and each of these segments was scored as natural lands/intact habitat (score 0), disturbed habitat including roads or agriculture (score 1), or urban/industrial/suburban lands (score 2). These scores were averaged to determine a weighted edge index for each site. We determined the last variable by drawing a polygon around the arrays of a site with the program Topo USA (DeLorme). The polygon extended to any borders or barriers fragmenting the habitat landscape the arrays were within. Variable 1 and 3 were calculated in square kilometers.

### Statistical Analyses

The proportion of recaptured animals proved too low to apply mark-recapture population estimates: after 3 years the average proportion of recaptures was only 17%, with a range of 0–47% across sites. Instead we used the total numbers of individuals captured in each array as our measure of abundance. The individuals were summed across sample periods for each year. The sum was divided by the number of trapping days to produce a capture rate for each array. Capture rate was log-transformed so that we could use parametric assumptions. At one site (Marron Valley) an extensive brush fire in the first year denuded all vegetation, so it was excluded from the analysis.

Exploratory data analysis revealed that 99.6% of the total variance in log capture success was due to within-year variation and only 0.4% to among-year variation. Consequently, we summed capture success across the 3 years to get an overall capture rate for each site to serve as the dependent variable in subsequent analyses. Of the 256 arrays, 169 of those (about two-thirds) had no horned-lizard captures over the 3 years, and we never observed any horned lizards incidental to our sampling at these arrays. In addition, 86.4% of the variance in capture rate was due to within-site variation and only 13.6% to among-site variation. We thus envision the abundance of horned lizards as a hierarchical process. First, there is an absence/presence process (0–1) that determines whether or not horned lizards will occur at an array. Then, given that they occur, another process controls abundance. The explanatory variables that affect each process may be different. We therefore conducted two separate analyses with these two processes in mind.

First, we ignored arrays in which no lizards were trapped and concentrated on arrays where horned lizards occurred (87 arrays across 13 sites). We then followed the procedure outlined by Ver Hoef et al. (2001). We first assumed that errors were independent and performed a stepwise regression with a $p$ value to enter and $p$ value to remove of 0.05. The usual test statistics ($F$ values) are here invalid to the extent that the residuals are autocorrelated (Godway & Cressie 1990). But the effect is such that any covariates included in the final model at this stage may later become significant once autocorrelation in the residuals is properly accounted for, but any variables excluded at this preliminary stage cannot later become significant when autocorrelation is assumed (Cressie 1991; Legendre 1993; Lennon 2000).

We then used a regression model that included autocorrelation and the covariates that were significant in the previous analysis. We assumed a spherical model for a variogram describing the autocorrelation and used spatially restricted maximum likelihood (SRML in SAS PROC MIXED) to estimate all parameters. This model assumes isotropy; that is, the autocorrelation and variogram depend only on distance, not direction or spatial position. To determine whether isotropy represented a reasonable assumption, we produced two-dimensional correlograms using the Matlab programs in EasyKrig 2.1. We

**Table 2.   Explanatory variables measured in the vicinity of each pitfall trap array.**

| Type of variable | Measurement* |
|---|---|
| Location | latitude (degrees) |
| | longitude (degrees) |
| | elevation (m) |
| | slope (degrees) |
| | aspect (degrees) |
| Vegetation structure | mean canopy height (m) |
| | shrub index (hits on transect) |
| | grass and herbs index (hits on transect) |
| Flora (based on all line-transect hits of plants) | typical coastal sage-scrub shrubs (%) |
| | typical chaparral shrubs (%, log) |
| | trees (height over 3 m, %; could not be normalized) |
| | grass and herbs (%, log) |
| | other (%) |
| | total vegetative cover (%) |
| Soils (based on all line-transect hits at ground) | frequency of leaf litter (log) |
| | frequency of sandy soil (log) |
| | frequency of cryptogamic soils (log) |
| | frequency of organic soils (log) |
| | frequency of moss |
| | frequency of bare rock |
| Ants (species scored) | Argentine ants (*Linepithema humile*) |
| | harvester ants (includes *Messor* and *Pogonomyrmex*) |
| | *Crematogaster* |
| | carpenter ants (*Camponotus*) |

*Units and transformation used to normalize the variable are in parentheses.*

did not detect obvious directional differences in the spatial patterns of autocorrelation. A general discussion of SRML is provided by Cressie (1991). To explore presence-absence, we used logistic regression and followed a forward stepwise process with the same local variables as for the multiple regression.

At the regional scale, all 21 sites were treated as independent. Site averages (across all arrays) for each of the independent variables were calculated. These averages were used with the three site-specific variables in a stepwise multiple linear regression with a *p* value to enter and remove of 0.10. In addition, we produced a kriged surface map of horned-lizard abundance (log capture rate +1) over the southern California region spanned by our study sites. Point-to-point universal kriging (Ver Hoef 1993) was performed on the 21 sites in Arc View (ESRI) through a least-squares fit to an exponential variogram (Kriging Interpolator 3.2, ArcView Spatial Analyst extension, M. Boeringa, Gemeentewaterleidingen Amsterdam, the Netherlands). We used a fix radius and a grid divided into 0.0101 decimal degrees. Finally, because juveniles potentially have different activity periods, diet (Suarez et al. 2000), and predators, we repeated the stepwise multiple linear regression at the regional scale. To do this, we used the proportion of lizards captured that were juveniles as the dependent variable to examine the effect of the site-independent variables on recruitment.

## Results

### Influence of Habitat at the Local Scale

#### ABUNDANCE

We captured 578 lizards. At the 13 sites with horned lizards, we detected between 3 and 92 lizards per site (Table 1; Fig. 2). Sites with no or few captures one year typically had few captures across all years. Also, different sites showed different temporal patterns, indicating a significant site-by-year interaction. Of the 28 explanatory variables, only 4 were retained in the stepwise model when we considered only arrays and sites that had captures: (1) presence of organic soils, (2) presence of Argentine ants (negatively associated with horned-lizard captures); (3) chaparral floristic components (positively associated); and (4) percentage of trees. We checked the residuals for outliers and homoscedasticity for the model as a whole and from leverage plots for each of the dependent variables. No outliers were observed, and the residuals were approximately normal except for the leverage test on the percentage of trees. The frequency distribution of this variate was highly skewed because the majority of sites had no trees. Hence, this variate was eliminated from the model. The resulting model explained about one-third of the overall variance in capture rates (Table 3).
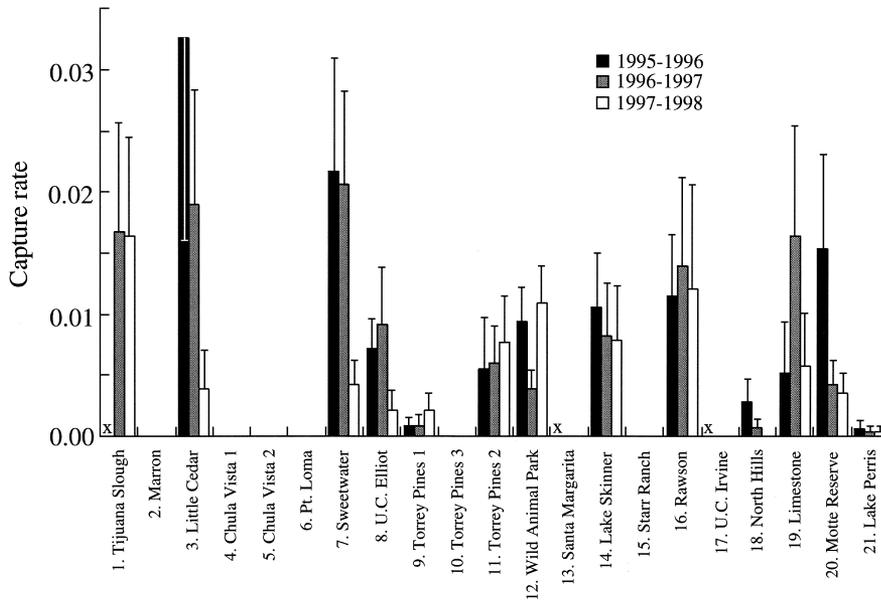
*Figure 2. Average capture success of horned lizards across all seasons by site and year (with 1 SE). An x indicates that a site was not sampled in 1995. Numbers correspond to locations in Fig. 1.*

When these three variables were added as covariates to the SAS PROC MIXED, the fitted spherical covariance function, expressed as a variogram (Cressie 1991), was not significantly different from horizontal. That is, for horned lizards, unlike the orange-throated whiptail lizards (*Cnemidophorus hyperythrus*) analyzed by the same system (Ver Hoef et al. 2001), we could detect no significant spatial autocorrelation in capture success rates over these distances (from about 100 m to 100 km). This result was not altered by considering different functional forms for the variogram shape (exponential or gaussian). This same result was obtained even when arrays without captures were added to the analysis. We also constructed variograms individually for the four

sites with horned lizards and the most arrays (Skinner, Elliot, Wild Animal Park, and Limestone Canyon). At this finer scale, we again found no significant pattern of spatial autocorrelation. Consequently, in subsequent analyses we treated each array as independent.

### PRESENCE-ABSENCE

The best stepwise model showed that horned-lizard presence was positively associated with the absence of Argentine ants and the presence of sandy soils and chaparral floristic components (Table 3). This combined model was significant ( *p* value < 0.0001) but accounted for only about 14% of the total variance. Argentine ants were

**Table 3.** Multiple-regression statistics, with log overall capture success at arrays where horned lizards were present as the dependent variable, presence or absence of horned lizards at each array as the dependent variable, and log overall capture success of horned lizards at each site as the dependent variable.

| *Dependant variable* | *Effect* | *Estimate* | *SE* | p |
|---|---|---|---|---|
| Overall capture | log organic soils | −0.87 | 0.182 | 0.0001 |
| success at each | Argentine ants | −0.992 | 0.269 | 0.0005 |
| array | log percent chaparral | 0.366 | 0.159 | 0.025 |
| | intercept | −2.045 | 0.434 | 0.005 |
| | whole model | $n = 87$ arrays | $R^2 = 29.3$ | <0.0001 |
| Presence or | Argentine ants | −1.202 | 0.269 | <0.0001 |
| absence at each | log sandy soil | 1.457 | 0.412 | 0.0004 |
| array | log percent chaparral | 0.901 | 0.228 | <0.0001 |
| | intercept | 1.169 | 0.557 | 0.036 |
| | whole model | $n = 247$ arrays | $R^2 = 14.21$ | <0.0001 |
| Overall capture | *Crematogaster* ants | 0.005 | 0.002 | 0.0297 |
| success at each | *Camponotus* ants | 0.0169 | 0.003 | 0.0002 |
| site | log canopy height | −0.011 | 0.004 | 0.027 |
| | log percent chaparral | 0.004 | 0.002 | 0.037 |
| | intercept | −0.027 | 0.006 | 0.0006 |
| | whole model | $n = 20$ sites | $R^2 = 67.4$ | 0.0013 |

the most highly correlated variable and provided a negative effect. The next most predictive variable was harvester-ant abundance, which, because it was strongly negatively associated and colinear with that of Argentine ants ($p < 0.0001$), did not enter into the multiple logistic regression. Sandy soils were strongly negatively associated with organic soils ($p < 0.0001$), which was one of the selected variables in the multiple regression resulting from the use of abundance data, so the logistic model and the linear regression on abundance identified similar sets of predictors.

### Regional Scale

At the regional scale, we characterized each site by averaging each of the local variables across arrays. These measures were supplemented with three landscape variables describing the amount of natural habitat occupied by the site and the extent that its edge was urbanized or disturbed. We entered four environmental variables in the stepwise multiple linear regression (Table 3): *Crematogaster* ants (positive effect), *Camponotus* ants (positive effect); mean canopy height (negative effect), and percentage of chaparral (positive effect). This total model explained 67.4% of the variance. The sites' latitudes, longitudes, and elevations, and the second-order terms of these spatial variables, were not significant, suggesting that regional trends in horned-lizard abundance cannot be as-

cribed simply to climatic trends paralleling geographic position. A kriged surface of capture success showed low numbers in and near coastal urban centers (Fig. 3).

The urban-edge index we calculated using a method based on a geographic information system (GIS) was itself highly positively correlated with mean abundance of Argentine ants (Fig. 4) and negatively with mean abundance of *Camponotus* ant as measured in the field. These two variables accounted for 64.2% of the variation in the edge index in a multiple linear regression.

Juvenile activity (summed over sites and years) peaked in August, unlike adult activity, which was highest in April (Fig. 5). The overall percentage of juveniles at each site varied from 0 to 71%. Percentage of juveniles (as a dependent variable) was not significantly correlated with the capture rate of all horned lizards. Instead, the Argentine-ant index was the only significantly correlated variable ($R^2 = 58.1\%$, $p > 0.0025$) and had a strong negative effect.

## Discussion

At both spatial levels of analysis we explored, horned lizards were more common in areas with native ants and few or no Argentine ants (i.e., chaparral vegetation) and with porous soils relatively free of organic debris. Their spatial pattern of abundance was patchy at even the smallest spatial scales. This is seen in the absence of spa-
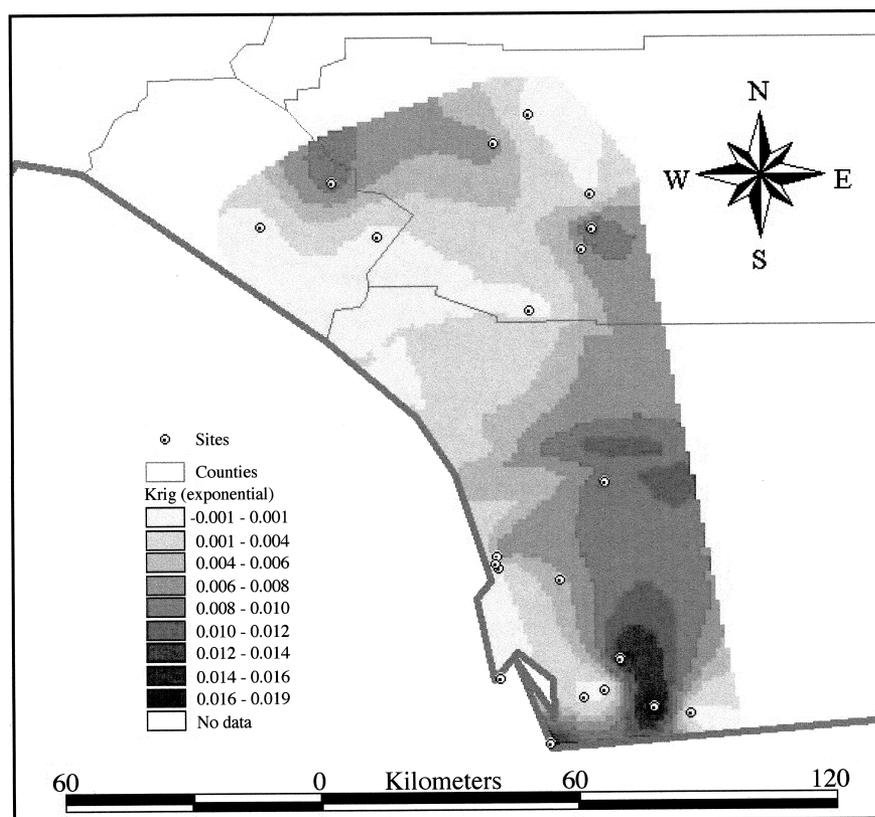


*Figure 3. An interpolated surface of horned-lizard abundance (log capture rate +1). Contours were produced by universal kriging with an exponential variogram.*
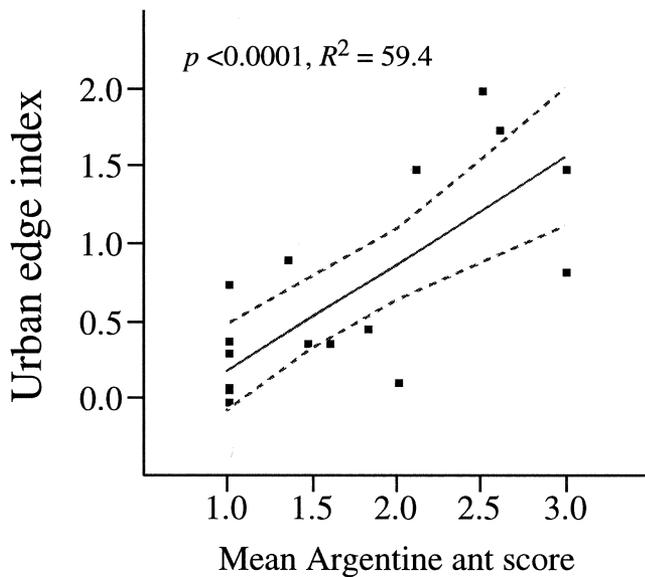
$$p < 0.0001, R^2 = 59.4$$

Figure 4. *Relationship between our measure of urban edge around a site and the average score of Argentine ant abundance across arrays. The edge index ranges from 0 to 2, with 0 indicating that the site was completely surrounded by native vegetation and 2 indicating that the site was surrounded by urban development. Linear-regression statistics and 95% confidence intervals are shown.*

whereas hatchling horned lizards raised on a diet of native ants maintain positive growth rates in the lab, those fed a diet of Argentine ants lose weight, and hatchlings fed arthropods typical of invaded areas average growth rates near zero (Suarez & Case 2002). In our study, we found that a site's Argentine-ant score was highly negatively correlated with the abundance of juveniles. Horned lizards produce large clutches of relatively small eggs (Pianka & Parker 1975; Vitt & Price 1982; Goldberg 1983; Pianka 1986), and the strong disparity in size between hatchlings and adults suggests that high initial growth is necessary for lizards to reach reproductive maturity by the second year. In addition, horned lizards are sit-and-wait predators (Pianka & Parker 1975) and may not be able to adjust behaviorally to the changes in prey diversity typical of invaded habitats. This combination of traits may make coastal horned lizards particularly vulnerable to changes in prey availability associated with the invasion of Argentine ants into scrub habitats in this region (Suarez et al 1998; Suarez et al. 2000) and may explain both the regional and local patterns seen in this study.

The negative association between Argentine ants and several groups of native ants was also found for the ant communities of small habitat fragments in urban San Diego (Suarez et al. 1998). Ant communities were surveyed in 40 isolated fragments of coastal sage scrub in San Diego County, California. The spatial scale of these fragments was much smaller than that of our study. Large fragments used by Suarez et al. (1998) averaged about 100 ha, whereas large sites in our study included several square kilometers of natural habitat. Across these small urban fragments, native ant diversity was positively correlated with the size of the fragment and negatively correlated with the density of Argentine ants and the number of years since the fragment was isolated from continuous scrub land. In addition, other groups of arthropods respond negatively to Argentine ants in these small fragments, even after differences due to edge effects alone are accounted for statistically (Bolger et al. 2000). This suggests that the regional effect of Argentine ants, like those we report here for the coastal horned lizard, may extend to other species as well. It should be
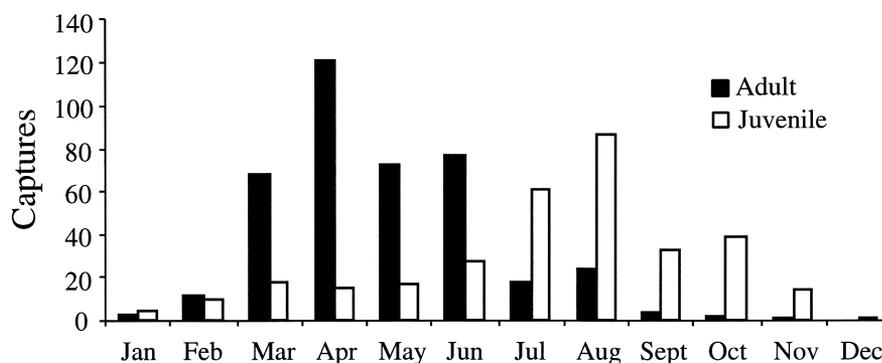
tial autocorrelation in our dependent variables, even at the scale of the array (approximately 100 m). The dependent variables (Table 2) that best explain the relative abundance of horned lizards include the absence of Argentine ants and the presence of native ants, particularly carpenter ants.

Horned lizards avoid eating Argentine ants (Suarez et al. 2000). Analysis of coastal horned-lizard fecal pellets reveal that in areas lacking Argentine ants, the diet of wild horned lizards consists primarily of ants (over 95% of prey intake), particularly harvester ants. In areas where Argentine ants have invaded, however, horned-lizard diets change significantly, incorporating more of other species of arthropods (Suarez et al. 2000). Furthermore,

Figure 5. *Number of captures of adult and juvenile coastal horned lizards by month, summed across sites and years. This figure includes data from additional sites in southern California for which we did not have the ecological measurements to include in the full analysis.*

noted, however, that the success of Argentine ants may be limited by water availability in arid regions (Holway 1998*b*; Suarez et al. 1998), and it remains to be seen if exotic ants will affect coastal horned-lizard populations in more inland sites, where they are farther from human development.

The edaphic correlates identified in our analysis are consistent with horned-lizard behavior. Because horned lizards are relatively slow-moving and depend more on crypsis than speed to escape predation, they seem to prefer soils that provide good traction yet muffle their movements. Several discrepancies between the three analyses we conducted may be due to the close association of groups of the environmental variables. For example, Argentine ants were themselves negatively correlated with the native ant components, significantly so except for *Camponotus*. The urban-edge index, as gathered at the regional scale from GIS layers, was highly correlated with ant community characteristics but was not as predictive of horned-lizard abundance.

The overall explained variance was highest at the largest spatial scale, a feature often seen in spatial analyses (Levin 1992). Many random events influence the particular movements of a single lizard; patterns become more evident when movements are averaged over many individuals and wider areas of land. Because an array may sample only a portion of an individual horned lizard's home range, the environmental attributes at that spot may not adequately describe the entire home range. When characteristics are averaged over several arrays, as in our regional analysis, patterns of relative abundance become clearer. The explained variance in this model was about 67%, compared to 29.3% and 14.2% at the local scale.

We believe that our results have implications for large-scale reserve-design schemes. Because it is impractical and prohibitively expensive to ground-truth all or even most points, a species' presence or absence is typically inferred from habitat characters that can be determined by remote sensing. These images are then categorized into a set of habitats based on conspicuous vegetative and edaphic characters that can be scored from the images. At a regional spatial scale with coarse resolution (1 mapping unit = 1000 ha) and broad habitat types—such as boreal forest, tundra, or desert, as in the Gap Analysis Program—this method is useful for predicting the presence of sets of animal species. Our study shows that some of the best predictors (i.e., ant species) are not obtainable from a remote-sensing venue and that their surrogates that are GIS–based are not as predictive. Similarly, in a study reported elsewhere, Ver Hoef et al. (2001) found that the best predictor of the abundance of orange-throated whiptail lizards (*Cnemidophorous hyperythrus*) in this same system is *Crematogaster* ants, which are also negatively affected by Argentine ants in small urban fragments (Suarez et al. 1998) and at the scale of arrays in this study.

The penetration of exotic species into natural areas can deterministically reduce the effective size of a reserve in proportion to the distance in which they penetrate. Habitat destruction has reduced the total area suitable for populations of coastal horned lizards, and much of the remaining habitat is unsuitable due to the penetration of Argentine ants and the subsequent displacement of the native ant species horned lizards need as prey. In addition, other factors such as increased predator abundance (Crooks & Soulé 1999) may further reduce horned-lizard survivorship in this fragmented system. Although stochastic, demographic, and environmental processes are often invoked as the cause of extinction of isolated populations, our results implicate deterministic processes as major contributors to population declines and as forces that may influence the distribution of species at the landscape level (Caughley 1994; Woodruffe & Ginsberg 1998).

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