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Effect of land cover, habitat fragmentation and ant colonies on the distribution and abundance of shrews in southern California

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Summary

1. Because effects of habitat fragmentation and anthropogenic disturbance on native animals have been relatively little studied in arid areas and in insectivores, we investigated the roles of different land covers, habitat fragmentation and ant colonies on the distribution and abundance of shrews, *Notiosorex crawfordi* and *Sorex ornatus*, in southern California.

2. *Notiosorex crawfordi* was the numerically dominant species (trap-success rate 0.52) occurring in 21 of the 22 study sites in 85% of the 286 pitfall arrays used in this study. *Sorex ornatus* was captured in 14 of the sites, in 52% of the arrays with a total trap-success rate of 0.2. Neither of the species was found in one of the sites.

3. The population dynamics of the two shrew species were relatively synchronous during the 4–5-year study; the peak densities usually occurred during the spring. Precipitation had a significant positive effect, and maximum temperature a significant negative effect on the trap-success rate of *S. ornatus*.

4. Occurrence and abundance of shrews varied significantly between sites and years but the size of the landscape or the study site had no effect on the abundance of shrews. The amount of urban edge had no significant effect on the captures of shrews but increased edge allows invasion of the Argentine ants, which had a highly significant negative impact on the abundance of *N. crawfordi*.

5. At the trap array level, the percentage of coastal sage scrub flora had a significant positive, and the percentage of other flora had a significant negative effect on the abundance of *N. crawfordi*. The mean canopy height and the abundance of *N. crawfordi* had a significant positive effect on the occurrence of *S. ornatus*.

6. Our study suggests that the loss of native coastal sage scrub flora and increasing presence of Argentine ant colonies may significantly effect the distribution and abundance of *N. crawfordi*. The very low overall population densities of both shrew species in most study sites make both species susceptible to extinction in isolated habitat fragments due to environmental stochasticity, and anthropogenic disturbance.

Key-words: Argentine ant, edge effect, habitat fragmentation, population dynamics, shrews.

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Introduction

Because of the rapid fragmentation of natural habitats in many areas, distribution and abundance studies

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over large geographical areas are needed to detect local differences in species habitat preferences. Compared to forested habitats, the effects of reduced habitat size and increase in edge habitat have been relatively little studied in arid areas. In contrast to fragments and edges created in forested landscapes, the vegetation cover, moisture levels and temperatures in habitat fragments in arid landscapes with relatively little vegetation are likely to remain more similar to those of

original continuous habitats (Saunders, Hobbs & Margules 1991).

In this paper, we investigate the occurrence and abundance of shrews in fragmented and continuous habitats in southern California. This area, especially San Diego county, has been recognized as one of the 'hot spots' of threatened biodiversity of fish, mammals and plants in the United States (Dobson *et al.* 1997). The fragmentation of once contiguous habitats in San Diego and surrounding counties throughout the last 100 years as rapid urban and suburban development has led to extinction-limited relictual small mammal populations with limited possibilities for recolonization due to the matrix of habitats constantly inhospitable to the small mammals.

Several studies have examined the effect of habitat fragmentation on rodent communities (Dickman & Doncaster 1987; Bowers *et al.* 1996; Ims & Andreassen 1999) also in coastal southern California (Soulé, Albers & Bolger 1992; Bolger *et al.* 1997; Chase *et al.* 2000). In contrast, little research has been undertaken on the impact of habitat fragmentation on insectivore communities anywhere. Because species differ in body size, diet, physiology and in their demographic responses to local environmental factors, disturbance and in the role of movement in their life histories (Ims & Andreassen 1999), a landscape that appears fragmented for one species may be continuous for another.

Shrews of the genus *Sorex* are widely distributed and abundant in many parts of the Northern Hemisphere. *Sorex* shrews are known for their high metabolic rate compared to similar-sized other mammals (Taylor 1998). Also, the population turnover is rapid in *Sorex* shrews (Rudd 1955) and thus, during late fall, winter and early spring, the populations consist exclusively of immature animals born during the previous summer (Newman 1976).

In our study sites in southern California, only two species of shrews occur. The ecology of both species is poorly known. The ornate shrew, *Sorex ornatus* (Merriam 1895), is morphologically a typical member of the genus *Sorex*. Unlike *Sorex* shrews in general, however, torpor-like behaviour has been reported in this species (Newman & Rudd 1978). *Sorex ornatus* is also known to live in stable groups in the wild during a non-reproductive period (see Rychlik 1998). *Sorex ornatus* occurs in California from approximately 39°N latitude southward discontinuously to the tip of Baja California (Owen & Hoffman 1983). Several subspecies are currently recognized, some of which are considered endangered (Owen & Hoffman 1983; Maldonado *et al.* 2001). The subspecies occurring in our study areas is *Sorex ornatus ornatus* (Owen & Hoffman 1983). The typical weight of adult *S. ornatus* in our study areas is 5 g (Juha Laakkonen, unpublished data).

The only species of the genus *Notiosorex*, the grey shrew, *Notiosorex crawfordi* (Coues 1877), is found throughout the south-western United States and northern Mexico inhabiting more xeric habitats than

most other shrews (Armstrong & Jones 1972). *Notiosorex crawfordi* is capable of entering short-term torpor (Lindstead 1980). Genetic differences are known between *N. crawfordi* from different parts of its wide distribution area, and three subspecies/species are recognized based on morphology (Carraway & Timm 2000). The *N. crawfordi* from our study sites belongs to the *Notiosorex crawfordi crawfordi*. The typical weight of adult *N. crawfordi* in our study areas is 3 g (Juha Laakkonen, unpublished data). *Notiosorex crawfordi* has been reported to be more social than other shrews and to live in high densities on small areas (Hoffmeister & Goodpaster 1962). Most ecological studies of this species have been carried out outside California (Armstrong & Jones 1972; Simons, Szaro & Belfit 1990), or are based on studies of relatively few individuals (Fisher 1941; Cunningham 1956; Coulombe & Banta 1964).

The purpose of this study was to compare the spatial variation in abundance and distribution of *S. ornatus* and *N. crawfordi* in fragmented and continuous habitats in southern California. The effect of abiotic and biotic factors on the ecology of shrews was analysed in an effort to gain insight to the habitat requirements of these shrew species, and to study the effect of fragmentation of habitats on the distribution of these shrews. By measuring relevant habitat variables at each trapping array instead of mapping gross vegetation communities, we hoped to gain information at two spatial levels, within-site and between-site. We hypothesize that due to the differences in their morphological and physiological characteristics, which in turn may affect their foraging frequency, the two shrew species differ in their response to fragmentation, land-cover variables and environmental factors.

Materials and methods

SPATIAL SAMPLING AT 22 STUDY SITES

We sampled the shrew abundance in 22 study sites (Fig. 1, Table 1) at two scales: the trapping arrays and the sites. The study localities range from sea level to elevations over 680 metres, and incorporate the diversity of habitat types present on the coastal slope of southern California. We expect differences in habitat composition to be associated with a broad scale north-south axis (latitude climate gradient), an east-west axis (elevational and rainfall gradient), and a natural land/urbanized axis associated with differing degrees of habitat fragmentation of natural lands (Westman, O'Leary & Malanson 1981). Consequently, sites were selected to span with replication these three prime dimensions. Since trapping arrays are potentially attractive to vandals and poaching, it was also necessary to ensure that the chosen sites had restricted access from the public.

A complete description of each site is in Fisher & Case (2000). The habitats include coastal sage scrub, coastal sand dunes, maritime succulent scrub, chaparral, oak woodland and coniferous forest types. Many study

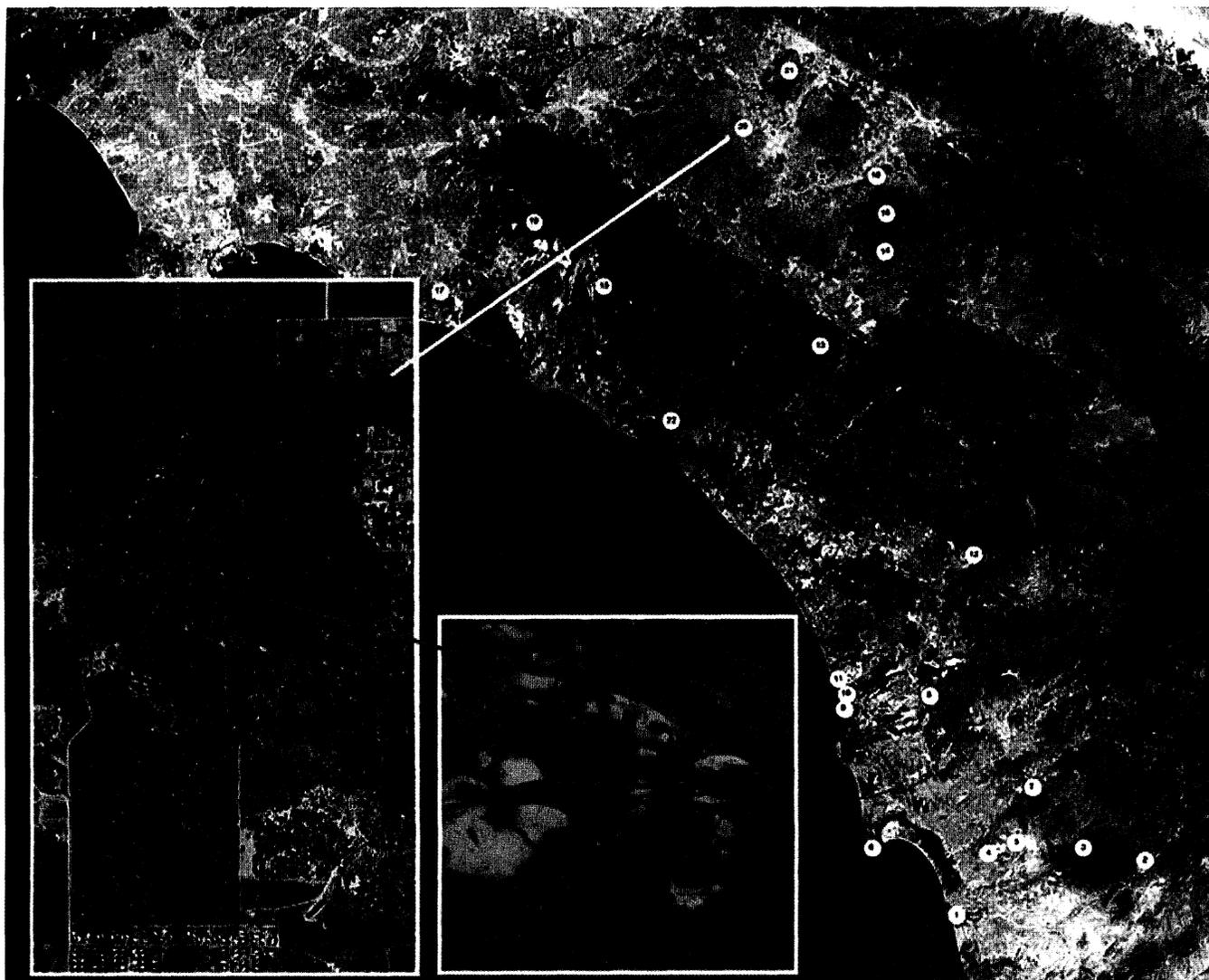


Fig. 1. Satellite photograph of southern California showing the locations of each of the 22 study sites (1 cm = 8 km). Names and details of each site are shown in Table 1. Inset is an aerial photo of one study site, Motte Rimrock Reserve, with dots showing the locations of each array (1 cm = 200 m). The smaller inset is another aerial photo showing a single array, which consists of seven pitfall traps connected by a drift fence (length of each arm = 15 m).

sites were dominated by California sagebrush (*Artemisia californica*), chamize (*Adenostoma fasciculatum*), buckwheat (*Eriogonum fasciculatum*), brittle bush (*Encelia farinosa*), lemonadeberry (*Rhus integrifolia*), black sage (*Salvia mellifera*), lauren sumac (*Malosma laurina*) and/or scrub oak (*Quercus berberidifolia*) (Sawyer & Keeler-Wolf 1995). Many study sites included patches of grassland. Sage scrub and chaparral habitats were most effectively sampled because most arrays were in these habitats which were the main focus of this study. The inland areas experience higher evapotranspiration during the summer than the coastal areas, resulting in differences in vegetation gradients (Westman *et al.* 1981). The boundaries of the mainly coastal study areas representing isolated habitat fragments are delineated by urban and suburban development. The inland areas are more continuous, relatively undisturbed habitat. Sites which are physically close together (e.g. Torrey Pines 2 and 3 or Chula Vista 1 and 2) are separated typically by major highways.

TRAPPING METHODS

Each of these study sites contained 5–30 pit-fall drift-fence arrays used originally to capture reptiles for a long-term reptile-monitoring project (Case & Fisher 2000; Fisher & Case 2000). Pitfalls, however, are also generally considered to be the most effective method to capture shrews (Wilson, Russell & Rasanayagam 1996). Smaller habitat fragments had fewer arrays than large natural lands (Table 1). Each array consists of seven 20-litre plastic buckets, connected by shade cloth drift-fences with 15-metre arms in a 'Y' shape, except that the arms are allowed to make gentle bends around trees, shrubs and boulders to minimize habitat alteration (see Case & Fisher 2000 for figures). A total of 2002 pitfall traps (individual buckets) in 286 arrays were used. The placement of arrays within sites is haphazard but arrays are at least 100 m apart from their centres. Multiple precautions were taken to reduce field mortality. Each bucket had PVC pipes of assorted sizes

Table 1. The location and geographical variables of the study sites from the largest area to the smallest one. The edge index was calculated by estimating the size of intact habitat in each site, and dividing that by the number of 500 m sides in each corresponding site that could be fitted to the site without crossing a road (see text for details). The trap-success rate shows the number of individuals caught per 100 trap-nights (a trap-night equals one pitfall left open for 24 h)

Site	Fig. 1 locations	Coordinates	Area of the landscape (km ²) and (no. of arrays)	Sample area (km ²)	Altitude (m)	Trap-success rate		
						Edge index	<i>N. crawfordi</i>	<i>S. ornatus</i>
Starr Ranch	(15)	117-48 33-60	461	5-02	252-530	0	0-86	0-57
Wild Animal Park	(12)	117-01 33-09	397	1-13	141-255	0-75	1-00	0-43
Little Cedar Ridge	(3)	116-90 32-61	243	1-02	338-443	0	0-43	0-14
Marron Valley	(2)	116-82 32-59	243	3-02	369-469	0	0-23	0-06
U.C. Elliott Reserve	(8)	117-11 32-89	120	1-42	166-218	0-92	0-20	0-06
Rawson	(16)	117-02 33-63	103	2-55	543-686	0	0-21	0-04
Lake Skinner	(14)	117-08 33-57	103	6-36	452-514	0-1	1-00	0-09
Sweetwater Reserve	(7)	116-97 32-72	99	0-90	90-197	0	0-86	0-14
St. Margarita Reserve	(13)	117-16 33-46	42	0-38	243-265	0-125	0-86	1-00
Lake Perris	(21)	117-19 33-86	41	8-84	477-536	0-32	0-13	0-00
Limestone Canyon	(19)	117-56 33-72	40	5-98	327-470	0-084	0-43	0-28
North Hills	(18)	117-04 33-70	12	1-99	545-580	0-07	0-70	0-00
Tijuana Slough	(1)	117-13 32-54	11	3-1	0-164	0-476	0-10	0-28
Motte Rimrock Reserve	(20)	117-23 33-80	7	1-88	557-593	0-4	0-57	0-00
Point Loma Reserve	(6)	117-23 32-67	5-5	1-16	22-113	0-38	0-86	0-00
Chula Vista 2	(5)	117-00 32-66	1-5	0-12	87-158	1	0-28	0-00
Torrey Pines State Park 3	(10)	117-24 32-92	1-5	0-79	11-71	0-38	0-11	0-86
Torrey Pines State Park 1	(9)	117-23 32-91	1-5	0-4	92-107	0-83	0-14	0-28
UC Irvine Reserve	(17)	117-83 33-65	1-1	0-24	43-76	1-75	1-40	0-00
Torrey Pines State Park 2	(11)	117-23 32-94	0-8	0-45	54-122	2	0-00	0-00
Chula Vista 1	(4)	117-05 32-64	0-4	0-15	88-106	1-5	0-43	0-00
Camp Pendleton	(22)	117-50 33-34	*	*	0-640	*	0-57	0-28

*Sample locations were spread throughout the habitat on site, which includes a matrix of development impacts. Thus these variables are not comparable.

for cover, cotton balls for insulation and wet sponges for moisture. Insects were also always available.

For 18 of these sites, sampling began in spring 1995 but for four (Camp Pendleton, UC Irvine, Santa Margarita, and Tijuana slough) sampling did not commence until spring 1996. Sampling was conducted at each study site for 10 consecutive days every 6 weeks, spread evenly across all seasons. About one-third of the sites were sampled simultaneously and then closed while the next third were sampled and so on, finally rotating back to the original third of the sites. This rotation was repeated throughout the study period (1995–99). The mean number of trapping days for a site was 196 (range from 100 to 256).

Traps were checked once every 24 h in the morning. The traps were kept closed between the sampling periods. Shrews found live in the buckets were identified and released unmarked, so the number of captures probably includes multiple captures. Besides identification of the species, the array and pitfall of each capture was recorded. The abundance of shrews was measured as captures (both dead and alive shrews), and presented as a trap-success rate (the number of individuals caught per 100 trap-nights; a trap-night equals one pitfall (one bucket) left open for 24 h).

SHREWS

We did not gather information about the sex and age of the live shrews in the field mainly because these are often difficult to determine without necropsy. Shrews found dead were stored in alcohol for taxonomic studies, and sampled later for endoparasites (Juha Laakkonen, unpublished data). Thus, it was possible to gain information about the sex and age of the shrews caught during different seasons. This subset of the total captures was also used to confirm the identification (according to Carraway 1995) of the species by the field workers.

REGIONAL VARIABLES

We characterized each site with three regional 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). The first two of these variables were determined by drawing 500-metre diameter circles around each array and then connecting the arrays of a site into a convex polygon. The area within this polygon that contained open space was determined using the program Topo USA (DeLorme), and was considered the sampled area. The perimeter of this polygon was divided into 500-metre segments and each of these segments was then scored as natural lands/intact habitat (score 0), disturbed habitat including roads, agriculture (score 1), or urban/industrial/suburban (score 2). These scores were then averaged to determine a weighted edge index for each site. The last variable was determined by drawing a polygon around the arrays of a site using the program Topo USA

Table 2. The mean, standard error (SE) and range (minimum and maximum) of the array-specific ($N = 286$) habitat and landscape variables recorded in this study

Variable	Mean	SE	Range
Location			
Elevation (metres)	280.90	12.53	0–686
Slope (degrees)	11.05	0.38	0–40
Aspect (degrees)	–0.23	0.04	–1–1
Vegetation			
Mean canopy height (metres)	1.05	0.12	0–15
Density of shrubs	56.07	1.62	0–95
Density of grasses and herbs	38.99	1.95	0–130
Flora			
% Coastal sage scrub flora	39.17	1.78	0–96
% Chaparral flora	13.78	1.36	0–87
% Trees	5.25	1.09	0–100
% Grass and herbs	20.58	1.41	0–95
% Other	5.40	0.66	0–72
Total % cover	81.46	1.14	0–100
Soils			
Frequency of leaf litter	48.98	1.76	0–100
Frequency of sandy soils	21.25	1.50	0–100
Frequency of cryptogamic soils	3.20	0.38	0–45
Frequency of bare rock	2.41	0.31	0–27
Frequency of organic soils	21.41	1.42	0–96
Frequency of moss	3.32	0.57	0–55

(DeLorme) that extended to any borders or barriers fragmenting the habitat landscape the arrays are within. The area variables were calculated in squared kilometres. We also characterized each site by the average (across array) measures of the local variables (see below).

LOCAL VARIABLES

At the local level, we determined the latitude (degrees), longitude (degrees) and elevation (metres) using a GPS receiver (with real time differential), the slope (degrees) and aspect (degrees) using a protractor and compass (Table 2). Because many microhabitats were present within the study areas, the flora and vegetation were recorded in the vicinity of each array following established protocols of the California Native Plant Society (Sawyer & Keeler-Wolf 1995; Table 2). The flora and vegetation at each array site were measured during the first year of sampling using two 25 m orthogonal line transects. These transects went north and south of the centre of the bucket of each array, and points were taken every 0.5 metres along the transect for plant species, canopy height, soil type and litter depth. Then, the proportion of coastal sage scrub and chaparral species was determined using 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 cryptogamic crust. The Marron Valley site experienced an extensive brush fire in 1995 completely denuding all vegetation; it was therefore excluded from the habitat variable analyses.

ANT COLONIES

During April–June 1997, 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 (harvester ants), carpenter ants and the species *Crematogaster californica* (see Suarez, Bolger & Case 1998) were determined in buckets at each array by visual searches (Fisher *et al.* unpublished data). The effect of the categorical presence of different types of ant colonies to the abundance of shrews was analysed separately from habitat variables.

CLIMATIC FACTORS

The minimum and maximum temperatures during the trapping period were recorded using thermometers placed in each site. The effect of rain was estimated by recording rain on a scale from zero to two depending on the intensity and duration of the rain during the 10-day trapping period (0 = no rain, 1 = moderate rain on 1, or light rain on a few days, 2 = heavy rain at least on 1 day, or moderate rain on several days during the trapping period). Estimation of the effect of rain during the previous 10-day trapping period (6 weeks earlier) of the site was also analysed using the same categories.

DATA ANALYSIS

Between sites

We analysed spatial and temporal variation in the abundance of both shrew species at the 14 study sites where both species occurred using a three-way anova, with the logarithm of the number of individuals per trap night as the dependent variable, and trapping area, year and species as independent variables.

Area and edge effects

Linear regression was used to examine the effect of size of the landscape of each study site, the size of the

area sampled and the disturbance and modification (edge effect) of the habitat on shrew abundance. The trap-success rates were arcsin transformed, and the non-normal independent variables were normalized with a log transformation, including the size of the landscape of each study site and the size of the area sampled. Camp Pendleton study site was excluded from these analyses due to variation in disturbance in that site.

Habitat, climatic and faunal variables

Since arrays are spatially clustered, we needed to determine the degree of spatial autocorrelation in shrew abundance. First, we assumed a general exponential model for a variogram describing the spatial autocorrelation of shrews testing separately all arrays, and only those where shrews occurred (see Cressie 1991; Chapter 2). This variogram was not significantly different from horizontal. That is, for shrews, unlike the case for orange-throated whiptail lizards (*Cnemidophorus hyperythrus*) analysed from the same system (ver Hoef *et al.* 2000), we could detect no significant spatial autocorrelation in capture success rates over these spatial distances (from about 100 m to 100 km). This same result was true even when the zero-capture arrays were added to the analysis. Since no significant autocorrelation was found, the arrays were considered independent and linear and stepwise multiple linear regression analyses were used to analyse the effect of habitat variables on the abundance of the shrews (Tables 3 and 4). The non-normal independent variables were normalized with a log transformation. The explanatory variable cover was excluded from all analyses because it could not be normalized.

The effect of ants on shrew abundance was analysed with categorical Kruskal–Wallis analysis of variance. The Kruskal–Wallis test was also used to analyse the effect of month, rainfall during the 10-day sampling period and rainfall during the previous 10-day sampling period to the abundance of shrews. Linear regression was used to examine the effect of maximum and minimum temperatures to the normalized trapping indices of both shrew species.

Table 3. Linear and stepwise multiple linear regression analyses table for abundance of *Notiosorex crawfordi* in all study areas from 1995 to 1999. Includes all variables that were significant when analysed separately. Abundance is the log transformed number of captures per trap night. VIF = Variance inflation factors

Source	Coefficient	Standard error	T-test	P	VIF
Constant	-1.88353	0.17575	-10.72	0.0000	
Slope	0.01252	0.00646	1.94	0.0546	1.3
Density of scrubs	-0.00126	0.00207	-0.61	0.5447	1.8
% other flora	-0.18525	0.08797	-2.11	0.0371	1.2
% grass and herbs	0.19131	0.09002	2.13	0.0354	2.3
% chaparral flora	0.06664	0.06666	1.00	0.3192	2.0
% sage scrub flora	0.00558	0.00199	2.80	0.0058	2.7
Density of grasses	-0.00257	0.00173	-1.49	0.1397	2.3

$R^2 = 0.23$, Regression $F = 5.72$, $P < 0.001$ ($N = 143$).

Table 4. Logistic regression model of habitat and landscape parameters and abundance of *Notiosorex crawfordi* to account for variation across arrays for the occurrence of *Sorex ornatus* in all study areas from 1995 to 1999. Includes all variables that were significant when analysed separately

Source	Coefficient	Standard error	Coefficient	P
Constant	0.96929	1.04752	0.93	0.3548
Mean canopy height	1.69833	0.64900	2.62	0.0089
Frequency of leaf litter	0.00890	0.00776	1.15	0.2513
% grass and herbs	0.18560	0.35562	0.52	0.6017
Density of scrubs	0.01182	0.00788	1.50	0.1337
Abundance of <i>N. crawfordi</i>	1.17197	0.38552	3.04	0.0024

Deviance = 236.67, $P = 0.01$, d.f. = 189 ($N = 195$).

Except for the autocorrelation analyses (MATLAB®, Mathworks, Natick, MA, USA), Statistix® (Analytical Software, Tallahassee, FL, USA) for Windows statistical software package was used in all analyses. The normality of variables was tested with the Wilk–Shapiro procedure. Throughout this paper, we accept a probability value of < 5% as statistically significant.

Results

TOTAL NUMBER OF CAPTURES

Total sampling effort for the study was 404 327 trap-days. A total of 2752 shrews were captured. *Notiosorex crawfordi* was the numerically dominant species with 2129 captures (77% of the total sample). A total of 623 *S. ornatus* were captured. The total number of shrews caught in any particular study site during the entire study period ranged from 0 to 397 (*N. crawfordi*; from 0 to 381, and *S. ornatus*; from 0 to 123). The overall trap-success rate was 0.68 (pooled data; 0.52 for the *N. crawfordi* and 0.2 for the *S. ornatus*). Only *N. crawfordi* was detected in seven (32%) of the study sites (Chula Vista 1 and 2, Motte, North Hills, Perris, Point Loma, UCI, Table 1). None of the sites had only *S. ornatus*. Neither of the shrew species were found at one (4.5%) of the sites (Torrey Pines 2).

Examination of the sex and age data from the subset of the sample ($N = 137$ for *N. crawfordi* and $N = 75$ for *S. ornatus*) showed that there was no significant difference between the sexes in the numbers they were caught, or the season they were caught (not shown, Juha Laakkonen *et al.* unpublished data). The rapid turnover of shrew populations was also seen in this subset. Thus, the age structure of the population was relatively homogeneous during the winter and spring months when most of the shrews were captured. Shrews born during the previous year were maturing during the early winter, and gravid females were caught from February through May. Juvenile *N. crawfordi* were also captured in late summer, which indicates that the breeding season of this species is longer than that of *S. ornatus*. Within species, pooled data was used in the following analyses.

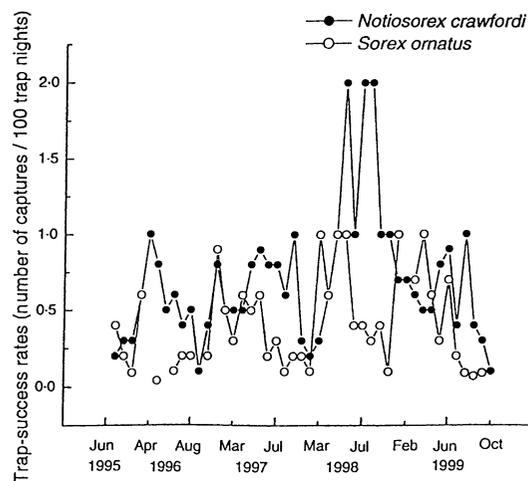


Fig. 2. Captures of shrews, *Notiosorex crawfordi* and *Sorex ornatus*, showed as trap-success rates in the 22 study sites in southern California from spring 1995 to autumn 1999 (pooled data). In four sites the sampling did not commence until spring 1996. The trap-success rate is the number of individuals captured per 100 trap nights (a trap-night equals one pitfall left open for 24 h).

ANNUAL AND SEASONAL DENSITY VARIATIONS

The general annual and seasonal density variations of the shrews are shown in Fig. 2 (pooled data from all study sites). Based on capture rates the population dynamics of *N. crawfordi* and *S. ornatus* were relatively similar during the 4–5-year study period (Fig. 2) except during the late spring and summer 1998. While populations of *S. ornatus* showed the seasonal decline from winter and early spring peak, the abundance of *N. crawfordi* was exceptionally high during this time compared to other years of the study.

Kruskal–Wallis analysis of variance on monthly captures of shrews showed interspecific differences between species. Most *N. crawfordi* were captured in May, April and August (in that order, $P = 0.16$ between months) but there were no significant pairwise differences among the means of different months. Most *S. ornatus* were captured in March, April and May ($P = 0.02$) but there were no significant pairwise differences among the means of different months

(some months were sampled more often than others). Precipitation during the trapping period and during the previous trapping period had a significant positive effect on the number of captures of *S. ornatus* (Kruskal–Wallis test; $P = 0.003$ and $P = 0.02$, respectively) but not on *N. crawfordi* ($P = 0.23$ and $P = 0.16$). Linear regression analyses of the maximum temperature during the trapping period showed a significant negative effect ($P = 0.009$) on the number of captures of *S. ornatus*. The minimum temperature had no significant effect ($P = 0.99$). Neither of these variables had any significant effect on captures of *N. crawfordi* ($P = 0.35$ and $P = 0.92$, respectively).

EFFECT OF YEAR OF STUDY, SITE AND SPECIES

Differences between all three independent variables were highly significant (trapping site $P < 0.001$, year $P < 0.001$, and species $P < 0.001$). Site–species interaction was significant ($P = 0.002$) suggesting that the abundance of the two shrew species depended on the site. The site–year and year–species interactions were not significant ($P = 0.14$ and $P = 0.10$).

EFFECT OF SITE SIZE AND DISTURBANCE

None of the independent variables (size of the study site landscape, size of the area sampled and edge effect) had a significant effect on the number of captures of the two shrew species (not shown). In *S. ornatus*; however, the negative effect of disturbance (edge effect) was approaching significance ($P = 0.06$).

EFFECT OF HABITAT AND LANDSCAPE VARIABLES

N. crawfordi was captured in 242 (85%) of the 286 arrays. The number of captures of *N. crawfordi* in each array varied from zero to 87 (mean 7.47, SE 0.58). This number of captures was divided by the number of days this array was trapped during the study to give an estimate of the abundance of shrews in this array. This value was used as the dependent variable in linear regression analyses. Each habitat and landscape variable was tested separately, and only the significant ones were used in the stepwise and multiple linear regression (Table 3). The final model ($R^2 = 0.20$; regression $F = 17.72$; $P < 0.001$) showed that the percentage of coastal sage scrub flora (Fig. 3a) had a significant positive effect ($P < 0.001$) and other, non-specified flora (Fig. 3b), had a significant negative effect ($P = 0.003$) on the abundance of *N. crawfordi*. We checked the residuals for outliers and normality for the model. One outlier was found (a high slope value in one of the arrays in St. Margarita), and removed from the final analyses.

Sorex ornatus was captured in 150 (52%) of the 286 arrays. The number of captures of *S. ornatus* in each

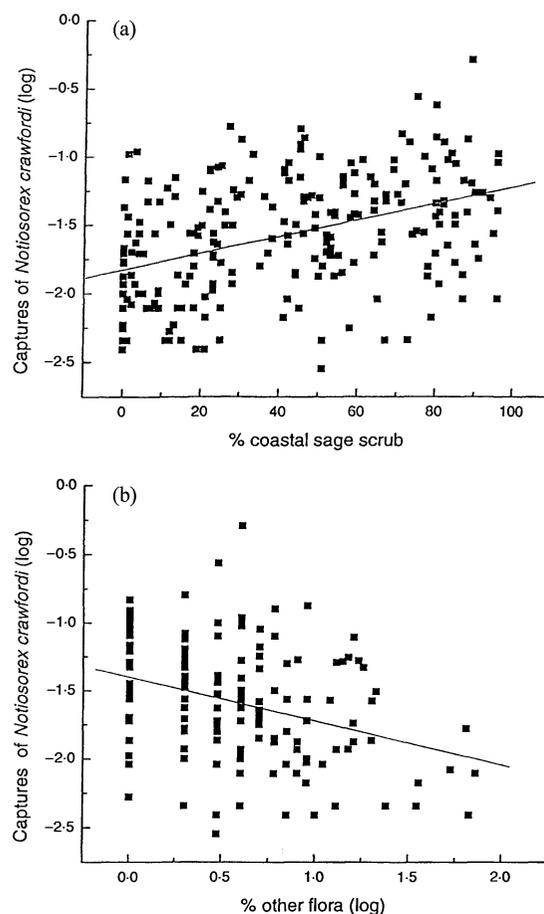


Fig. 3. Regression showing the effect of (a) the percentage of coastal sage scrub flora in an array and (b) the percentage of other flora in an array on the number of captures of *Notiosorex crawfordi* (log transformed trap-success rate = the number of individuals captured per 100 trap nights (a trap-night equals one pitfall left open for 24 h)). Both regressions are statistically significant.

array varied from zero to 23 (mean 2.18, SE 0.22). Linear regression could not be used for analyses of *S. ornatus* because a log transformation did not normalize its distribution (due to the large number of array with no captures of *S. ornatus* during the entire study). Logistic regression was used to analyse the effect of habitat and landscape variables to the presence or absence of *S. ornatus*. As with *N. crawfordi*, each variable was tested separately and only the significant ones were used in the stepwise multiple regression (Table 4). In the final model (deviance = 297.85; $P = 0.002$; d.f. = 230), the mean canopy height ($P < 0.001$) and abundance of *N. crawfordi* ($P = 0.01$) had a positive effect on the occurrence of *S. ornatus*.

PRESENCE OF ANT COLONIES

The Kruskal–Wallis analysis of variance showed that the Argentine ants had a negative effect on the abundance of *N. crawfordi* ($P < 0.001$) but that this shrew species was more abundant in arrays where *Crematogaster* ant colonies were common ($P = 0.03$). No effect

was found between abundance of *N. crawfordi* and carpenter ants or harvester ants (not shown). Analysis of variance showed that none of the ant species colonies had significant effect to the abundance of *S. ornatus* (not shown).

Discussion

This study showed considerable spatial differences in the abundance and distribution of *Notiosorex crawfordi* and *S. ornatus* in southern California (Table 1). Because of the wealth of empirical evidence (Lande 1987; Bolger *et al.* 1991; Stacy & Taper 1991; McCoy & Mushinsky 1994; Robinson *et al.* 1995) showing that local animal populations persist longer in large patches of suitable habitat than in small patches, it is surprising that the size of the study site or the size of the surrounding landscape had no effect to the abundance of *N. crawfordi* or *S. ornatus*. As for the latter species, this can be explained at least partly by the location of the different sized study sites. Due to the urban development along the coast, most of the small study sites were at or close to the coast where the habitat is more mesic than inland, and thus more suitable for *S. ornatus* (see below).

The better adaptation of *N. crawfordi* against desiccation results in higher abundance, wider habitat range (Duncan & Corman 1991; this study) and larger distribution area (Cunningham 1956; Hoffmeister & Goodpaster 1962; Coulombe & Banta 1964; Armstrong & Jones 1972) of *N. crawfordi* compared to those of *S. ornatus*. Since the population densities and territories of shrews are relatively small, *N. crawfordi* may be able to survive even in small fragments (such as the UC Irvine study site, Table 1) if suitable habitat is available. The apparent ability of *N. crawfordi* to utilize whatever cover is available (Cunningham 1956; Hoffmeister & Goodpaster 1962; Armstrong & Jones 1972) is likely to also help it to survive in disturbed habitats with man-made covers (piles of brush). The wide habitat range of *N. crawfordi* illustrates that its often-used common name, desert shrew, is misleading.

There is clear evidence that habitat fragmentation reduces the movement of small mammals (Wolff, Schaubert & Edge 1997). Due to their small size, however, the movement of shrews might be less effected by fragmentation than that of most other mammals (Lindenmayer, Cunningham & Pope 1999). Thus, shrews may be able to survive in smaller fragments than larger species including other small mammals (rodents; Bolger *et al.* 1997). This is supported by the fact that *N. crawfordi* occurred in 21 of the 22 (> 95%) study sites, including many of the smallest ones (Table 1). Many of our study sites were not entirely isolated fragments, however, and thus we could not analyse the effect of the age of the fragments on the captures of shrews. The negative effect increasing age of a fragment on small animal diversity is well documented (Bolger *et al.* 1997).

Although shrews may be able to survive in small fragments, environmental stochasticity, disturbance

and invasion of non-native species, however, will increase the chance of extinction of animals such as shrews, whose population density is continuously small. Extinction due to environmental stochasticity or disturbance is likely to have occurred in one of our study sites (Torrey Pines 2). Although the size of the site and the habitat in Torrey Pines 2 are very similar to the Torrey Pines 1 and 3 sites, no shrews were found in the former during the entire study. Compared to the latter two areas, Torrey Pines 2 suffers from high edge effect (and high number of Argentine ants), being entirely isolated by houses and roads. Despite the short distance between Torrey Pines 3 (which is connected to Torrey Pines 1) and 2 (1.5 km by air), immigration to Torrey Pines 2 from the former sites is not possible for shrews due to a major road. Distance effects on small animal occurrence in fragments have been shown to be weak (Soulé *et al.* 1992), and shrews are relatively poor dispersers (Hanski & Kaikusalo 1989). As for rodents, the urban barriers are likely to impose a very high degree of isolation for shrews.

We found no single variable that could explain the absence of *S. ornatus* in six of the sites. These sites differ in location, size, altitude, edge effect and invasion by Argentine ants. The sites lacking *S. ornatus*, however, had no moist habitats such as riparian, marsh or woodlands.

In contrast to clear spatial differences in the abundance of *N. crawfordi* and *S. ornatus*, the annual variations in the abundance of these shrews were relatively similar indicating that similar environmental conditions favour both species at the annual scale (Fig. 2). The population density of shrews remained relatively similar between years, which may help these species to survive better than some of the rodent species (Bolger *et al.* 1997; also Andrén 1994), especially since the edge effect is disproportionately greater for species with larger than smaller home ranges (Bowers *et al.* 1996).

It is not known whether population densities of *N. crawfordi* and *S. ornatus* show any multi-annual cycles, and this study was not long enough to reveal any patterns in the dynamics of the two shrew species. Elsewhere, depending on the locality, population densities of shrews show (Sheftel 1989) or do not show (Henttonen *et al.* 1989) regular multi-annual cycles, but in most areas the shrew densities fluctuate according to the season.

Seasonal fluctuation in shrew density was seen also in our study, but there were also some interspecific differences. Especially during the last 2 years of the study, *S. ornatus* reached annual peak densities earlier during the year than *N. crawfordi* (Fig. 2). The earlier peak in number of captures in *S. ornatus* was also seen in monthly comparison of absolute numbers of captures (see Results). This difference is explained at least partly by the increased activity of *S. ornatus* during and after rainfall, and its avoidance of hot temperatures (see Results).

Except for some seasonal peaks of *S. ornatus*, *N. crawfordi* was the more abundant shrew species in

general. *N. crawfordi* was already more abundant than *Sorex* in the Pleistocene deposits of the Rancho La Brea tar pits (Compton 1937), which indicates that the interspecific difference in abundance may have existed for some time.

Precipitation during the 10-day trapping period had an immediate positive impact on the captures of *S. ornatus*. Precipitation during the previous 10-day trapping period had a lesser but significant effect on the number of captures of this species. Environmental moisture has been found to be one of the primary factors determining the local abundance and diversity of shrews (Getz 1961; Coulombe & Banta 1964; Simons *et al.* 1990; however, Neet & Hausser 1990), and rainfall has also been shown to increase the activity and widespread movement of shrews (Doucet & Bider 1974; Pankakoski 1979). The restriction to moist areas most probably results from a large turnover of water by shrews due to their high metabolism. Moist areas may also attract their invertebrate prey (Churchfield 1990). It is of interest that although it occupies drier regions than most species of *Sorex* shrews, the abundance of *S. ornatus* correlated with increased moisture. No clear relation between moisture and number of captures of *N. crawfordi* was seen in this study but results of Simons *et al.* (1990) showed that increased moisture correlated with the abundance of *N. crawfordi* in southern Arizona.

We have no information about the effect of predation on shrews in our study sites. Many mammalian predators do not readily eat shrews unless rodent densities are low but predatory birds, especially owls, prey on shrews (Cunningham 1956; Armstrong & Jones 1972; Korpimäki & Norrdahl 1989; see Bolger *et al.* 1997). In warmer areas, snakes may also be important predators of shrews (Wallace & Diller 1990).

The positive effect of the abundance of *N. crawfordi* on the presence of *S. ornatus* most probably results from similar general environmental requirements of the two shrew species. We did, however, find some differences in habitat preference. The percentage of typical coastal sage scrub habitat was the primary factor related to the abundance of *N. crawfordi* (Fig. 3, Table 3). This result and the negative effect of other flora on *N. crawfordi* (Fig. 3, Table 3) indicate that as the native flora diminishes due to the fragmentation and invasion of exotic plants, the abundance of *N. crawfordi* is likely to decrease. Interestingly, Bolger *et al.* (1997) showed that the area of scrub habitat in fragments was the most significant predictor of rodent species diversity in coastal southern California.

Most previous studies (Getz 1961; Spencer & Pettus 1966; Yahner 1983; Churchfield *et al.* 1997; however, Wrigley, Dubois & Copland 1979) suggest that the amount of plant cover does influence habitat preferences of shrews but that the vegetation type is not important *per se*. Results of our study indicated that coastal sage scrub shrub habitat is preferred by *N. crawfordi* over other habitat types in southern California.

Since coastal sage scrub habitat covered a major part of our study sites, however, it is difficult to separate the effect of habitat type and cover for the habitat preference of shrews. The explanatory variable cover could not be included in the analyses because most sites had a very high percentage of cover (Table 2).

The canopy height was the main variable explaining the presence of *S. ornatus* (Table 4). This may be related to the moister microclimate and/or large amount of debris under large trees. Previous studies have also documented the association between *Sorex* shrews and tall woody foliage (Yahner 1983). Very few arrays had trees (Table 2), however, and within site other factors may be more important.

Argentine ants are known to have a negative effect on many native animal species (see Suarez *et al.* 1998; Fisher *et al.* unpublished data). This study showed that Argentine ants also have a negative effect on the abundance of *N. crawfordi*. The reason for this is not known, but the fact that Argentine ants can change or reduce the native non-ant arthropod community (Cole *et al.* 1992; Bolger *et al.* 2000) may affect the prey availability of shrews. Since Argentine ants appear to be dependent on moisture (Cole *et al.* 1992) they may be expected to favour similar habitats to shrews. We found no significant relationship between the abundance of *S. ornatus* and Argentine ants. This may be due partly to the small number of *S. ornatus* in many study areas. It is not known whether the positive association between *N. crawfordi* and *Crematogaster* ant colonies is due to similar habitat requirements, or whether these ants are important prey of shrews. Like other native ants, *Crematogaster* ants are affected negatively by Argentine ants (Suarez *et al.* 1998).

In real islands, significant interspecific differences in extinction rates have been found between shrews, and these differences were negatively correlated with body size (Peltonen & Hanski 1991). Larger species are less affected by environmental stochasticity than are smaller species, smaller species being more sensitive to temporal variation in food availability (Hanski & Kaikusalo 1989). The differences in physiology most probably explain why the smaller shrew species was more widespread and abundant in our study areas.

One species is often numerically dominant in each shrew community. The lesser productivity of forests of North America has been mentioned as a cause for the dominance of a shrew species with a small body size (*S. cinereus*) in contrast to a dominance of a larger one in Europe (*S. araneus*; Hanski & Kaikusalo 1989). This may also explain the lower densities of shrews in forested areas of North America (Kirkland & Findley 1999, Table 5) compared to those in Europe and Siberia (Sheftel 1989). The results of this study support the conclusions of previous studies (Kirkland, Parmenter & Skoog 1997; Kirkland & Findley 1999) that in Nearctic areas, a major difference between sorcid communities in the sagebrush-steppe and forested habitats is the low density of shrews in the former habitat.

Table 5. Abundance of *Notiosorex crawfordi* and some *Sorex* species in western United States. For comparison, abundance from a more mesic area in the eastern United States is included. The trap-success rate shows the number of individuals caught per trap/100 trap-nights (a trap-night equals one pitfall left open for 24 h). Note that the length of the trapping period, and the trapping season varied in each study. Pitfalls were used in all studies with or without drift fences

Species	Locality	Habitat	Trap-success rate	Reference
<i>N. crawfordi</i>	Southern Arizona	Riparian, upland habitat	5	Simons <i>et al.</i> 1990
<i>N. crawfordi</i>	Southern Arizona	Riparian, various	0.25–6.5*	Duncan & Corman 1991
<i>N. crawfordi</i>	Southern California	Coastal sage brush Chaparral	0.52 (0.6)**	This study
<i>Sorex</i> spp.	Colorado	Sedge marsh, subalpine forest, clear-cut	0.02–0.5	Spencer & Pettus 1966
<i>Sorex</i> spp.	Southern Wyoming	Montane, intermontane	1***	Brown 1967
<i>Sorex</i> spp.	South-western Wyoming	Sagebrush-steppe	0.032	Kirkland <i>et al.</i> 1997
<i>Sorex</i> spp.	North-central New Mexico	Conifer forests	5.9	Kirkland & Findley 1999
<i>S. ornatus</i>	Southern California	Coastal sage brush, Chaparral	0.2 (0.5)**	This study
<i>Sorex</i> spp.	Southern Pennsylvania	Deciduous forest	14.6	Kirkland & Findley 1999

*Transformed to correspond captures per trap; the original trap-success rates were given per array which included four pitfalls;

trap-success rate in January–April (peak breeding season); *approximation; the exact number of trapping days not reported.

Thus, extensive trapping effort with pitfalls is required to document the distribution and assemblage of shrews in drier habitats of western North America (see also Kirkland *et al.* 1997).

Conclusions

As predicted, the two shrew species differed in their response to land-cover variables and environmental factors. *N. crawfordi* was still widespread within the coastal sage scrub habitats in southern California but it was relatively abundant in only a few places. The occurrence of *S. ornatus* was mosaic, and it was significantly associated directly (precipitation) and indirectly (microclimate provided by trees) with moisture. In contrast to our prediction, we did not find any differences between shrew species in their response to fragmentation. Fragmentation and urbanization, however, enable the invasion of Argentine ants, which had a strong negative effect on the abundance of *N. crawfordi*. The fact that coastal sage scrub habitat has been dramatically reduced from its former extent by conversion for human use indicates that further reduction of these habitats threaten the abundance of this shrew species in southern California. Because habitat fragmentation may induce changes in space use, social relationships and interspecific interactions of shrews which translate into genetic and demographic effects, more research is needed on the social structure, behaviour and diets of *N. crawfordi* and *S. ornatus* to provide further insights into the long-term effects of habitat fragmentation on the southern California shrew populations.

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