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Factors influencing the variation in capture rates of shrews in southern California, USA

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We examined the temporal variation in capture rates of shrews *Notiosorex crawfordi* (Coues, 1877) and *Sorex ornatus* (Merriam, 1895) in 20 sites representing fragmented and continuous habitats in southern California, USA. In *N. crawfordi*, the temporal variation was significantly correlated with the mean capture rates. Of the 6 landscape variables analyzed (size of the landscape, size of the sample area, altitude, edge, longitude and latitude), sample area was positively correlated with variation in capture rates of *N. crawfordi*. In *S. ornatus*, longitude was negatively correlated with variation in capture rates. Analysis of the effect of precipitation on the short- and long-term capture rates at 2 of the sites showed no correlation between rainfall and capture rates of shrews even though peak number of shrews at both sites were reached during the year of highest amount of rainfall. A key problem confounding capture rates of shrews in southern California is the low overall abundance of both shrew species in all habitats and seasons.

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Introduction

Because of various methodological and biological reasons, detailed density estimates of shrews are rare, and usually do not include analysis of the variation in densities (Smallwood and Smith 2001). Since shrews typically die rapidly in traps, their density estimates are usually based on removal trapping. In general, removal methods with shrews have generated higher density estimates than live-trapping (Smallwood and Smith 2001). However, without separate assessment using trap lines to detect shrews immigrating into the trapped area, the effective trapping area cannot be defined (Sarrazin and Bider 1973, Bury and Corn 1987), making it problematic to convert numbers to density. The use of trapping methods other than the preferred pitfall techniques (Smallwood and Smith 2001) usually under-

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estimates the abundance of shrews. One often neglected factor affecting spatial and temporal density estimates of shrews is their activity level. Since capture rates of shrews are proportional to their activity level (Sarrazin and Bider 1973), the significantly increased soricid activity on rainy nights (Getz 1961, Vickery and Bider 1978, Bury and Corn 1987, Kirkland *et al*. 1998) may confound estimates of their relative abundance based on the assumption that the probability of capture is constant throughout the trapping period.

The recent studies on shrews occupying arid habitats of western North America indicate that some of these habitats can support relatively species-rich assemblages (Williams 1984, 1991, Kirkland *et al*. 1997, Laakkonen *et al*. 2001) but their abundance is consistently low. In an attempt to determine factors influencing such low estimates of density of shrew populations, we examined the temporal variations in capture rates of the desert shrew *Notiosorex crawfordi* (Coues, 1877), and the ornate shrew *Sorex ornatus* (Merriam, 1895), from southern California, USA, in relation to the overall abundance, area of habitat fragmention, location (coastal vs inland), altitude and disturbance (edge effect) of the study sites.

Our previous study (Laakkonen *et al*. 2001) showed that unlike in *S. ornatus*, the capture rate of *N. crawfordi* was not affected by rainfall during the trapping period (or during the previous trapping period). In this study we further analyzed the effect of precipitation on the capture rates by studying the effect of short term (during the trapping period), monthly, and annual precipitation on the capture rates of shrews at 2 sites differing in the amount of annual rainfall. Although precipitation had no significant effect on the short-term capture-rates (Laakkonen *et al*. 2001), we predicted that high levels of monthly and annual rainfall would increase the long-term capture rates of *N. crawfordi* due to the increase in their prey populations (Lindstedt 1980), as has been documented for other shrew species (Holling 1959, Butterfield *et al*. 1981, Henttonen *et al*. 1989).

Although trap-success studies, such as ours, provide only a surrogate of the shrew densities, it allows comparison to other similar shrew studies, providing much needed information (Smallwood and Smith 2001) on shrews for which abundance estimates in large areas are lacking.

Material and methods

The data was collected from 20 sites used in our earlier study from 1995 (1996 in some cases) until 1999 (for details of the trapping periods see Laakkonen *et al*. 2001). Additional trapping was done in some areas in 2000 and 2001. The trapping did not end at the same time in all sites (trapping period ranged from 2–6 years; Table 1).

A complete description of each study site is described in Fisher and Case (2000). The habitats include coastal sage scrub, coastal sand dunes, maritime succulent scrub, chaparral, oak woodland, and coniferous forest. The boundaries of the mainly coastal study areas representing isolated habitat fragments are delineated by urban development. The inland areas are more continuous, relatively undisturbed habitat; they also experience higher evapotranspiration during the summer than the coastal areas that results in vegetation gradients.

Table 1. The location and geographic 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 mean number of individuals caught per 100 trap-nights (a trap-night equals one pitfall left open for 24 h) in April–May. CV – coefficient of variation, *n* – number of years sampled.

Site	Coordinates	Area of the landscape (km^2)	Sample area (km^2)	Mean altitude (m)	Edge index	Trap-success rate				*n*
						Notiosorex crawfordi		*Sorex ornatus*		
						CV	Mean	CV	Mean	
Starr Ranch	117.48 33.60	461	5.02	431	0	50	0.27	77	0.71	5
Wild Animal Park	117.01 33.09	397	1.13	218	0.75	42	0.94	171	0.41	6
Little Cedar Ridge	116.90 32.61	243	1.02	403	0	61	0.18	145	0.46	5
Marron Valley	116.82 32.59	243	3.02	409	0	137	0.20	182	0.13	5
U.C. Elliott	117.11 32.89	120	1.42	195	0.92	91	0.10	101	0.34	5
Rawson	117.02 33.36	103	2.55	627	0	153	0.04	143	0.05	4
Lake Skinner	117.08 33.57	103	6.36	478	0.1	129	0.24	92	0.01	5
Sweetwater	116.97 32.72	99	0.90	108	0	96	0.78	130	0.32	6
St. Margarita	117.16 33.46	42	0.38	308	0.125	100	1.16	104	2.00	5
Lake Perris	117.19 33.86	41	8.84	510	0.32	87	0.20	–	–	5
Limestone Canyon	117.56 33.72	40	5.98	393	0.084	111	0.42	126	0.65	5
North Hills	117.04 33.70	12	1.99	555	0.07	74	0.59	–	–	5
Tijuana Slough	117.13 32.54	11	3.1	43	0.476	196	0.19	104	0.40	5
Motte Rimrock	117.23 33.80	7	1.88	574	0.4	73	0.58	–	–	4
Point Loma	117.23 32.67	5.5	1.16	53	0.38	83	0.49	–	–	6
Chula Vista 2	117.00 32.66	1.5	0.12	126	1	74	0.35	–	–	5
Torrey Pines 3	117.24 32.92	1.5	0.79	44	0.38	57	0.15	103	0.94	2
Torrey Pines 1	117.23 32.91	1.5	0.4	99	0.83	141	0.21	59	0.99	2
UC Irvine	117.83 33.65	1.1	0.24	58	1.75	55	1.09	–	–	6
Chula Vista 1	117.05 32.64	0.4	0.15	99	1.5	16	0.68	–	–	5

Table 2. Correlation matrix (Spearman's r_S) between the coefficient of variation (CV) used as an index of the temporal variance in the occurrence of shrews and the mean number of shrews (a separate value for each species) captured per 100 trap-nights, and between six landscape variables (see Table 1) predicted to effect the population stability in 18 study sites in southern California. * $p < 0.05$, ** $p < 0.01$ (Spearman Rank Correlation test).

Shrew species	Mean number of captures/ Landscape variables	CV
Notiosorex crawfordi	Mean number of *N. crawfordi*	– 0.46*
(n = 18 sites)	Mean number of *S. ornatus*	– 0.50
	Landscape area	0.13
	Sample area	0.48*
	Mean altitude	0.11
	Edge index	– 0.37
	Longitude	– 0.11
	Latitude	– 0.10
Sorex ornatus	Mean number of *S. ornatus*	– 0.18
(n = 11 sites)	Mean number of *N. crawfordi*	– 0.02
	Landscape area	0.17
	Sample area	– 0.40
	Mean altitude	– 0.02
	Edge index	– 0.27
	Longitude	– 0.73**
	Latitude	– 0.34

The effect of rainfall on shrew captures was studied at 2 sites with 2 years (Pt. Loma) and 1 year (Wild Animal Park – WAP) of new data added to the original study (Laakkonen *et al*. 2001). Data on the minimum and maximum temperatures, and precipitation during the trapping periods were recorded using thermometers placed at each site, and by recording the intensity and duration of rainfall during the 10-day trapping period and during the previous 10-day trapping period (6 weeks earlier; for details see Laakkonen *et al*. 2001). Besides site-specific data during trapping, monthly and annual data on temperatures and precipitation were collected by the National Weather Service at the site (WAP), or from a nearby weather station (data for Pt. Loma) at Lindberg Field airport located about 8 km north of Pt. Loma. These data were used in analyses of the effect of rainfall on shrew captures.

Trapping methods

Each of the study sites contained 5 to 20 pitfall, drift-fence arrays (for details see Case and Fisher 2000). Sampling was conducted at each study site for 10 consecutive days every 6 weeks, spread evenly across all seasons. Traps were checked in the morning, once every 24 hours. The traps were kept closed between the sampling periods. Shrews found live in the buckets were identified and released unmarked, so the numbers of captures probably include an unknown proportion of recaptures. The capture rate (trap-success rate) was defined as the number of individuals caught per 100 trap-nights (a trap-night equals one pitfall left open for 24 h). Due to the low overall abundance of shrews in all study sites, pooled data of all sex and age groups were used in all analyses. Our previous study (Laakkonen *et al*. 2001) showed that there was no significant difference in numbers between the sexes, or in the season they were caught. As an index for the variation in the number of captures of shrews, we computed the coefficient of variation (CV). We used the April–May capture rates for the comparison between years because at this time of year both mature and immature shrews are present in the population. Thus, these capture rates correspond to the autumn value usually used to estimate the density variations of temperate shrew populations. Also, in late spring, there is little rain and no extreme temperatures which could significantly influence the activity of shrews in southern California. Because sites were not trapped at exactly the same time (see Laakkonen *et al*. 2001), we did not attempt to analyze the spatial synchrony between sites.

Data analysis

We analyzed the correlation between CV and the mean number of the shrew species, and between CV and six landscape variables (Table 2; for details of the landscape variables see Table 1 and Laakkonen *et al*. 2001) using the Spearman Rank Correlation test. This test also was used to analyze the relationship between shrew captures and annual rainfall (Fig. 1). Kruskal-Wallis test was used to analyze the effect of monthly precipitation, rainfall during the 10-day and during the previous 10-day sampling period, and the maximum and minimum temperatures during the trapping periods to the shrew density estimates (Fig. 1). Statistix (Analytical Software, Tallahassee, FL, USA) for Windows statistical software package was used in all analyses.

Results

The coefficient of variations for *N. crawfordi* ranged from 16 to 196 (mean $\bar{x} = 90$), and for *S. ornatus* from 77 to 182 ($\bar{x} = 125$, Table 1; includes the sites with at least 4 years of data). The mean number of shrews caught per 100 trap-nights in spring varied from 0.04 to 1.16 ($\bar{x} = 0.47$) for *N. crawfordi*, and from 0.01 to 2.00 ($\bar{x} = 0.5$) for *S. ornatus* (Table 1; Torrey Pines sites were excluded because they represented only 2 years of data).

In *N. crawfordi*, temporal variations in capture rates were greatest in small populations, and in large study areas (Table 2). The variation in capture rates increased significantly from the coast towards the inland sites in *S. ornatus*.

The annual or monthly rainfall had no significant effect (Fig. 1) on capture rates of shrews at Pt. Loma ($r_s = 0.03$ and $p = 0.42$ for *N. crawfordi*) or at WAP ($r_s = 0.5$ and $p = 0.58$ for *N. crawfordi*, $r_s = 0.36$ and $p = 0.16$ for *S. ornatus*). Precipitation during the trapping period and during the previous trapping period had no significant effect on the captures of shrews at either site ($p = 0.84$ and $p = 0.75$ for *N. crawfordi* at Pt. Loma, and $p = 0.14$ and $p = 0.83$ for *N. crawfordi*, $p = 0.99$ and $p = 0.51$ for *S. ornatus* at WAP). The minimum or maximum temperatures during the trapping period showed no effect on the captures of *N. crawfordi* ($p = 0.56$ and $p = 0.52$ at Pt. Loma, $p = 0.39$ and $p = 0.37$ at WAP) or on captures of *S. ornatus* at WAP ($p = 0.26$ and $p = 0.61$).

Discussion

As in many species of shrews (Hanski 1989), the variations in capture rates were greatest in small populations of *N. crawfordi* (Table 2). No such correlation was found in *S. ornatus*. Even though the mean abundance in spring was similar in both

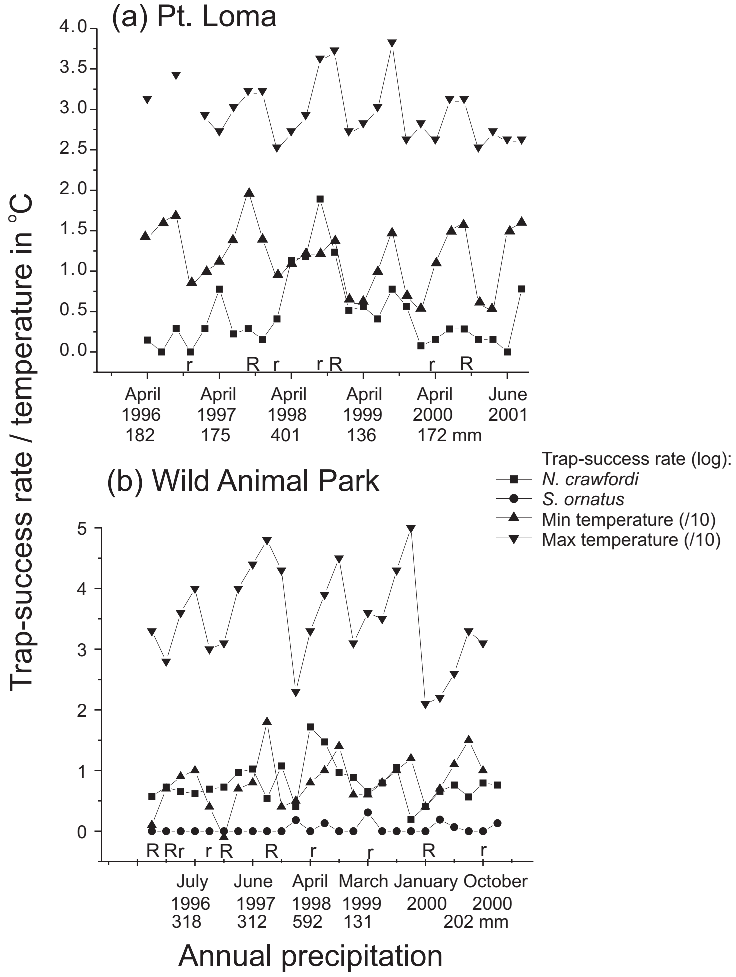

Fig. 1. Log-transformed trap-success rate of shrews, and minimum and maximum temperatures (°C) during each trapping period at Pt. Loma (a) and Wild Animal Park (b) study sites from 1996 to 2001 (2000 for WAP). The temperature values have been divided by 10 to fit the scale. The letters R and r on the x-axis indicate light and heavy rain (respectively) during the trapping period. Annual precipitation values are shown at the bottom of the figure (National Weather Service). The long-term annual precipitation average at Pt. Loma is 257 mm (86 years of data), and 344 mm at WAP (16 years of data; National Weather Service). Note that only *Notiosorex crawfordi* occurs at Pt. Loma.

species, the capture rates of *S. ornatus* were lower than those of *N. crawfordi* much of the year in most sites (Laakkonen *et al.* 2001, Fig. 1). This indicates that seasonal variation in activity is likely to result in greater sampling error in capture rates of *S. ornatus* compared to those of *N. crawfordi*. Within coexisting shrew species, the temporal variation has been found to be higher in the generally less abundant species in short-term (Hanski 1989, Table 3) and in longer-term studies (16–18

Table 3. Temporal fluctuations in the numbers of coexisting shrew species from United States and from northern Europe (studies were chosen based on similar length of the study period). CV – coefficient of variation (100 standard deviation divided by the mean). Mean – the number of individuals caught per 100 trap-nights. *n* – the number of years over which CV and mean were calculated. Pitfalls with or without drift fences were used in North American studies; snap traps and/or pitfalls in all other studies. * The southern California values are averages of all the sites with at least 4 years of data (*N* = 18 sites for *N. crawfordi* and *N* = 11 sites for *S. ornatus*). ** Calculated from the data given in the original paper.

Species	Locality	CV	Mean	*n*	Reference
Notiosorex crawfordi	Southern California*	90	0.47	4–6	This study
Sorex ornatus		125	0.50		
Sorex cinereus	South-western Wyoming	89**	0.03	7	Kirkland *et al*. 1997
Sorex cinereus fontinalis	South-central Pennsylvania	54	3.40	4	Kirkland *et al*. 1998
Sorex hoyi		41	0.88		
Sorex fumeus		65	0.77		
Sorex araneus	Eastern Finland	34	17.2	8	Skarén 1972
Sorex cacutiens		131	6.2		
Sorex spp. (mostly *S. araneus*)	Southeastern Norway	70	0.64**	7	Sonerud 1988
Sorex araneus	Eastern Finland	48	12.9	5	Hanski 1989
Sorex caecutiens		168	14.2		

years; Ivanter 1976, Kaikusalo 1980). Within a region, however, a low abundance does not necessarily translate into high temporal variation (Table 3). Despite the arid conditions of southern California (low precipitation and lack of snow), the temporal variation of the two species of shrews and their interspecific differences in CV, are remarkably similar to those of shrew species from mesic environments (Table 3). It should be noted, however, that CV is affected by trapping methods.

The body size of a species has many predictable effects on its occurrence on a real island (Hanski 1986) or a habitat fragment. Compared to *S. ornatus*, *N. crawfordi* has a smaller body size which means smaller individual food requirements and potentially greater population density resulting in a smaller role for demographic stochasticity at a given site. Smaller body size, on the other hand, should make *N. crawfordi* more vulnerable to environmental stochasticity and interspecific competition (Hanski 1986, 1989). *N. crawfordi* has, however, many specializations against desiccation (Lindstedt 1980, Laakkonen 2002), which enable it to avoid unfavourable environmental conditions and short term food shortage.

Of the landscape variables, only size of the sample area was significantly correlated with the temporal variation of *N. crawfordi* captures (Table 2). The tendency of shrews residing in southern California to occupy only part of the study sites (Laakkonen *et al*. 2001) may influence the correlation between CV and size of the site sampled. In *N. crawfordi*, 33–53% and, in *S. ornatus*, 46–85% of the shrews were captured from the 3 arrays with most captures within a site (J. Laakkonen *et al*., unpubl.). In density estimates of *Sorex* in general, smaller sites have often been associated with higher densities (Smallwood and Smith 2001). The mean size of our study sites (2.32 km^2) was larger than that (0.02 km^2) of the previous studies (Smallwood and Smith 2001). In *S. ornatus*, temporal variation was highest in inland sites. This correlation could be due to a more stable microclimate in coastal habitats (see below).

Similar to the results of our previous analysis of 22 sites (Laakkonen *et al*. 2001), a graphical analysis showed a peak in captures in the rainy year of 1998 (Fig. 1). At Pt. Loma, the average rainfall exceeded the 1998 value of 401 mm once in a decade. The limited rainfall data (16 years) available from WAP showed only one annual precipitation value higher than the one recorded in 1998 (National Weather Service). We found, however, no significant relation between any of the climatic variables and captures of *N. crawfordi* or *S. ornatus* (Fig. 1). However, our previous study (Laakkonen *et al*. 2001) had shown that the captures of the latter species were affected by rain and maximum temperatures. There are several possible explanations for this lack of correlation. Because the overall abundance of both species of shrews was low, capture of a few individuals in a site at a particular time may have had a significant effect on the temporal variation in capture rates when sites are analyzed separately (see also Bury and Corn 1987). Since most rainfall occurs during the most active period of reproduction, activity and movement peaks associated with the mating period (Sarrazin and Bider 1973, Newman 1976, Rust 1978, Hays and Lidicker 2000) also may confound the analyses on the effect of rainfall and other climatic variables on the temporal variation in captures. Finally, the use of meteorological data recorded at a weather station may not accurately reflect the microclimate of a given site or individual trapping array. A marked feature of the climate in the San Diego area is the wide variation in temperature and rainfall within short distances attributable to variation in elevation. The seasonal rainfall averages about 25 cm per year along the coast, and increases with elevation and distance from the coast to up to 100 cm per year in the mountains (National Weather Service). Moisture due to oceanic fog drip contributes an additional 10 cm, at least in some coastal sites (J. Estburg, 1996, Records of fog drip at Torrey Pines State Reserve, unpubl.). Fog drip may be one of the factors contributing to the lack of significant correlation between capture rates of *N. crawfordi* and the annual rainfall at Pt. Loma. There is little information on factors associated with *N. crawfordi* captures elsewhere; however, a study conducted along an elevational gradient in southern Arizona (Simons *et al*. 1990) showed that captures of *N. crawfordi* correlated both spatially (vegetation type) and temporally (rainfall) with decreased aridity.

The low overall abundance of shrews is a key factor confounding the abundance estimates of shrews in southern California. In order to reduce stochastic variation in abundance estimates, studies of long-term density of shrews are needed. Also, since some habitat characteristics have a significant effect on the abundance of shrews in southern California (Laakkonen *et al*. 2001), studies of density should include several habitat types. Finally, because the amount of moisture available for shrews varies greatly between sites, the recorded climatic factors should be site-specific.

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