

SPECIES RICHNESS AND CALIFORNIA VOLES IN AN ANNUAL AND A PERENNIAL GRASSLAND

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ABSTRACT.—Populations of a common burrowing rodent, *Microtus californicus* (the California vole), thrive in ungrazed or lightly grazed grasslands in coastal California. Two sites ungrazed by livestock, one dominated by native perennial grasses and another dominated by invasive annuals, were evaluated over 2 consecutive years for the relationship between plant species richness and location of *M. californicus* burrow entrances (burrows). Plant species and burrows were sampled as present or absent in contiguous 1-m² quadrats on a 100-m² grid. Quadrats with burrows averaged significantly more plant species than quadrats without them (11.3 vs. 9.9 species, $P < 0.001$). Burrows found in 1996 were not correlated with species richness in 1995, suggesting that voles affect richness rather than seek it out. Vole burrow locations showed significant clumping on the annual site and trended toward clumping on the perennial site in both 1995 and 1996. Because voles seem to create a clumped pattern with their burrow entrances, the associated increase in plant species richness may have a strong effect on the overall structure of the plant community. A quantitative comparison of the 2 sites showed that the plant matrix of the perennial site contained flora of the annual site. This similarity in plant species composition may allow for similar treatment of our 2 types of sites and potentially other California grasslands. Undetected increases in vole populations with livestock grazing reduction may account for the erratic results from grasslands management research and the inconsistent success of derived management practices.

Key words: *Microtus californicus*, California, native grasses, plant community comparison, grassland management.

Plant species composition and richness respond variably to livestock grazing on California grasslands (Bartolome et al. 1980, Bartolome and McClaren 1992, Hatch et al. 1999). In other studies of grasslands, both North American (Waser and Price 1981, Harnett et al. 1996, Stohlgren et al. 1999) and worldwide (Pandey and Singh 1991, Belsky 1992, Noy-Meir 1995), grazing or its cessation inconsistently influenced species richness. Proulx and Mazumder (1998) reviewed much of the current research on the relationship between grazing (by all types of animals) and species richness. They concluded that research in this area had significant potential for improving management, but that nutrient-rich plant communities responded unpredictably to grazing.

We believe that the relationship between grazing and plant species richness could be masked by the interaction between primary grazers and other herbivores within the study systems. Most terrestrial grazing studies attribute main effects to livestock, large mammalian herbivores, or other species that make obvious disturbances (e.g., gopher mounds) without specific consideration of the impacts

of other, less obvious herbivorous animals. This is despite the fact that grazing, especially by livestock, and its partial or full cessation have a substantial effect on non-domesticated animals and other ecosystem processes in grasslands (Lidicker 1989, Jones and Longland 1999). We wanted to evaluate the impact of one of these covert grazers on plant species richness in coastal California.

Microtus californicus (the California vole), a common burrowing rodent in California grasslands, has the potential to interact with grazing and strongly affect plant species richness. This generally hidden species, which primarily eats the green shoots of emerging grasses during the wet winter season and grass seeds during the dry summer season (Batzli 1986), thrives in higher cover levels (Ostfeld and Klosterman 1986, Ostfeld et al. 1986) characteristic of ungrazed or lightly grazed sites (Borchert and Jain 1978). Cessation or reduction of grazing by livestock benefits *M. californicus* primarily by reducing predation, though food sources may also increase (Ostfeld and Klosterman 1986). Voles are known to affect some plant species in the California grasslands

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(Batzli and Pitelka 1970, Borchert and Jain 1978, Cockburn and Lidicker 1983, Lidicker 1989) and seem likely to impact plant species richness. However, this impact of voles on plant species richness has not been tested.

Because the direct effects of grazing seem more likely to be the dominant forces in heavily grazed sites, and because voles are primarily active only in sites with low livestock grazing pressure, we were interested in the impact of voles in ungrazed exclosures within the extensive grazed landscape. Our main null hypothesis was that the presence of *M. californicus* burrow entrances (burrows) would not be associated with a change in species richness nor be affiliated with any particular plant species. We also hypothesized that burrow entrances would have a random distribution across the study area. This hypothesis was designed to identify the scale of any impact of voles. In addition, we hypothesized that an annual- and a perennial-dominated site (the main types in this system) would have similar associations with voles and similar plant species richness and composition.

STUDY SITE

In 1995 we established 2 permanent 100-m² (10 × 10 m) sites in an East Bay Municipal Utility District watershed, 25 km northeast of San Francisco, California. The sites were within ungrazed and unburned exclosures of about 1000 m² each. The exclosures were established in 1991 as part of a grazing study and separated by about 100 m (Fehmi 1998). The sites have an elevation of 128 m, 60–70 cm of average annual (generally winter) rainfall, and frequent fog. The area was grazed moderately (half or less of the forage was used) year-round for at least 70 years before establishment of the exclosures. Prior to that time, heavy grazing probably took place episodically (R. Tripp unpublished data). The soil on both sites is a fine-loamy, mixed, mesic typic argixeroll (Los Gatos Loam; Welch 1977). The annual site has a slope of 31%, the perennial site a slope of 27%; they both have similar northwest aspects (309° and 303°, respectively). While we did not physically observe *M. californicus*, their burrows and characteristic aboveground runways are common in these ungrazed paddocks.

Three native perennial grasses (Bartolome and Gemmill 1981, Bartolome et al. 1986) dominated one site: *Nassella (Stipa) pulchra* (A. Hitchc.) Barkworth, *Nassella (Stipa) lepida* (A. Hitchc.) Barkworth, and *Danthonia californica* Bolander (the perennial site; Fig. 1). The other site was entirely without native perennial grasses and dominated by a mix of the annual grasses *Lolium multiflorum* Lam., *Bromus hordeaceus* L., and *Bromus diandrus* Roth (the annual site; Fig. 1). Distinct patches dominated by native perennial grasses are not unusual in the otherwise introduced annual landscape of California's coastal prairie (White 1967, Elliot and Wehausen 1974, Stromberg and Griffin 1996). However, these perennial patches are prized because of their native status (Bartolome and Gemmill 1981, Bartolome et al. 1986, Heady et al. 1991) and may be protected and managed differently from the annual-dominated grasslands (Heady et al. 1991, Hatch et al. 1999).

METHODS

Each site was gridded into series of square quadrats measuring 1 m². This allowed the presence/absence of plant species and the presence of vole burrows showing active use to be recorded in contiguous quadrats covering the entire area of each 100-m² site. This intensive sampling protocol, the need to sample while the plants were flowering (for positive identification), and our available resources restricted us to monitoring 2 sites. Sampling took place between late April and mid-June in both 1995 and 1996. An ANOVA was calculated to evaluate significant differences in plant species richness between quadrats with and without vole burrows, and to look at differences between years and site types. Because the individual quadrats within a site could be spatially autocorrelated, we used a 1000-iteration bootstrap technique to calculate the significance of the ANOVA terms (Venables and Ripley 1994). We also report significance at $P < 0.01$ to make the tests more conservative.

To determine how the effects of voles were distributed across the sites, we evaluated locations of vole burrows on both sites for distribution patterns departing from complete spatial randomness using Ripley's K-function ($L(t)$ values) on each of the contiguous grids (Fehmi 1998). The K-function is a 2nd-order method

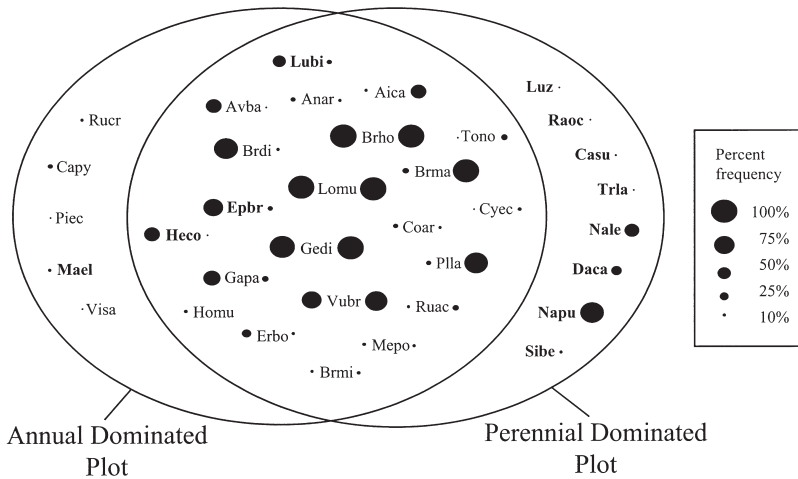


Fig. 1. Venn diagram of the average plant species composition for both years of the study. Native plants are in bold and the size of the dot adjacent to the name indicates the actual percent frequency of that plant species in 1-m² quadrats averaged over 1995 and 1996. The dot to the left of the name represents data for the annual site, and the dot to the right represents data for the perennial site. Species in the area overlapped by the 2 circles are represented on both sites. Names are the first 2 letters of the Latin binomial for each species as follows:

Aica, *Aira caryophylla*
 Anar, *Anagallis arvensis*
 Avba, *Avena barbata*
 Brmi, *Briza minor*
 Brdi, *Bromus diandrus*
 Brho, *Bromus hordeaceus*
 Brma, *Bromus madritensis*
 Casu, *Calystegia subcaulis*
 Capy, *Carduus pycnocephalus*
 Coar, *Convolvulus arvensis*
 Cyec, *Cynosurus echinatus*
 Daca, *Danthonia californica*
 Epbr, *Epilobium brachycarpum*
 Erbo, *Erodium botrys*
 Gapa, *Galium parisiense*
 Gedi, *Geranium dissectum*
 Heco, *Hemizonia congesta*
 Homu, *Hordeum murinum*
 Hovi, *Holocarpha virgata*

Lomu, *Lolium multiflorum*
 Lubi, *Lupinus bicolor*
 Luz, *Luzula* sp.
 Mael, *Madia elegans*
 Mepo, *Medicago polymorpha*
 Nale, *Nassella lepida*
 Napu, *Nassella pulchra*
 Picc, *Picris echinoides*
 Plla, *Plantago lanceolata*
 Raoc, *Ranunculus occidentalis*
 Ruac, *Rumex acetosella*
 Rucr, *Rumex crispus*
 Siga, *Silene gallica*
 Sibe, *Sisyrinchium bellum*
 Tono, *Torilis nodosa*
 Trla, *Triteleia laxa*
 Visa, *Vicia sativa*
 Vubr, *Vulva bromiodes*

relying on the variance between all point-to-point distances (reviewed in Haase 1995). The center of each quadrat formed the proxy location for all individuals present in the quadrat. A 95% confidence interval for each L(t) value was calculated using 1000 Monte Carlo simulations of data on a grid.

Spatial dependence between plant species and vole burrows was tested using 2-way contingency tables and chi-square statistics. Marginal totals were used to compute the expected values in the chi-square test. This indicates whether a plant species was found with, or away from, burrow entrances more often than expected. An odds ratio was calculated to

show the direction of the association between burrows and plants (positive or negative, Selvin 1995), and probabilities (P) were Bonferroni corrected as required (Selvin 1995). S-Plus 3.3 (Venables and Ripley 1994) was used for all calculations and simulations.

To quantify the differences between the sites, we used 2 separate types of measures. Simpson's and Shannon's equitability indices (as described in Begon et al. 1990) combine richness and abundance, giving measures of the evenness with which individuals are distributed among the species. The coefficient of community (CC; Jongman et al. 1995) uses only species richness to measure the difference

between sites. For the sites to be considered different, both the equitability and the community measures should show the sites are different. Simpson's and Shannon's calculations used the average relative frequencies of plants at each site from the quadrat data from both years. Relative frequency was calculated by dividing the observed frequency of a species by total frequency of all plants. A test for similarity was created with a 1000-iteration bootstrap of the Simpson's and Shannon's equitability indices. They were calculated with the frequency for each of 28 species randomly chosen from all observed frequencies.

The CC was calculated from species richness data of the 2 sites. To test the possibility of getting any particular value by chance, we again used a 1000-iteration bootstrap procedure to generate the distribution of the CC. First, 3 values for species richness of the surrounding hectare (an area that would include both sites) were estimated for the pool of available species. The available richness data were combined into different plot sizes (1, 4, 16, 25, and 100 quadrats), and regression was used to estimate the expected species richness of a hectare. The procedure was repeated 3 times: first using only the richest combination stratified by site and year, then using all the data, and finally using only the least rich combination. This resulted in high, middle, and low estimates of species richness of the hectare (the species pool). The simulation procedure drew 2 sets of species from the pool and calculated the CC 1000 times. The size of the sets of species matched those observed from the sites in this study.

RESULTS

Vole burrows on the annual site were found in 18% of the quadrats in 1995 (Fig. 2a) and 29% in 1996 (Fig. 2b). They were less common on the perennial site, occupying 5% of the quadrats in 1995 (Fig. 2c) and 14% in 1996 (Fig. 2d). Overall, plant species richness per quadrat varied between 5 and 17 species (Fig. 3), and quadrats with burrow entrances averaged significantly more species than quadrats without them (11.3 vs. 9.9 species, $P < 0.001$). Quadrats in 1996 were significantly more species rich than in 1995 (11.2 vs. 9.1 species, $P < 0.001$). There were no significant differences in species richness between the peren-

nial and annual sites (10.4 vs. 9.9 species, $P = 0.207$), and no significant interactions were detected. Burrow locations in 1996 were not associated with species richness in 1995 ($P = 0.542$), and there was no detectable relationship between richness in 1995 and in 1996 ($P = 0.600$). While 7 burrows were observed in the same quadrats both years, the location of burrows between years was not significantly correlated ($P = 0.269$).

Burrow entrances were significantly associated with 2 plant species in the quadrats in 1996. Positive association was found with *Carduus pycnocephalus* ($P < 0.001$) on the annual site, and a negative association was found with *Plantago lanceolata* ($P = 0.001$) on the perennial site. *Galium parisiense* trended toward a positive association on the annual site also in 1996 ($P = 0.049$). The spatial pattern of burrow entrances showed significant clumping on the annual site at distances between 1.5 and 3.0 m in 1995 (Fig. 4a) and between 1.0 and 4.0 m in 1996 (Fig. 4b). Although they were visibly clumped in 1995 (Fig. 2c) on the perennial site, there were too few burrows for statistical testing. The pattern of burrows on the perennial site in 1996 showed a nonsignificant trend toward clumping (Fig. 4c).

The sites had 22 species in common (Fig. 1), with 30 on the perennial site and 27 on the annual site. Eight natives were found only on the perennial site, and species other than the 3 native perennial grasses were infrequent. One native occurred only on the annual site and 3 occurred on both sites. When sites were evaluated for relative frequency of native plants, the annual site contained 20% natives vs. 22% in the perennial site.

Simpson's equitability index was 0.54 for the annual and 0.44 for the perennial site. With the bootstrapped standard deviation of 0.063, these sites did not differ significantly ($P = 0.11$). Shannon's equitability index was 0.87 for the annual site and 0.82 for the perennial site. The bootstrapped standard deviation was 0.030, so again the sites were not significantly different ($P = 0.09$). The CC for these 2 sites was 0.77. This can also be expressed as a 77% similarity for these 2 sites. Species richness of the hectare enclosing the 2 sites was estimated as being between 50 and 80, with a likely richness of 63. The probability of getting a CC as high as 0.77 by chance from a pool of 50 species (the most conservative test) was very

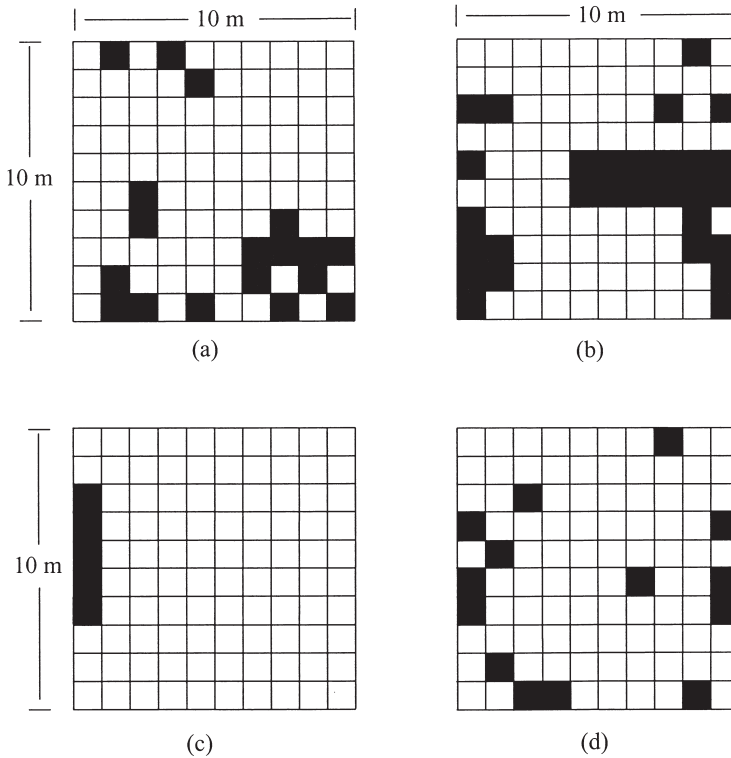


Fig. 2. Shaded squares showing *Microtus californicus* burrow entrance locations for each site in each year: (a) locations in 1995 on the annual site, (b) locations in the annual site in 1996, (c) locations in the perennial site in 1995, and (d) locations in the perennial site in 1996. Entrances were located as present or absent in 1-m² quadrats on a 100-m² square grid.

low ($P < 0.001$), with the probability decreasing as size of the pool increased. The CC expected for 2 sites with this pool of source species was 0.45 ($s = 0.069$), indicating that the 2 sites evaluated here are much more similar than could be expected by chance. With these commonly available community comparison metrics, we could quantify no significant differences in plant composition between the 2 sites other than the species they do not have in common.

DISCUSSION

Within our livestock exclosures, vole activity was associated with an increase in species richness of the plant community. There are 2 possible explanations for this association. Voles were correlated with the cause of (or themselves caused) species richness or they moved to areas with higher species richness. Because there were no observed relationships between plant

species richness in the same quadrats in 1995 and 1996, and because high richness sites in 1995 had no significant correlation with burrow locations in 1996, we feel that voles did not move to high richness sites between years. Instead, the results suggest that voles were associated with causes of higher richness. While concluding that voles directly caused these changes is premature, our data nonetheless suggest that voles may be a significant force in structuring plant communities on our site and potentially other California grasslands.

While specific vole activities potentially influencing plants are unknown, the observed positive and negative association of particular plants with rodent activity may result from several processes. There was more available light and less competing vegetation around vole burrows, and burrowing brings deeper soils to the surface. This might have presented a small, open soil patch that offered an advantage for some plants such as *Carduus pycnocephalus*

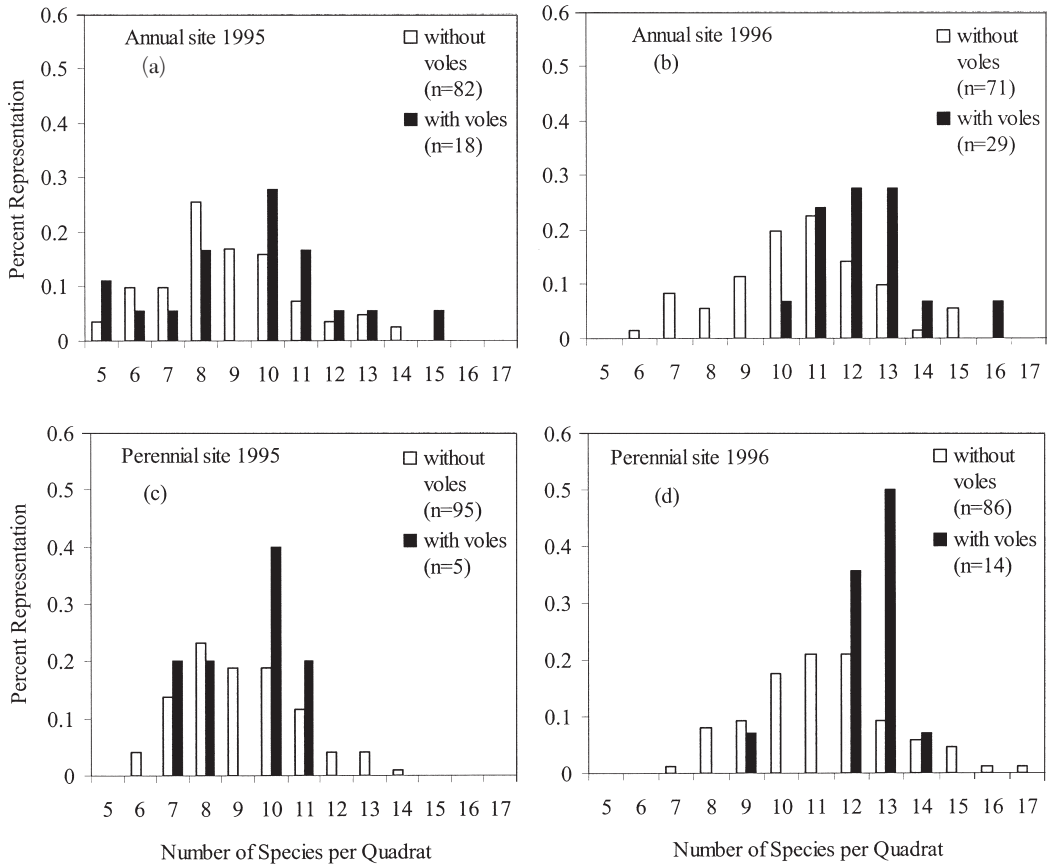


Fig. 3. Species richness of 1-m² quadrats by year and site. The number of quadrats for each level of species richness was divided by the number of quadrats (n) to give percent representation on the annual site in 1995 (a) and 1996 (b) along with the perennial site in 1995 (c) and 1996 (d).

(Stromberg and Griffin 1996) and the small-statured *Galium parisiense*. There also could have been fecal and urine deposits around these openings, changing the soil's nutritive value and adding seeds. Other studies have shown higher nutrient levels associated with rodent activity (Hobbs and Mooney 1995), but at least one study has shown lower levels due to microbial immobilization (Bradshaw and Goldberg 1989). Voles may have brought seeds near burrows either unintentionally or through stockpiling food sources (Batzli and Pitelka 1970). *Carduus* seeds may have blown on disturbed areas of the site, such as the area near vole burrows, in a manner similar to that of other members of the family Asteraceae, noted by Robinson and Quinn (1988). Borchert and Jain (1978) also noted vole activity associated with thistles (*Centaurea*), but their assumption

was that voles preferred thistles as habitat. A further analysis of our data showed no significant correlation ($P = 0.748$) between thistle locations in 1995 and burrow locations in 1996. This offers support for the idea that thistles located in the burrow entrances rather than the converse, though some combination of both may have occurred.

Vole burrows were negatively associated with *Plantago lanceolata* on the perennial site. Plants or seeds can be grazed preferentially near burrows (Batzli and Pitelka 1970). The loss of up to half the annual seed production of grasses has been attributed to rodents, particularly voles (Batzli and Pitelka 1970, Gulmon 1979). Vole seed preferences may structure the grasslands during years with large vole populations (Borchert and Jain 1978, Cockburn and Lidicker 1983), and the disturbance

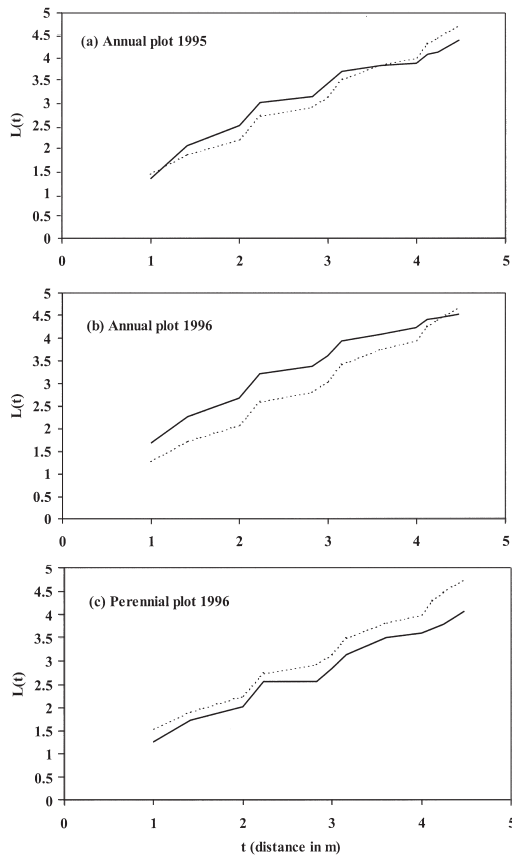


Fig. 4. Analysis of the *Microtus californicus* burrow entrance spatial patterns. Solid lines represent Ripley's $L(t)$ for each site; dashed lines represent the 95% upper confidence interval estimated from 1000 simulation runs. When the solid line is above the dashed line, significant clumping is present. (a) Annual site in 1995, (b) annual site in 1996, (c) perennial site in 1996. For actual locations, see Figure 2.

of burrows or tunnels may be detrimental to plants. Voles can destroy substantial amounts of vegetation through construction of above-ground runways (Ford and Pitelka 1984). They also mediate the effect of other animals since they are associated with reduced arthropod numbers (Batzli and Pitelka 1970). Despite substantial research into voles, they have not been routinely considered in comparisons of livestock grazing and plant species richness.

Given the burrow clumping and associated increased species richness in our data, we looked at other studies on grassland species richness to see which procedures might be expected to detect our high richness areas. Our sites did not have a homogeneous distri-

bution, with vole-impacted patches of up to 4 m² comprising only about 16% of the area sampled. Detection of this type of patchy distribution requires a different sampling approach than acceptable for more homogenous distributions. Our levels and distribution of richness would likely have been detected with the plant species richness sampling procedure of Waser and Price (1981), who used sixty-five 0.25-m² quadrats. They certainly would have been included in Stohlgren et al.'s 100-m² and 1000-m² quadrats. Procedures of other studies, such as Harnett et al.'s (1996) use of subsampling within four 1-m² quadrats, Belsky's (1992) 2-m² quadrats, or Stohlgren et al.'s (1999) ten 1-m² and two 10-m² quadrats, may not have included high species richness plots similar to ours. Our data suggest that well-distributed smaller samples are more likely to capture species richness variability than the same sampling area consolidated. Furthermore, sampling intensities in sites with fewer voles, such as our perennial site, need to be higher than on sites with more voles, such as our annual site.

The annual and perennial sites were more similar than expected. The species of the annual site were the main constituents of the matrix between perennial grasses in the perennial site, and both sites had similar species richness with vole-associated increases. The similarity in plant species composition also belies the use of the term *relict* (e.g., Heady et al. 1991) to describe patches dominated by native perennial grasses because on our site perennials seemed to be integrated into the annual grassland matrix. Vole use of both types of grassland, combined with other similarities between the two, may allow some reintegration of annual and perennial site management.

For annual site restoration or perennial site conservation, voles could be the episodic disturbance hypothesized as important for the recruitment of perennial grasses such as *Nassella pulchra*, *N. lepida*, and *Danthonia californica* (Bartolome and Gemmill 1981, Fehmi 1998). As discussed above, voles may impact 3- to 4-m² areas and have highly dynamic population fluctuations (Garsd and Howard 1981, Salvioni and Lidicker 1995). Together this implies a substantial episodic disturbance in this system. This idea finds further support from Hobbs and Mooney (1985, 1995), who found that time since disturbance by *Thomomys bottae*, the western pocket gopher, is

correlated with observed patterns of plant abundance in a California serpentine grassland. They further determined that most of the site is disturbed every 3–5 years by gopher activity, and that perennial grasses decrease after the exclusion of *T. bottae*. While the activity of voles is different from gophers, we believe these native rodents could create disturbances that could foster perennial recruitment.

While the inference space of this study is quite small, it implies that research done to date on the restoration, conversion, and conservation of California grasslands may have incorrectly interpreted the role of grazing management as a determinant of vegetation structure. Experimental treatments in these studies may have inadvertently combined the direct impact of livestock with an indirect response of voles. In the control or ungrazed treatments of livestock studies, the increased biomass and cover of vegetation greatly enrich vole habitat and allow vole populations to increase. Thus, the interacting effects of cattle and voles might explain the inconsistent results from grazing experiments and their derived management practices (Hatch et al. 1999), including seasonal grazing practices designed to maintain and enhance native perennial grasses (Dyer et al. 1996). Our conclusion is that grazing studies which control only livestock may not answer important questions about the forces that structure plant communities. Future studies need to better document the relationship between the plant community and vole activity, especially with experiments directly manipulating vole numbers.

ACKNOWLEDGMENTS

This research was partially supported by the East Bay Municipal Utility District and the University of California. We thank J. Battles, C. D'Antonio, and B. Allen-Diaz for suggestions and discussion. Comments of W. Lidicker and A. Dyer improved the organization and clarity of this manuscript.

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Received 24 April 2000
Accepted 9 November 2000