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Comparing pocket gopher (*Thomomys bottae*) density in alfalfa stands to assess management and conservation goals in northern California

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Abstract

Pocket gophers (*Thomomys bottae*) affect alfalfa (*Medicago sativa* L.) production in Yolo County, California, as well as the distribution of special status, rare species that either prey on gophers or use their burrows as habitat. Farming practices, as well as attributes of the landscape and of alfalfa fields, were compared to 134 estimates of gopher density among 35 alfalfa stands scattered throughout the County during 1992–1994. Gophers in alfalfa fields averaged only one-fourth the average density among published reports, and the range from low to high density was much smaller in alfalfa fields. Gopher density was greater at the field edge, especially during the first 2 years of stand production. Preference for the edge decreased by the third year of alfalfa production as gophers used the available space in the field interior. A stepwise multiple regression model could explain 73% of the variation in the 134 estimates of gopher density. This variation was explained by years since sowing of the alfalfa (standardized slope coefficient, $\beta \approx 0.52$), annual frequency of flood irrigation ($\beta \approx -0.43$), habitat area as a percentage of the landscape within a 500 m buffer around the field ($\beta \approx 0.31$), season of the year ($\beta \approx 0.25$), field size ($\beta \approx -0.20$) and percentage of sand within the top soil layer ($\beta \approx 0.16$). This model can be used to predict the distribution of special status species that depend on gophers, and can be used to guide conservation efforts by increasing the spatial extent of non-cultivated gopher habitat on suitable areas intervening alfalfa fields. Non-cultivated gopher habitat is currently rare in the valley portion of Yolo County. Gopher control failed to influence density to the magnitude sought by the alfalfa growers, and cessation of control would benefit both production and conservation goals in some alfalfa growing regions.

Keywords: Alfalfa; Conservation; Density; Gopher control; Habitat; Landscape; Pocket gophers; Soil; *Thomomys bottae*; Yolo County; California

1. Introduction

The density of pocket gophers (*Thomomys bottae*) affects ecological conditions and the management of resources in Yolo County, California. For example, gophers and their burrows create habitat for many other species (Vaughan, 1961), and affect the numerical distributions of special status, rare species in Yolo County (Smallwood, 1995; Erichsen et al., 1996; Smallwood et al., 1996, 1998). Gophers or their commensal burrow occupants are important prey items of Swainson's hawk (*Buteo swainsoni*), short-eared owl (*Asio flammeus*), greater Sandhill crane (*Grus canadensis tubida*), northern harrier (*Circus cyaneus*), white-tailed kite (*Elanus leucurus*), white-faced ibis

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(*Plegadis chihi*), prairie falcon (*Falco mexicanus*), and other species. Gopher burrows in grassland and vernal pool complexes, which are the natural habitats of pocket gophers in the Central Valley of California, are used for nesting or refuge by giant garter snake (*Thamnophis gigas*), California tiger salamander (*Ambystoma californiense*), western spadefoot toad (*Scaphiopus hammondii*), and western burrowing owl (*Athene cunicularia*). These species are listed by federal and state government agencies as Threatened, Candidates for listing, Species of Special Concern, or Fully Protected. The Swainson's hawk, a species listed as threatened in California, is particularly attracted to alfalfa, where these hawks do much of their foraging on gophers (Smallwood, 1995). Furthermore, like other fossorial animals, gophers and their burrows facilitate important ecological processes (Huntly and Inouye, 1988) such as soil formation (Grinnell, 1923; Mielke, 1977; Hole, 1981) and transport of spores of mycorrhizal fungi to plant roots (Maser et al., 1978).

In Yolo County, the vast majority of gophers construct their burrows in stands of alfalfa (*Medicago sativa* L.), which is the second most valuable crop and is an important rotation crop for the County's most valuable crop — tomatoes (*Lycopersicon esculentum*). Gophers are treated as a pest because they eat alfalfa plants, bury plants with soil mounds, disrupt irrigation flow, and create an uneven ground surface that damages machinery (Miller, 1953; Lewis and O'Brien, 1990; Loeb, 1990). This machinery, used for herbicide applications and alfalfa harvest, is driven across the alfalfa field many times during the 4–5 year life of the stand. The use of this machinery compacts the soil, thereby slowing soil penetration of water applied by flood or sprinkler irrigation. Miller (1953) estimated that gophers damage at least 25% of the alfalfa in the Sacramento Valley, California, and Luce et al. (1981) estimated that gophers reduce yield up to almost 50% in the mid-western US. One-third of the growers attempt gopher control using toxicants, but usually with little effect (Smallwood and Geng, 1997). Many growers are unaware that gophers also create void space with their burrows (Smallwood and Morrison, 1999a), which channels irrigation water past the compacted top soil layer to the deep root zone of alfalfa where it is most useful to the plants (Smallwood and Geng, 1997). Gophers can consume less alfalfa than is produced by irrigation via gopher burrows, for an average net gain in yield of 21% (Smallwood and Geng, 1997; also see Dalquest, 1948). Therefore, the factors influencing gopher density in alfalfa are thought also to influence the status of special status species as well as profit margins in this agricultural county.

Understanding the factors influencing gopher density would serve both production and conservation goals in agricultural landscapes. Recent syntheses of density estimates indicated serious shortfalls in understanding of density (Smallwood and Schonewald, 1998). The study area size was found to explain much of the variation in density when log density was regressed on log study area size for Falconiformes (Village, 1984; Smallwood, 1995), mammalian carnivores (Smallwood and Schonewald, 1996), primary mammalian herbivores (Blackburn and Gaston, 1996), and pocket gophers (Smallwood and Morrison, 1999b). The regression equations predicted densities that were consistently higher than would be expected of randomly selected study sites (Smallwood, 1995; Smallwood and Schonewald, 1996; Smallwood and Morrison, 1999b). This pattern emerged probably because investigators usually chose study sites based on a priori knowledge of high density. The high density areas are the naturally occurring population clusters (Taylor and Taylor, 1977, 1979; den Boer, 1981; Hanski, 1994). Density might decline as study area boundaries encompass more of the intervening animal-free space between the high density clusters. Therefore, our understanding of animal density might change significantly by choosing study sites in a non-conventional manner, such as randomly or systematically.

Some of the published estimates of gopher density were made in alfalfa stands, but like other estimates, these alfalfa stands were chosen for known high density of gophers, and revealed only that the study area size and body mass explained a substantial amount of the variation in gopher density (Smallwood and Morrison, 1999b). However, Smallwood and Morrison (1999b) found the 100 published estimates to vary 390-fold from low to high density and to average $53 \pm 49\,\text{ha}^{-1}$. None of the other measured variables could explain additional variation in gopher density, including counting method, estimation method, vegetation complex, and topography. Smallwood and Morrison (1999b) corroborated the speculations of Smallwood and Schonewald (1996) that investigators are biasing their results by choosing study sites based on a priori knowledge of high density.

The purpose of this study was to test whether the variation in gopher density among opportunistically chosen alfalfa stands can be explained by study area size (i.e., field size), as well as farming practices and attributes of the field and surrounding landscape. Williams and Cameron (1984) suggested that linear elements of the landscape provide dispersal corridors for gophers, so this study also tested whether pocket gopher density would be greater in fields surrounded by a greater density of road verges, railroad tracks, canal banks, and stream channels. Barnes (1971) suggested that juxtaposition of the study area to gopher habitat would affect density. This study tested whether gopher density in alfalfa correlates with the proportion of the surrounding area in alfalfa production or other land uses suitable for gophers and their dispersal. It also tested whether sandy soils would support more gophers, consistent with the results of Downhower and Hall (1966) and Davis et al. (1938). Season of the year also has been found to influence gopher density (Miller, 1946; Bandoli, 1981; Smallwood and Erickson, 1995). This study specifically tested whether gopher density in alfalfa relates to: (1) spatial extent of the alfalfa field; (2) age of the alfalfa stand; (3) season; (4) irrigation practices; (5) time since attempted gopher control; (6) field shape; (7) field edge versus interior conditions; (8) the composition and depth of soil; (9) the density of road verges, canal banks, railroad tracks, and other linear structures within 1000 m that can be used as corridors by dispersing gophers; and (10) the proportion of land within 500, 1000, and 3000 m of each alfalfa stand that is composed of other alfalfa stands, pastures, orchards, vineyards, grasslands, riparian vegetation, and other land uses and vegetation complexes usable by gophers. These influences not only would elucidate understanding of density, but they would improve the efficiency of gopher management on agricultural landscapes.

2. Methods

2.1. Study location

Observations of 15,008 active gopher burrows were mapped during 134 counts in 39 commercial stands of alfalfa (Table 1) grown by 15 farmers in the Counties of Yolo, Butte, and Solano, California (38°30′–39°22′N, 121°36′–122°4′W; 12–78 m elevation). The fields were chosen opportunistically by University of California Cooperative Extension Farm Advisors, and most were in Yolo County (Fig. 1). The soils were loams and clays, including the following FAO (1988) soil classifications (followed by the names of the Soil Taxonomy of National Resources Conservation Services, US Department of Agriculture): Cambisole (Brentwood silty clay loam), Vertisols (Capay silty clay, Willows soils — flooded), Luvisols (Hillgate loam, Marvin silty clay loam, Myers clay, Rincon silty clay loam, San Ysidro loam, Sycamore silt loam — flooded, Tehama loam, Zamora loam), Solonetz (Pescadero soils — flooded), Fluvisols (Reiff very fine sandy loam), Phaeozems (Sacramento soils — flooded), Cambisols (Sycamore complex — drained and flooded), Regosols (Yolo silt loam). Gopher burrow systems were counted during the summer and autumn of 1992, spring, summer and autumn of 1993, and spring and summer of 1994. Alfalfa in the Sacramento Valley is typically grown for 5 years in rotation with tomato, maize, and wheat (*Triticum aestivum* L.). It is flood irrigated along bordered strips and harvested 6 or 7 times from March to October. Some of the alfalfa stands were removed after the first sampling effort and some were planted 1–2 months prior to the last sampling effort.

2.2. Gopher mapping

Irrigation borders served as transect because gophers orient their burrows along these borders (Miller, 1957). The locations of gopher burrows were mapped in alfalfa fields using the pacing method of Smallwood and Erickson (1995), which relies on gopher territoriality separating individual burrow systems. Each burrow system typically contains one adult gopher (Miller, 1946; Hansen and Remmenga, 1961; Bandoli, 1981), so our density estimates were specifically of burrows, but indicative of the adult gopher population (Smallwood and Erickson, 1995). Gopher burrows in alfalfa tended to be a little farther apart than those counted in forest clear-cuts by Smallwood and Erickson (1995), so burrow centers were approximated at every 15 m wherever contiguous sign (i.e., fresh mounds and plugged feeding holes) made

Table 1
Attributes of the alfalfa fields where locations of gopher burrow systems were mapped in the Sacramento Valley, California

Field	Grower	No. of counts	Mean density ± S.D.	Hectares	Edge to interior ratio	Months since sowing upon first count
1	A	5	9.7 ± 5.9	55	67	22
2	A	5	16.1 ± 5.7	26	108	33
3	A	7	2.2 ± 2.2	19	94	8
4	A	8	7.7 ± 6.0	13	126	8
5	B	5	10.5 ± 3.4	17	126	33
6	B	1	31.7	12	126	66
7	B	2	11.2 ± 3.5	42	60	8
8	B	2	2.1 ± 2.3	33	90	8
9	C	5	25.7 ± 10.4	12	137	16
10	C	5	28.5 ± 11.3	7	160	18
11	C	4	16.8 ± 8.4	18	96	43
12	C	1	23.9	24	77	55
13	C	4	23.0 ± 9.8	17	114	31
14	C	5	15.4 ± 14.5	28	82	5
15	D	5	13.7 ± 7.8	30	80	18
16	D	4	2.2 ± 1.0	28	79	4
17	D	5	9.2 ± 7.3	20	100	4
18	D	4	24.4 ± 6.4	15	79	17
19	D	5	17.9 ± 9.8	21	154	16
20	E	5	13.5 ± 5.8	24	89	30
21	F	1	14.1	28	76	55
22	F	1	13.1	57	61	55
23	G	1	16.6	22	91	54
24	H	4	18.9 ± 13.8	17	108	33
25	I	1	32.8	63	50	55
26	J	5	2.7 ± 1.3	28	84	21
27	J	5	1.8 ± 1.2	23	91	10
28	J	3	1.5 ± 1.1	33	80	34
29	J	5	3.3 ± 1.6	17	100	21
30	J	3	0.2 ± 0.2	24	94	7
31	J	2	5.1 ± 0	8	238	22
32	K	5	28.3 ± 9.8	62	57	34
33	L	4	30.8 ± 7.4	32	75	19
34	L	2	26.2 ± 0	30	82	48
35	M	1	8.0	15	117	32
36	N	2	14.1 ± 13.3	4	199	66
37	N	2	4.9 ± 0	2	287	42
38	D	2	3.5 ± 2.5	23	87	30
39	D	2	4.3 ± 5.0	28	82	6

distinctions of individual burrow systems impossible. In other words, an additional burrow system was counted every 15 m when clear gaps between clusters of mounds could not be seen. Gopher burrows were counted within 7.7 m of each irrigation border, or within a 15.4 m wide strip transect. Density estimates were calculated by dividing the burrow count by the area of the strip transect.

Occupied gopher burrows were identified by the presence of recently excavated soil mounds and tunnel plugs. Recent gopher sign in alfalfa is easily identified, because the monthly flood irrigation causes the loosely arranged soil particles in recently excavated soil to coagulate, thus forming a smooth, hardened surface. The entire field was sampled along every other irrigation border during the first visit, and along

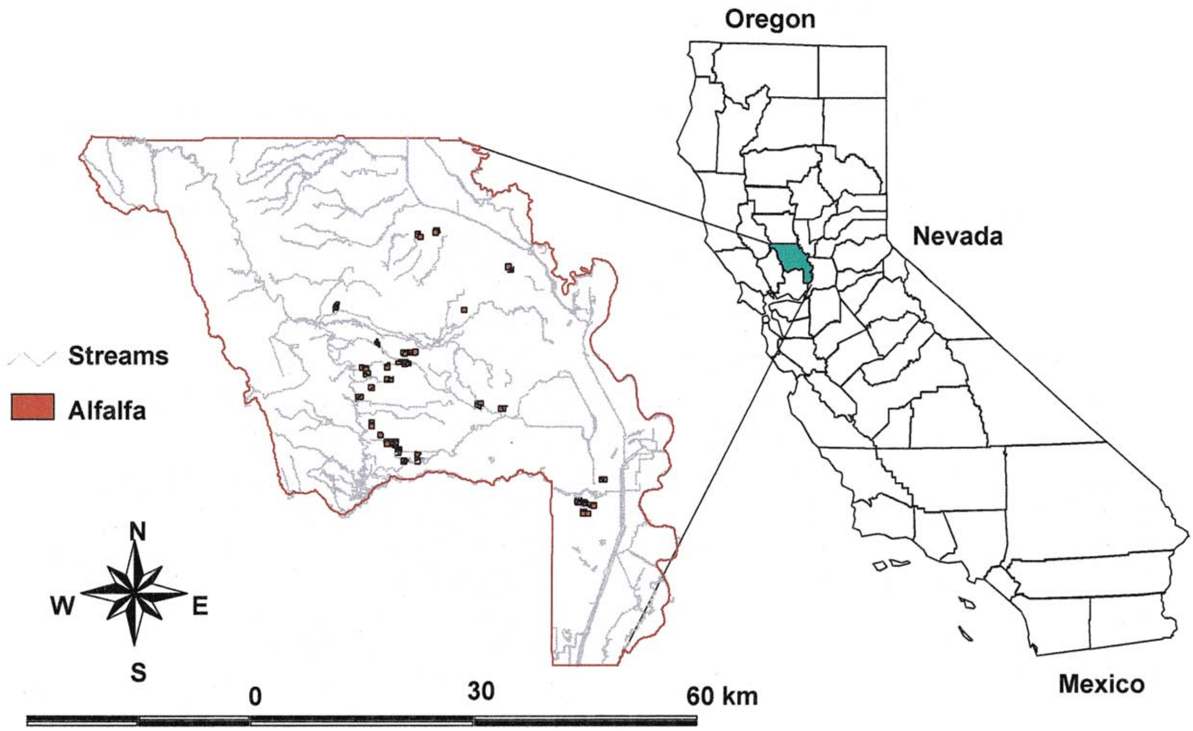

Fig. 1. Gopher burrows were mapped and counted within 35 alfalfa stands (shaded squares) in Yolo County, California, during 1992–1994.

every fourth or eighth border during later visits, once the distribution across the field had already been characterized during the earlier visits. (Density estimates did not differ significantly among counts made from every second, fourth or eighth irrigation border.) Gopher burrows were marked on maps of each alfalfa field, drawn at a scale of 1 cm = 20 m.

2.3. Cultural practices and field attributes

Farmers were interviewed to obtain information on age of stand (months since sowing), annual frequency of flood irrigation (all participating growers used flood irrigation), amount of water applied, gopher control practices, and total yield per month (harvest is monthly) and year. These data were collected for most fields. Although flood irrigation was developed partly as a gopher control practice (Dixon and De Ong, 1917), in this paper 'control' refers to application of strychnine bait to gopher burrows.

The effect of the field edge was analyzed by separating the gopher count and transect area into interior and edge sections at 20 m within the field perimeter, which should span the combined widths of 1–2 gopher home ranges. Therefore, gopher density estimates were compared among fields through time and on the edge and interior sections, along with multiple factors that could conceivably influence gopher density in alfalfa.

2.4. Landscape attributes

Arc/Info geographic information system (GIS) was used to combine spatial data representing land use, natural vegetation complexes, roads, streams and canals, and soils in Yolo County (Table 2). (Four alfalfa stands in Butte and Solana Counties were excluded due to lack of spatial data.) The land use data were provided by the California Department of Water Resources, which mapped agricultural and other land uses observed in 1989 from aerial photos at a scale of 1:24,000. These same photos were used by Smallwood and Yolo County personnel to digitize the patch boundaries of 26 vegetation complexes (Smallwood et al., 1998). All land uses surrounding each alfalfa

Table 2
Attributes of the alfalfa fields where gopher burrow distributions were mapped in Yolo County, and Pearson's correlation coefficient estimated between log density of gophers and each landscape and field attribute

Variable	Mean	S.D.	Minimum	Maximum	Correlation with log density
Gopher density in alfalfa field (number/ha)	14	10.2	0.2	32.8	–
Estimated number of gophers in alfalfa field	422	479	5	2328	0.61**
Hectares of alfalfa stand	26.9	14.0	7.3	62.8	0.04
Edge to interior ratio of alfalfa stand	97	35	50	238	0.10
Months since sowing of alfalfa	34	16	11	68	0.50**
Annual frequency of irrigation	6.9	2.2	4	11	−0.45**
Percent of field area composed of sandy soils	15.2	7.7	8.0	42.5	0.25**
Percent of field area composed of silty soils	24.0	4.6	11.5	30.8	−0.32**
Percent of field area composed of clay soils	35.0	5.8	20	48.5	0.01
Soil pH	7.6	0.4	6.5	8.3	−0.12
Soil organic matter (% of volume in top meter)	0.6	0.5	0	2.5	−0.05
Soil depth (cm)	23.7	6.1	5.0	36.0	−0.16
Soil bulk density ($g\,cm^{-3}$)	1.48	0.04	1.37	1.65	0.31**
Gopher habitat within 500 m (% of area)	26.8	19.7	0	75.2	0.42**
Gopher habitat within 1000 m (% of area)	26.0	15.2	0.4	53.1	0.35**
Gopher habitat within 3000 m (% of area)	23.6	6.6	6.4	43.8	0.30**
Alfalfa within 500 m (% of area)	25.8	16.5	1.9	73.0	0.40**
Alfalfa within 1000 m (% of area)	20.7	13.3	0.5	48.5	0.38**
Alfalfa within 3000 m (% of area)	13.7	5.2	2.6	25.4	0.26**
Natural vegetation within 500 m (% of area)	0.7	1.0	0	3.4	0.18*
Natural vegetation within 1000 m (% of area)	1.2	1.4	0	5.2	0.12
Natural vegetation within 3000 m (% of area)	4.5	4.5	0.2	21.9	0.21*
Meters of streams/canals in 1000 m buffer	3061	1965	0	7674	−0.38**
Meters of roads/highways in 1000 m buffer	6406	3613	0	14282	0.03

* $P < 0.05$.
** $P < 0.01$.

field were monitored and the landscape map updated during the study.

The GIS soil layers was used to estimate the percent of the area in each alfalfa field composed of sand, silt, and clay soils, based on the particle size distribution in the top soil layer. For example, sandy soils composed an average of 15% of the top soils among the 35 alfalfa fields sampled in Yolo County. Additionally, the weighted averages of pH, soil bulk density, and organic matter content, were estimated based on the proportional areas of the soil types and the typical association between these attributes and the soil types.

Sampling buffers were created using GIS around the boundaries of each alfalfa field in which gopher burrows were mapped and counted (Fig. 2). These buffer areas extended 500, 1000, and 3000 m for land use and vegetation complexes, and 1000 m for verges of roads, railroad tracks, and canals. The percent of the buffered area was estimated for each land use and vegetation complex. Each land use category and vegetation complex was rated for its habitat quality (Table 3), similar to the types of ratings summarized in Lidicker (1995). Ratings ranged between 0 and 1 corresponding with a gradient of gopher density typically observed between inhospitable lands and fourth year alfalfa stands. For example, gophers do not establish burrows in soils used for growing wheat, tomatoes, and rice, nor in soils supporting freshwater marsh. These land uses and vegetation complexes were rated zero (Table 3). Orchards were rated 0.5 because they typically support half the density of gophers compared to fourth year alfalfa (Smallwood, unpublished data; Smallwood, 1995). Marshy areas were rated 0.2 due to their upland areas and embankments, which typically support gophers. The habitat ratings were multiplied by the percentages of the corresponding land uses and vegetation complexes, and these products

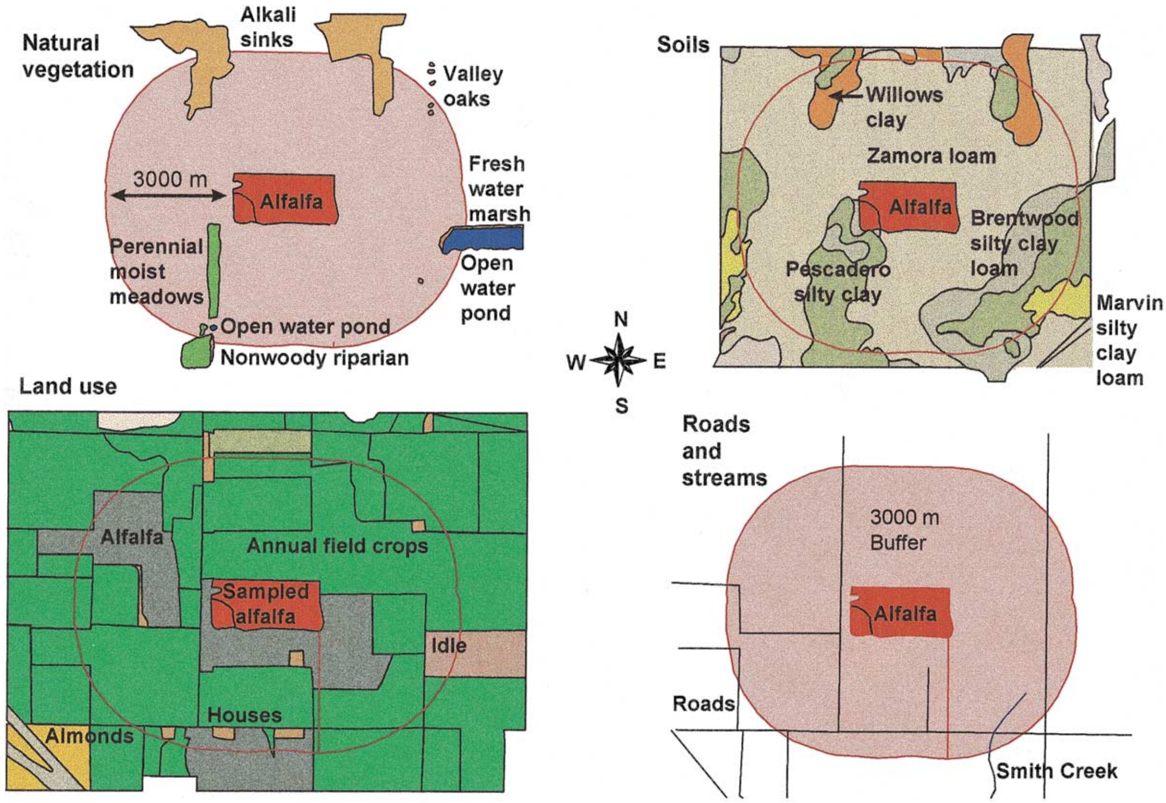

Fig. 2. An illustrated example of a 3000 m buffer that was constructed around an alfalfa stand using GIS, and containing data representing natural vegetation complexes, soils, land use, and possible dispersal corridors. The road verges and stream banks and certain vegetation complexes, soils, and land uses serve as gopher habitat and potential source areas for dispersing gophers.

Table 3
Land uses and vegetation complexes, their aggregation to categories and classes, and their gopher habitat quality ratings as a fraction of 1.0[a]

Landscape description	Rating as gopher habitat
Alfalfa, native grasses, freeways and railroads (verges), riparian valley oak (*Quercus lobata*), mixed riparian forest, cottonwood (*Populus fremontii* S.) forest, riparian willow (*Salix* spp.) scrub	1.0
Pasture, mixed pasture, native pasture, farmsteads, feedlots, lawn areas	0.8
Disturbed grassland (a mix of exotic species)	0.7
Native woodland, groves of black walnuts (*Juglans californica* S.), valley oaks scattered in agriculture, orchards and vineyards	0.5
Non-woody marsh/meadow	0.4
Eucalyptus (*Eucalyptus* spp.) groves	0.3
Perennial moist meadow, ruderal wetlands, freshwater marsh, vegetated open water, vernal pool, alkaline sink scrub, artificial wetlands, gravel wash along stream	0.2
Annual field crops, flowers and nursery, turf farm, idle land (previously cropped), urban, schools, extractive industries, warehouses, tank farms, substations, industrial, fruit and vegetable processing plant, sewage treatment plant, residential, airport runways, parking lots, oiled surfaces, reclamation site, open water pond	0.0

[a] Ratings ranged from 0 to 1, representing areas where gophers cannot occur to where they occur at higher densities, respectively.

were summed to estimate the total percentage of habitat within the buffers surrounding each alfalfa stand.

2.5. Analytical methods

Derived data from GIS overlays were added to existing data and a correlation matrix was examined to identify inter-correlated variables and to estimate correlation coefficients between gopher density and the independent variables. Linear least-squares regression analysis was used to test hypotheses, and a stepwise variable entry was used to construct a multivariate model. In this model, the standardized slope coefficient, β, informed of each variable's relative contribution to the total sum of squares explained by the model. To test for the effects of stand age and season, all 134 counts of burrows were used in multiple regression analysis, including multiple counts from the same field whenever they were available.

3. Results

3.1. Gopher density

Gopher density in alfalfa varied only 43-fold from low to high density, and averaged only $14 \pm 10\,\mathrm{ha}^{-1}$. Density regressed on study area size predicted no difference in density between the smallest and largest alfalfa fields sampled ($r^2 = 0$):

$$\log \mathrm{density} = 0.895 + 0.014 \log \mathrm{hectares} \qquad (1)$$

Although the estimated annual amount of water applied to alfalfa fields did not correlate with gopher density ($r = 0.04, n = 111, P = 0.70$), the annual frequency of irrigation did ($r = -0.32, n = 111, P < 0.001$). Gopher density did not correlate with the edge to interior ratio nor with alfalfa yield during the month preceding the gopher burrow count.

Gopher density in alfalfa was most responsive to the age of the stand (time since sowing), season, edge versus interior field conditions, annual frequency of irrigation, and gopher control. The log density increased with log months since sowing ($r = 0.50, n = 133, P < 0.01$). Average gopher density increased as average alfalfa yield decreased until the fifth year of production, when gopher density reached an asymptote and average alfalfa yield returned to levels indicative of young stands (Fig. 3). As the gopher population increased into the third year of production, the 95% confidence intervals widened. Although gopher density differed among years of production (ANOVA: $F = 9.7$, d.f. $= 4, 133$, $P < 0.001$), Tukey's Honestly Significant Difference test produced P-values near 1.0 among third, fourth, and fifth years of production for both field edges and interiors. The densities between first and second years along the edge were significantly different at the 5% level, but not within the interiors. The differences between either first or second years to the third, fourth, and fifth years were significant at the 1% level for both edge and interior densities.

Average gopher density increased during spring to an early summer peak, then declined into autumn (ANOVA: $F = 6.1$, d.f. $= 3, 133$, $P < 0.001$). This seasonal trend in gopher density corresponded with the trend in alfalfa yield until late-summer and autumn, when gopher density no longer decreased at the rate of alfalfa yield (Fig. 3).

3.2. Edge versus interior

Gopher density was consistently greater along the field edge than in the interior (paired-samples: $t = 8.34$, d.f. $= 133$, $P < 0.001$). Using the Smirnov two-sampled test of the null hypothesis that two samples represent the same population (Conover, 1971), the frequency distributions of density at the field edge and interior differed at the 1% level during the first and second years of production, at the 10% level during year 3, at the 5% level during year 4, and they did not differ significantly during the fifth year. For brevity of presentation in Fig. 4, data were consolidated between the first 2 years and among the last 3 years, as warranted by the corresponding lack of significant differences in density. Gophers appeared to invade the fields along the edges, then proceeded to saturate the field with burrows as the alfalfa stands grew older.

3.3. Landscape context of alfalfa stands

The estimates of both density and number of gophers varied widely among the 35 alfalfa fields (Tables 1 and 2). Most of these alfalfa fields were grown on Yolo loam soils, but these varied in

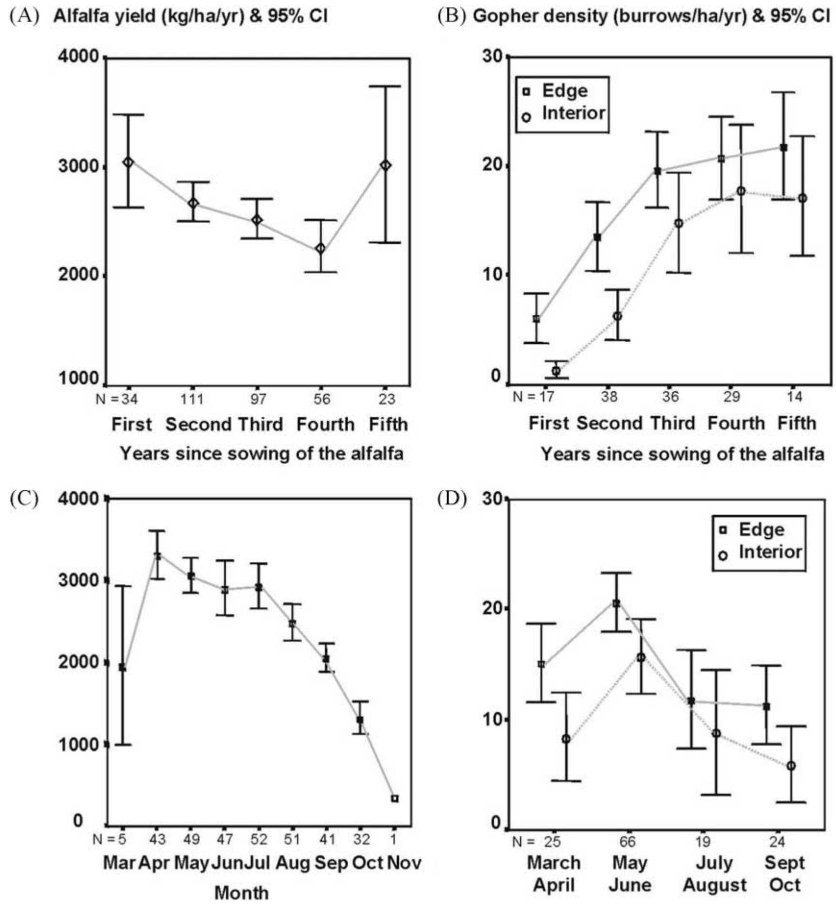

Fig. 3. Comparison of (A) annual and (B) seasonal trends in alfalfa yield with (C) annual and (D) seasonal trends in gopher density along the field edge and within the interior.

consistency in percentage of sand, silt, and clay particles. However, the tillage used during other phases of the rotation, and the deep-ripping used after alfalfa production, would have changed the soil particle size distribution, the depth of the top soil layer, the organic matter content, the soil bulk density, and the pH. The soil attributes were therefore useful only as indicators of soil conditions in each field.

Some alfalfa fields were almost completely isolated from other alfalfa fields within 500–3000 m, whereas others were adjacent to multiple alfalfa fields comprising up to 73% of the surrounding area. The alfalfa within 500 m appeared to serve as most of the source habitat from which gophers could originate ($r = 0.91$, $P < 0.001$). Alfalfa served as the dominant habitat of gophers on the valley portion of Yolo County (Table 2). Natural vegetation useful for gophers averaged only 0.7% of the 500 m buffer (an average of 1.3 ha per the average buffer of 187 ha) and only 4.5% of the 3000 m buffer (an average of 158 ha per the average buffer of 3555 ha).

Some of the landscape attributes were correlated. For example, the percentage of alfalfa within 1000 m increased with more sandy soils ($r = 0.57$, $P < 0.001$), and decreased with more silty soils ($r = -0.62$, $P < 0.001$). The percentage of natural vegetation within 1000 m decreased for fields with higher clay content ($r = -0.51$, $P < 0.001$). The length of stream within 1000 m of the field increased with increasing depth of soil ($r = 0.42$, $P < 0.001$) and

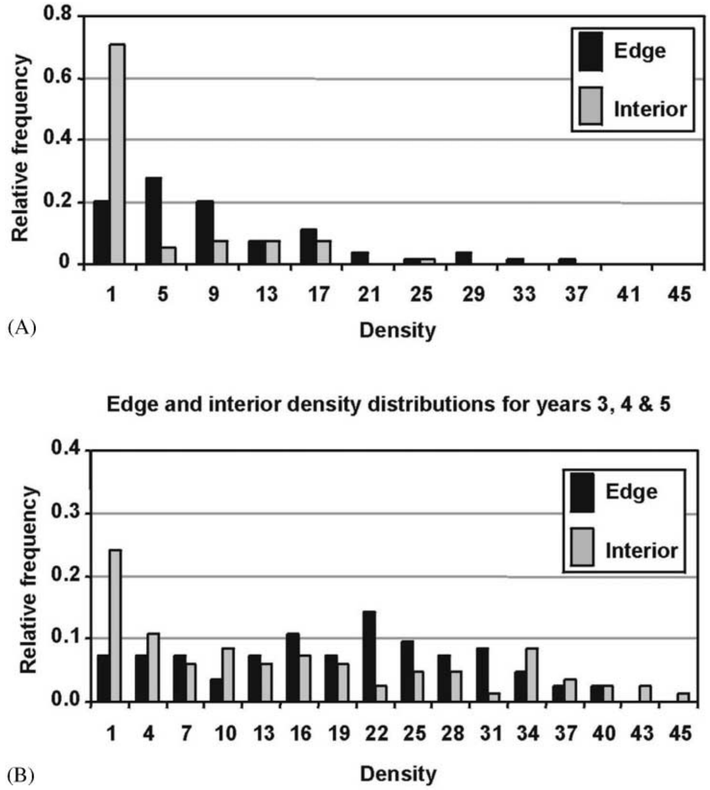

Fig. 4. Shifts in relative frequency distributions of gopher density at the field edge and interior in (A) first and second year stands and (B) third, fourth and fifth year stands.

higher percentages of silty soils ($r = 0.39$, $P < 0.001$). The frequency of irrigation decreased in fields with higher soil bulk density ($r = -0.41$, $P < 0.001$). The soil attributes were highly inter-correlated and could only be used one at a time in developing linear models so as to avoid multicollinearity.

3.4. Multivariate model of gopher density

Landscape attributes explained a substantial amount of the variation in gopher density among the alfalfa fields we studied in Yolo County ($R^2 = 0.73$, root MSE = 0.28, d.f. = 6, 109, $P < 0.0001$; Table 4). Stand age and the annual frequency of irrigation explained the most variation in log density, and source area within 500 m and the season of the year explained the next largest amounts of variation (β in Table 4). By accounting for the effects of stand age and annual frequency of flood irrigation, field size was recognized as a significant explanatory variable (Fig. 5). After regressing log density on log age of stand, annual frequency of irrigation, season, percent sand in soil, and log hectares of transect, the unstandardized residuals correlated negatively with the percentage of available habitat as the size of the buffer increased (Fig. 6). In other words, source areas for gophers appeared to occur nearby each alfalfa stand.

3.5. Gopher control

Gopher control appeared to be more effective among populations subjected to control efforts 7–18 months previously (ANOVA: $F = 3.05$, d.f. = 5, 133, $P < 0.012$), especially in the field interiors (Fig. 7). However, the variable representing months since gopher control did not meet the tolerance level of 0.05

Table 4
Unstandardized (*b*) and standardized (*β*) slope coefficients estimated for predictor variables of log density, using linear least-squares regression[a]

Predictor variable	Regression coefficients			
	a	*b*	S.E. of *a* and *b*	*β*
Intercept	−0.077	–	0.30	–
Habitat area (%) within 500 m of field	–	0.0083	0.002	0.312
log months since sowing of alfalfa	–	1.094	0.115	0.520
Annual frequency of irrigation	–	−0.104	0.014	−0.428
Season of year	–	0.199	0.041	0.250
log hectares of transect (field size)	–	−0.549	0.153	−0.201
Percent sand in field's top soil layer	–	0.0089	0.003	0.155

[a] The unstandardized slope coefficient is useful for model prediction of density, and the standardized slope coefficient informs of the variable's relative contribution to the total sum of squares explained by the model.

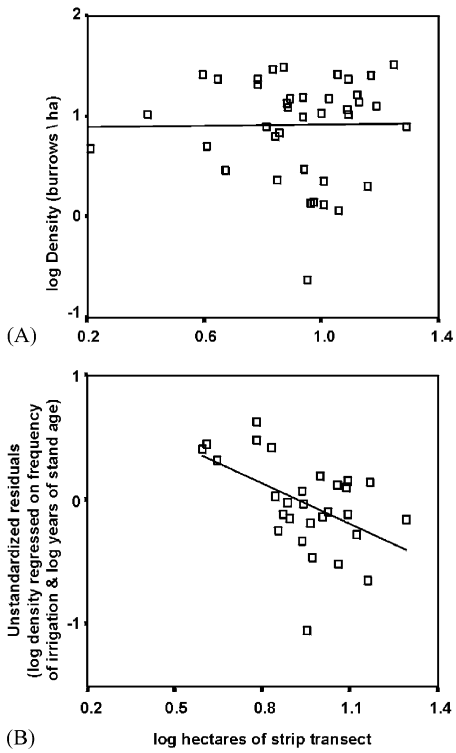

Fig. 5. Density of gophers and field size. Gopher density in alfalfa stands apparently did not change with increasing field size (A) as it had among study sites chosen based on prior knowledge of high density (Smallwood and Morrison, 1999b), but the pattern observed at other sites emerged when considering the effects of annual frequency of irrigation and age of alfalfa stand (B).

for inclusion in the multiple regression of density. Also, the unstandardized residuals from the multiple regression did not differ by months since gopher control in the same manner nor magnitude as did density. After removing the effects of stand age, frequency of irrigation, and field size, which apparently interacted with months since control, gopher density at the field edge did not differ significantly with months

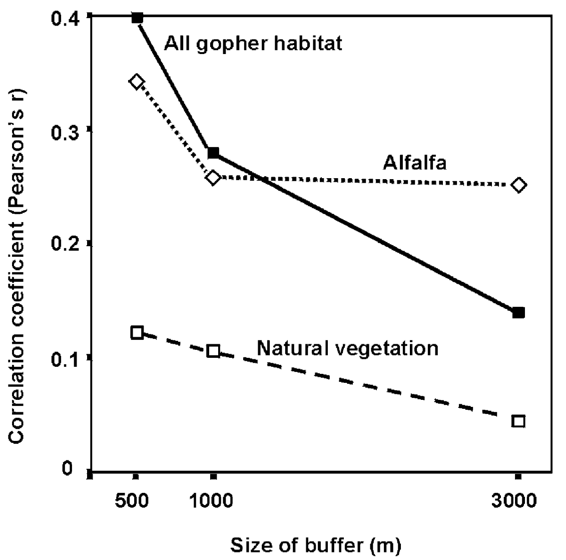

Fig. 6. Correlation between gopher density and size of buffer. The correlation declined between the residual variation in density and the available gopher habitat surrounding the alfalfa field as the buffer size increased, especially when examining only the available alfalfa around the sampled field.

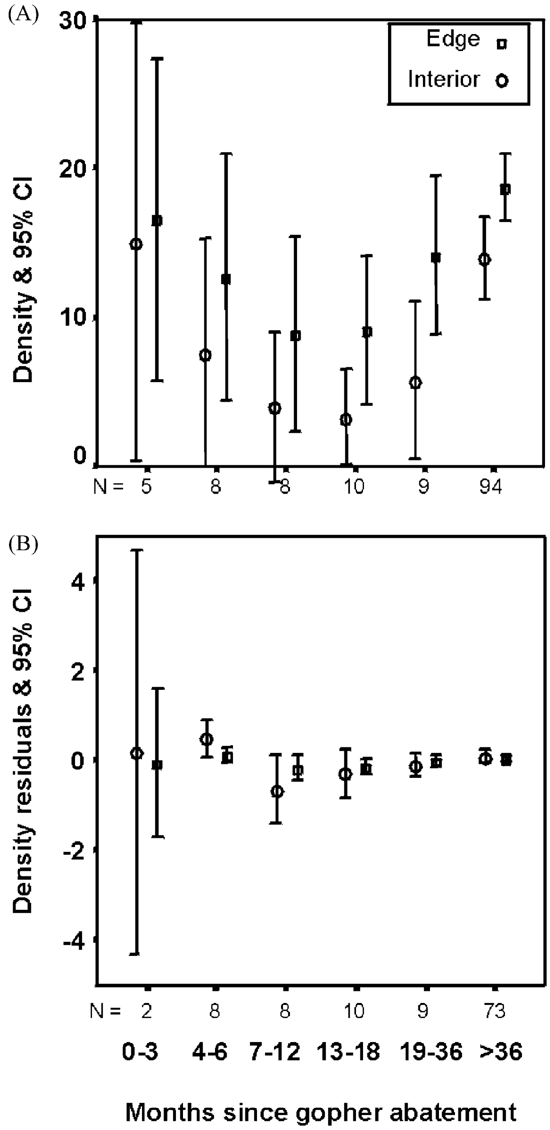

Fig. 7. Gopher control and gopher density. Although gopher density appeared to decline until 18 months since poisoning gophers (A), this decline vanished after considering the effects of annual frequency of irrigation, age of alfalfa stand, and size of field (regression residuals, B).

since control (ANOVA: $F = 1.94$, d.f. $= 5, 109$, $P < 0.094$), and gopher density in the field interiors was highest 4–6 months following control (ANOVA: $F = 3.16$, d.f. $= 5, 109$, $P < 0.011$).

4. Discussion

4.1. Gopher density

Gopher density averaged per alfalfa field did not decline with increasing study area size in the same manner as among conventional study sites (Smallwood and Morrison, 1999b). It was originally believed that this pattern would result by not choosing study sites based on prior knowledge of high density. However, gopher density in alfalfa declined with study area size, once the effect of stand age, management practices, and landscape context were considered (Fig. 5). Although alfalfa is a rich resource for gophers, the pattern of gopher density in alfalfa resembled the pattern observed in other plant communities. Also, gopher density in alfalfa averaged four times less than elsewhere. This difference in density was due to: (1) inclusion of young alfalfa stands in the sample that had yet to be invaded by gophers; (2) an average study area of 25 ± 14 ha, which was >10 times larger than the average study area of 2.4 ± 8.9 ha used for published estimates; and (3) frequent flood irrigation. This study added to the argument that investigator choice of study site and study area size substantially influences the density estimate (Smallwood and Schonewald, 1996).

Quantifying the effects of succession on gopher density was constrained to the period of time during which each alfalfa stand was grown, which was usually 5 years. After planting, the stand improved with a slowly increasing gopher density for about a year, then degraded as the gopher density grew beyond one gopher per 100 m of irrigation border, or 6.7 gophers/ha (Smallwood and Geng, 1997). Gopher density increased rapidly between 1 and 1.5 years, and saturated most stands after 2.5–4 years. One 7-year old alfalfa stand remained saturated with gophers, and the stand appeared healthy with an unbroken and lush canopy. What the gopher populations would have done in older stands of alfalfa remains unknown. Gopher density increased with age of cover crop in vineyards as a power function through 10 years since sowing (Smallwood, 1996).

Gopher density in alfalfa changed seasonally, as if tracking the yield. October is when gopher populations typically peak in number (Miller, 1946; Howard and Childs, 1959; Reid et al., 1966; Bandoli, 1981), but in alfalfa the number of active burrows were fewest during October. Average gopher density in field interiors was declining through October, along with average alfalfa yield, whereas gopher density along the field edges had stabilized by this time (Fig. 3). Gopher density in alfalfa might have declined during autumn due to the intense predation by large foraging groups of Swainson's hawks preparing for their annual migration to Central and South America in early October (Smallwood, 1995). The field edge may provide some sanctuary for gophers during this time, perhaps because they are not as frequently forced to the ground surface during flood irrigation.

The field edge was typically the first part of the field inhabited by gophers following sowing of the alfalfa, and also harbored the greatest proportion of survivors of seasonally inclement conditions and gopher control efforts. The field edge likely harbored survivors whose progeny colonized new and previously vacated burrows in the field interior. The field edge was preferred by gophers from sowing of the alfalfa stand to its rotation to the next crop. Similarly, Black and Montgomery (1991) reported highest gopher densities along the margins of a colluvial deposit, where the soils were deeper and easier to excavate than surrounding soils. The soils at the edges of alfalfa fields may also be deeper and easier to excavate, but some other quality might also render edges attractive to gophers.

The numerical distribution of invading gophers into a first year alfalfa field tracked the yield gradient (Smallwood and Geng, 1997), indicating that gophers searched for optimal resource patches (Tilman, 1983; Hanski, 1994), which also might have corresponded with nitrogen content in the soil and higher plant biomass (Tilman, 1983). After the first year of invasion, the numerical distribution became dependent on the previous distribution during the early phase of the invasion. The locations of new burrows (home ranges) becomes influenced more by existing burrows than by the spatial pattern of preferred resources. In other words, as the invasion progressed beyond the field edge and first few interior clusters, the gopher distribution in that field came to be influenced by factors that were intrinsic as well as extrinsic to the population. Such a transition would explain the shift in skewness and kurtosis among frequency distributions of density as the stands grew older (Fig. 4). Right skewness and leptokurtosis, indicative of an aggregated distribution, both decreased from the first 2 years to the last 3 years as the initial population clusters along the field edges and most productive alfalfa patches spread into the field. As gophers saturated the field from the edge, the distribution shifted from clumped to regular, and theoretically graded through random during the middle stages of field invasion.

Gopher density in alfalfa, adjusted by management practices, the time needed for population growth, and landscape context, still changed with the size of the field in a log–log pattern similar to Smallwood and Morrison (1999b), and the regression slope for the populations within the field interiors was similar to the slope estimated for published estimates (−0.58 versus −0.45, respectively). The physical and biological forces underlying this log–log relationship between density and field size are open to speculation. For example, gophers removed by farmers or predators from the interiors of increasingly larger fields might be replaced at an increasingly slower rate, similar to the patterns quantified for predatory arthropods recovering from the spraying of pesticides on commercial stands of wheat (Duffield and Aebischer, 1994), thereby leaving increasingly larger vacant areas at any given time.

Previous estimates of gopher density were made without any quantification of the landscape conditions, thus preventing any hypothesis testing for landscape effects other than crude comparison of text descriptions among study sites (Smallwood and Morrison, 1999a,b). Smallwood and Morrison (1999a,b) used Kuchler (1949) classification to aggregate the diverse descriptions of vegetation from among the published reports of gopher density, but they were unable to explain any of the variation in gopher density using this approach. Descriptions of soil and surrounding land cover and land uses were too gross and too rare for comparison among these studies.

Contrary to expectations, gopher density appeared to be unaffected by the density of road verges, canal banks, railroad embankments and stream corridors. Based on previous studies involving other species of gophers (Williams and Baker, 1976; Williams and Cameron, 1984) and other species of Rodentia (La Polla and Barrett, 1993), it was thought that gopher density and their rate of spread into new alfalfa stands would be increased by more linear elements along which they can disperse. The effects of these linear elements of the landscape were likely hidden by the abundance of alfalfa surrounding most of the alfalfa stands sampled in this study. After all, these linear elements surrounded alfalfa stands, orchards, and other land uses supplying dispersing gophers. Whether gophers moved along these linear elements during dispersal seemed to be irrelevant, possibly because much of the landscape matrix was alfalfa.

Alfalfa production supports most of the gophers in the valley portion of Yolo County, because non-agricultural vegetation occurs in isolated, small patches throughout the County. The Yolo Bypass cannot support gophers because the excessive runoff periodically floods out all gophers attempting to live there. Recent surveys within the Yolo Bypass (the flood basin for the Sacramento River) have turned up no sign of pocket gophers (Smallwood, unpublished data from 1997). Source populations for invasion of new alfalfa stands therefore occur mostly in nearby alfalfa stands, the density of which depends on the soil particle distributions that include more sands. As each stand is rotated out of production every 5 years or so, virtually the entire population of gophers within the stand is destroyed. Each new alfalfa stand undergoes invasion and burrow construction by gophers, but is saturated by gopher burrows at half- to two-thirds the stand's production life. Therefore, gophers occur in a checkerboard pattern in Yolo County, in which most populations are undergoing a growth phase.

Alfalfa production excludes most of the special status species that use gopher burrows for refuge or nesting, because these species require gopher burrows that persist longer than they do in alfalfa. Removing alfalfa also displaces all, and destroys many, of the burrowing owls, tiger salamanders, western spadefoot toads, giant garter snakes, and other special status species residing in the gopher burrows. For this reason, these special status species cannot benefit from the high numbers of gophers supported by alfalfa production, and they are restricted to the vegetation complexes occurring at the thin margins of crop production within the agricultural landscape. Alfalfa stands may even serve as ecological sinks for these rarely-occurring commensal species.

Avian predators of gophers have fared better than the commensal species, given the dominance of alfalfa rotation on the landscape. In fact, flood irrigation enhances the foraging opportunities for such species as Swainson's hawk, white-tailed kite, and northern harrier. If the area in alfalfa production were to decline substantially due to changing market conditions, then the number of avian predators would also decline due to their reduced food supply. In some cases, these numerical declines would likely cause serious conservation problems for species that are already rare. Sandier soils and alfalfa production appear to be the dominating factors regulating the numerical patterns of pocket gophers in the valley portion of Yolo County, and thus also dominate the numerical patterns of many other species that rely on gophers for food or their burrows for refugia.

4.2. Gopher control

Gopher control was not warranted in most, if not all, Sacramento Valley alfalfa. Smallwood and Geng (1997) found evidence for gopher-caused damage to alfalfa to be over-estimated, especially in light of the benefits gophers bring to alfalfa production. Gophers increase their own food supply with their burrowing (Dalquest, 1948; Smallwood and Geng, 1997), and in so doing in alfalfa, they also increase alfalfa yield to the grower (Dalquest, 1948). The increase in average alfalfa yield during the fifth year of production could not have been realized had gophers caused significant damage to alfalfa beforehand (Fig. 3). Nevertheless, many alfalfa growers will continue to attempt gopher control, and so control effectiveness ought to be assessed.

Application of strychnine baits reduced gopher density in the interiors of pre-saturated alfalfa stands, but not to the levels that would achieve the goals of the growers attempting the control. Where control was attempted, gopher density usually increased at the same rate as in the other fields (Smallwood and Geng, 1997), probably because recruitment of small mammals into vacated ecological space occurs rapidly at the field scale (Sullivan, 1979, 1986). Hansen and Remmenga (1961) found gopher density to increase rapidly to even higher levels 1 year following a trap-out of gophers, and Smallwood (1999) found gophers in forest clear-cuts to have densities 2–12 times greater where the gophers were controlled compared to those not controlled 1 year previously. Alfalfa growers applying poison baits are unlikely to control gophers from alfalfa fields in California's Sacramento Valley (Loeb, 1990). Control in fourth and fifth year stands should not even be attempted. The only effective control using poison would be to apply the baits to the field edges and internal population clusters in first and second year stands or in very large stands.

The old gopher control method of flood irrigation (Dixon and De Ong, 1917) reduced gopher populations more effectively as its annual frequency was increased. Flood irrigation forced many gophers to the ground surface where they were heavily preyed upon by hawks, herons, snakes, and coyotes (*Canis latrans*). This increased predation pressure, combined with increased burrow degradation, may have overwhelmed the capacity of gopher populations to fully recover. However, flood irrigation has benefited the predators of gophers (Smallwood and Geng, 1993), including the legally defined rare Swainson's hawk (Smallwood, 1995). In loamy soils, where gophers provide a net benefit to alfalfa growers (Smallwood and Geng, 1997), increasing the height and width of irrigation borders would provide gophers greater refuge from flood irrigation and would still benefit the growers and the predators of gophers. In sandy soils, where gophers likely do not benefit growers by channeling water to the deep root zone, irrigation borders could be minimized, thereby denying gophers refuge from flood irrigation.

This study provided incomplete understanding of the factors influencing gopher density. For example, alfalfa stands were in production for too few years to observe gopher population responses to declining yields following the growth phase of the gopher population. Also, gopher body mass tends to be larger in alfalfa than in nearby natural areas (Patton and Brylski, 1987), and reproduction is year-round with more litters per female (Miller, 1946; Patton and Brylski, 1987; Loeb, 1990). By increasing body mass intra-specifically, alfalfa might also influence density, if density is truly a function of body mass (Smallwood and Morrison, 1999b). A landscape study of gophers in and around alfalfa fields, along with body mass estimates, would help identify the effects of changing spatial scale on gopher distribution. Such a study, especially using spatial analysis by distance indices, or SADIE (Perry, 1995), could further define how human interpretation of animal density changes due to study design and investigator perception (Wiens, 1989; Levin, 1992; Smallwood and Schonewald, 1998) versus spatial grain perceived by the species' individuals (Kotlier and Wiens, 1990; Holling, 1992).

5. Conclusions

Choosing study sites without first knowing the gopher distribution reduced the influence of study area size on explaining the variation in density estimates, and other variables emerged as significantly related to density. According to Smallwood and Geng (1997) and this study, comparisons of pocket gopher density need to account for: (1) edge versus interior patch conditions; (2) seral stage (e.g., age of alfalfa stand); (3) availability of habitat nearby; (4) spatial extent of the study area; (5) productivity (nitrogen content of soil, according to Tilman (1983); (6) season; (7) resource management practices affecting disturbance frequency; and (8) sufficiently long time periods (Connell and Sousa, 1983) to account for spatial shifting of populations (Taylor and Taylor, 1979) and inter-annual variability in population size (Cyr, 1997). This study found that gopher density appeared unaffected by the extent of potential dispersal corridors surrounding each alfalfa field, perhaps because gophers dispersed effectively across the landscape matrix — upland fields. The percent of potential gopher habitat within 500 m of each field was more predictive of gopher density than was the percent of habitat within 1000 or 3000 m. Gopher density is complex, indicating that population density is often defined too simplistically for operational use in ecology and for agricultural management practices. Density comparisons can be more useful by qualifying estimates by the conditions of each of the eight factors just listed. By systematically quantifying the effects of various factors on animal density, ecological theory will become more predictive and natural resources management should become more effective.

Flood irrigation forces gophers to the ground surface where they were preyed upon by special status, rare species, thereby facilitating the achievement of conservation goals. However, the field edge and the irrigation borders provide refuge from flood irrigation and the survivors and immigrants quickly repopulate the interior portions of the field. Gopher control efforts using poisons failed to achieve the goals of the growers.

In some alfalfa growing regions, cessation of gopher control would save money while also maintaining the benefits to alfalfa production through soil formation and beneficial symbiotic relationships, and it would facilitate conservation goals for special status, rare species. In these areas, gopher survival during flood irrigation should be encouraged by providing taller and perhaps wider irrigation borders. In sandy soils where gophers provide less benefit to the growers, irrigation borders should be minimized in height and width to deny gophers that refuge. Application of poison baits should be discontinued due to ineffectiveness and hazard to non-target species.

Because non-cultivated gopher habitat is rare in the valley portion of Yolo County, it was concluded that alfalfa serves as the principal habitat of gophers. However, special status species that are commensal with gophers cannot survive the rotation period of alfalfa. The results of this study should be used to encourage a greater spatial extent of permanent gopher habitat in areas of alfalfa production, such as planted grasslands along road verges, canal banks and other portions of Yolo County not used to grow crops. Such efforts could contribute substantially to the conservation of the special status species in the area, and might even enhance alfalfa production due to the benefits that gophers bring to soils in alfalfa stands (Smallwood and Geng, 1997).

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References

Bandoli, J.H., 1981. Factors influencing seasonal burrowing activity in the pocket gopher, *Thomomys bottae*. J. Mamm. 62, 293–303.

Barnes Jr., V.G., 1971. Response of pocket gopher populations to silvicultural practices in Central Oregon. In: Black, H.C. (Ed.), Wildlife and Forest Management in the Pacific Northwest. School of Forestry, Oregon State University, Corvallis, pp. 167–174.

Black, T.A., Montgomery, D.R., 1991. Sediment transport by burrowing mammals, Marin County, California. Earth Surf. Proc. Landforms 16, 163–172.

Blackburn, T.M., Gaston, K.J., 1996. Abundance–body size relationships: the area you census tells you more. Oikos 75, 303–309.

Connell, J.H., Sousa, W.P., 1983. On the evidence needed to judge ecological stability or persistence. Am. Nat. 121, 729–824.

Conover, W.J., 1971. Practical Nonparametric Statistics. Wiley, New York.

Cyr, H., 1997. Does inter-annual variability in population density increase with time? Oikos 79, 549–558.

Dalquest, W.W., 1948. Mammals of Washington. Univ. Kansas Publ. Mus. Nat. Hist. 2, 1–444.

Davis, W.B., Ramsey, R.R., Arendale Jr., J.M., 1938. Distribution of pocket gophers (*Geomys breviceps*) in relation to soils. J. Mamm. 19, 412–418.

den Boer, P.J., 1981. On the survival of populations in a heterogeneous and variable environment. Oecologia 50, 39–53.

Dixson, J., De Ong, E.R., 1917. Control of the Pocket Gopher in California. University of California Press, Berkeley, CA.

Downhower, J.F., Hall, E.R., 1966. The pocket gopher in Kansas. Univ. Kansas Mus. Nat. Hist. Misc. Publ. 44, 1–32.

Duffield, S.J., Aebischer, N.J., 1994. The effect of spatial scale of treatment with dimethoate on invertebrate population recovery in winter wheat. J. Appl. Ecol. 31, 263–281.

Erichsen, A.L., Smallwood, K.S., Commandatore, A.M., Fry, D.M., Wilson, B., 1996. White-tailed kite movement and nesting patterns in an agricultural landscape. In: Bird, D.M., Varland, D.E., Negro, J.J. (Eds.), Raptors in Human Landscapes. Academic Press, London, pp. 166–176.

FAO (United Nations Food and Agriculture Organization), 1988. FAO–UNESCO soil map of the world, revised legend. World Soil Resources Report 60. Food and Agriculture Organization, Rome, Italy.

Grinnell, J., 1923. The burrowing rodents of California as agents in soil formation. J. Mamm. 4, 137–149.

Hansen, R.M., Remmenga, E.E., 1961. Nearest neighbor concept applied to pocket gopher populations. Ecology 42, 812–814.

Hanski, I., 1994. Spatial scale, patchiness and population dynamics on land. Phil. Trans. R. Soc. London B 343, 19–25.

Hole, F.D., 1981. Effects of animals on soils. Geoderma 25, 75–212.

Holling, C.S., 1992. Cross-scale morphology, geometry and dynamics of ecosystems. Ecol. Monogr. 62, 447–502.

Howard, W.E., Childs Jr., H.E., 1959. Ecology of pocket gophers with emphasis on Thomomys Bottae Mewa. Hilgardia 29, 277–358.

Huntly, N., Inouye, R., 1988. Pocket gophers in ecosystems: patterns and mechanisms. Bioscience 38, 786–793.

Kotlier, N.B., Wiens, J.A., 1990. Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. Oikos 59, 253–260.

Kuchler, A.W., 1949. A physiognomic classification of vegetation. Ann. Assoc. Am. Geogr. 39, 201–210.

La Polla, V.N., Barrett, G.W., 1993. Effects of corridor width and presence on the population dynamics of the meadow vole *Microtus pennsylvanicus*. Land Ecol. 8, 25–37.

Levin, S., 1992. The problem of pattern and scale in ecology. Ecology 73, 1943–1967.

Lewis, S.R., O'Brien, J.M., 1990. Survey of rodent and rabbit damage to alfalfa hay in Nevada. Vertebr. Pest Conf. 14, 116–117.

Lidicker Jr., W.Z., 1995. The landscape concept: something old, something new. In: Lidicker Jr., W.Z. (Ed.), Landscape Approaches in Mammalian Ecology and Conservation. University of Minnesota Press, Minneapolis, MN, pp. 3–19.

Loeb, S.C., 1990. Reproduction and population structure of pocket gophers (*Thomomys bottae*) from irrigated alfalfa fields. Vertebr. Pest Conf. 14, 76–81.

Luce, D.G., Case, R.M., Stubbendieck, J.L., 1981. Damage to alfalfa fields by plains pocket gophers. J. Wildl. Manage. 45, 258–260.

Maser, C., Trappe, J.M., Nussbaum, R.A., 1978. Fungal–small mammal interrelationships with emphasis on Oregon coniferous forests. Ecology 59, 799–809.

Mielke, H.W., 1977. Mound building by pocket gophers (Geomyidae): their impact on soils and vegetation in North America. J. Biogeogr. 4, 171–180.

Miller, M.A., 1946. Reproductive rates and cycles in the pocket gopher. J. Mamm. 27, 335–358.

Miller, M.A., 1953. Experimental studies on poisoning pocket gophers. Hilgardia 22, 131–166.

Miller, M.A., 1957. Burrows of the Sacramento Valley pocket gopher in flood-irrigated alfalfa fields. Hilgardia 26, 431–452.

Patton, J.L., Brylski, V., 1987. Pocket gophers in alfalfa fields: causes and consequences of habitat-related body size variation. Am. Nat. 130, 493–506.

Perry, J.N., 1995. Spatial analysis by distance indices. J. Anim. Ecol. 64, 303–314.

Reid, V.H., Hansen, R.M., Ward, A.L., 1966. Counting mounds and earth plugs to census mountain pocket gophers. J. Wildl. Manage. 30, 327–334.

Smallwood, K.S., 1995. Scaling Swainson's hawk population density for assessing habitat-use across an agricultural landscape. J. Raptor Res. 29, 172–178.

Smallwood, K.S., 1996. Managing vertebrates in cover crops: a first study. Am. J. Alt. Agric. 11, 155–160.

Smallwood, K.S., 1999. Abating pocket gophers (*Thomomys* spp.) to regenerate forests in clearcuts. Environ. Conserv. 26, 59–65.

Smallwood, K.S., Erickson, W.A., 1995. Estimating gopher populations and their abatement in forest plantations. For. Sci. 41, 284–296.

Smallwood, K.S., Geng, S., 1993. Alfalfa as wildlife habitat. Calif. Alfalfa Symp. 23, 105–108.

Smallwood, K.S., Geng, S., 1997. Multi-scale influences of gophers on alfalfa yield and quality. Field Crops Res. 49, 159–168.

Smallwood, K.S., Morrison, M.L., 1999a. Estimating burrow volume and excavation rate of pocket gophers (Geomyidae). Southwest. Nat. 44, 173–183.

Smallwood, K.S., Morrison, M.L., 1999b. Spatial scaling of pocket gopher (Geomyidae) density. Southwest. Nat. 44, 73–82.

Smallwood, K.S., Schonewald, C., 1996. Scaling population density and spatial pattern for terrestrial, mammalian carnivores. Oecologia 105, 329–335.

Smallwood, K.S., Schonewald, C.M., 1998. Study design and interpretation for population estimates of mammalian carnivores. Oecologia 113, 474–491.

Smallwood, K.S., Nakamoto, B.J., Geng, S., 1996. Association analysis of raptors on an agricultural landscape. In: Bird, D.M., Varland, D.E., Negro, J.J. (Eds.), Raptors in Human Landscapes. Academic Press, London, pp. 177–190.

Smallwood, K.S., Morrison, M.L., Beyea, J., 1998. Animal burrowing attributes affecting hazardous waste management. Environ. Manage. 22, 831–847.

Smallwood, K.S., Wilcox, B., Leidy, R., Yarris, K., 1998. Indicators assessment for Habitat Conservation Plan of Yolo County, California, USA. Environ. Manage. 22, 947–958.

Sullivan, T.P., 1979. Repopulation of clear-cut habitat and conifer seed predation by deer mice. J. Wildl. Manage. 43, 861–871.

Sullivan, T.P., 1986. Understanding the resiliency of small mammals to population reduction: poison or population dynamics? In: Richards, C.G.J., Ku, T.Y. (Eds.), Control of Mammal Pests. Taylor & Francis, London, pp. 69–82.

Taylor, L.R., Taylor, R.A.J., 1977. Aggregation, migration and population mechanics. Nature 265, 415–421.

Taylor, R.A.J., Taylor, L.R., 1979. A behavioral model for the evolution of spatial dynamics. In: Anderson, R.M., Turner, B.D., Taylor, L.R. (Eds.), Population Dynamics. Blackwell Scientific Publications, Oxford, pp. 1–28.

Tilman, D., 1983. Plant succession and gopher disturbance along an experimental gradient. Oecologia 60, 285–292.

Vaughan, T.A., 1961. Vertebrates inhabiting pocket gopher burrows in Colorado. J. Mamm. 42, 171–174.

Village, A., 1984. Problems in estimating Kestrel breeding density. Bird Study 31, 121–125.

Wiens, J.A., 1989. Spatial scaling in ecology. Funct. Ecol. 3, 385–397.

Williams, S.L., Baker, R.J., 1976. Vagility of local movements of pocket gophers (Geomyidae: Rodentia). Am. Midl. Nat. 96, 303–316.

Williams, L.R., Cameron, G.N., 1984. Demography of dispersal in Attwater's pocket gopher (*Geomys attwateri*). J. Mamm. 65, 67–75.