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Fire, Vegetation Changes, and Population Fluctuations of Townsend's Ground Squirrels

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ABSTRACT.—Townsend's ground squirrels (*Spermophilus townsendii*) are important prey for raptors and other predators in the Snake River Birds of Prey Area in southwestern Idaho, an area undergoing drastic vegetation changes induced by fire. We used 54 transects of burrow entrances done in 1982 and recensused in 1986–1989 to determine how the vegetation changes were affecting squirrel populations and if Townsend's ground squirrels will continue to provide a stable prey base for these predators. The mean number of active burrow entrances/ha decreased from 194 in 1982 to 68 in 1988. Burrow densities were highest and had the lowest annual variation in winterfat (*Ceratoides lanata*)-Sandberg's bluegrass (*Poa secunda*) communities. Big sagebrush (*Artemisia tridentata*)-dominated communities had intermediate burrow densities, whereas shadscale (*Atriplex confertifolia*) communities had the lowest burrow densities. Burrow densities were highly variable in exotic annual communities, and negatively correlated with cheatgrass (*Bromus tectorum*) and other exotic annuals in all communities. Widespread conversion of desert shrublands to exotic annual-dominated communities by wildfires appears to be creating an increasingly unstable prey base for raptors in the Snake River Birds of Prey Area.

INTRODUCTION

In the Snake River Plain of southwestern Idaho, Townsend's ground squirrels (*Spermophilus townsendii idahoensis*) are a critical food source for nesting prairie falcons (*Falco mexicanus*), and important prey for red-tailed hawks (*Buteo jamaicensis*), ferruginous hawks (*B. regalis*) (Steenhof and Kochert, 1985, 1988), badgers (*Taxidea taxus*) (Messick and Hornocker, 1981), western rattlesnakes (*Crotalus viridis*) and gopher snakes (*Pituophis catenifer*) (Diller and Johnson, 1988). Consequently, population fluctuations of Townsend's ground squirrels have a major impact on the food supply of many predators in the Snake River Plain, and Townsend's ground squirrels should be considered a keystone species (Gilbert, 1980) in this ecosystem.

In nine species of ground squirrels (*Spermophilus*), populations are known to vary 1.18 to 2.67-fold between minimum and maximum levels (Boag and Murie, 1981). In a 7-yr study, Townsend's ground squirrels at five 1-ha live-trapping grids in the Snake River Birds of Prey Area, southwestern Idaho, fluctuated 2.45-fold, from 7.6 to 18.6 yearlings and adults/ha (Smith and Johnson, 1985). Johnson *et al.* (1987) reanalyzed Smith and Johnson's (1985) live-trapping data to include the effective trapping area, which slightly reduced the above density estimates but not the magnitude of the fluctuations.

In recognition of the importance of Townsend's ground squirrels in the Snake River Birds of Prey Area, Nydegger and Smith (1986) investigated the relationship between Townsend's

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ground squirrel densities and vegetation type using burrow entrance transects. They found ground squirrel densities were highest in winterfat (*Ceratoides lanata*) and lowest in shadscale (*Atriplex confertifolia*) communities, with intermediate densities in big sagebrush (*Artemisia tridentata*) communities.

In the spring of 1986, many observers in the Snake River Birds of Prey Area believed, on the basis of casual observations, that Townsend's ground squirrel populations had declined markedly from previous years (M. Kochert, pers. comm.). Because of rapid and drastic vegetation changes in the Snake River Plain caused by the introduction of exotic annuals (Yensen, 1980; Kochert and Pellant, 1986), a possibility existed that the perceived population decline was a permanent result of vegetation changes rather than a normal population fluctuation.

Consequently, this study was initiated to monitor population trends of Townsend's ground squirrels in the Snake River Birds of Prey Area. A secondary goal was to investigate in more detail the relationship between vegetation and ground squirrrel densities found by Nydegger and Smith (1986). We were especially interested to learn if the altered habitats were supporting ground squirrel populations equivalent to those in native vegetation.

STUDY AREA

The Snake River Birds of Prey Area is a 243,000-ha tract of desert rangeland under multiple-use management administered by the U.S. Bureau of Land Management, and located on the Snake River Plain in Ada, Elmore and Owyhee counties, southwestern Idaho, at ca. 900–950 m elevation. The topography is of low relief with occasional lava buttes; the canyon of the Snake River cuts through the southwestern portion of the area.

The climate is arid (110–350 mm annual precipitation), with most of the precipitation falling as rain or snow between November and April. Summers are hot and dry with little green vegetation available for ground squirrels to eat after late June. Male Townsend's ground squirrels enter torpor by June, followed by females and then pups by early July and the population remains below ground until emergence in late January-early February (Smith and Johnson, 1985).

Historically, as illustrated in Figure 1, pristine vegetation in the Snake River Birds of Prey Area consisted of three major vegetation types (Yensen, 1980). (1) Big sagebrush communities occurred on deep, well-drained, neutral pH soils. Open stands of big sagebrush were interspersed with Thurber's needlegrass (*Stipa thurberiana*), with moderate amounts of Sandberg's bluegrass (*Poa secunda*) and squirreltail (*Sitanion hystrix*), and lesser amounts of Great Basin wild rye (*Elymus cinereus*), Indian ricegrass (*Oryzopsis hymenoides*), and bluebunch wheatgrass (*Agropyron spicatum*), all perennial bunchgrasses. There were 6–7 common forbs, including arrowleaf balsamroot (*Balsamorhiza sagittata*). (2) Winterfat communities occurred on deep, fine silt soils (Fautin, 1946; Billings, 1949). Sandberg's bluegrass was the dominant grass, with some Indian ricegrass and squirreltail and several forb species. (3) Shadscale communities occurred on shallow, poorly drained, saline soils. Dominant grasses were Indian ricegrass and needle-and-thread (*Stipa comata*) with squirreltail and some Sandberg's bluegrass. Globe mallow (*Sphaeralcea* spp.) and several native mustards were the principal forbs.

The pristine vegetation has been modified by overgrazing by cattle of early settlers, loss of topsoil, invasion of exotic annuals, especially cheatgrass (*Bromus tectorum*) and wildfires (Yensen, 1980, 1981). Most species of bunchgrasses and forbs are now much less common in modern communities and the short-lived, grazing and fire-resistant Sandberg's bluegrass and squirreltail are now the most common native grasses (Fig. 1).

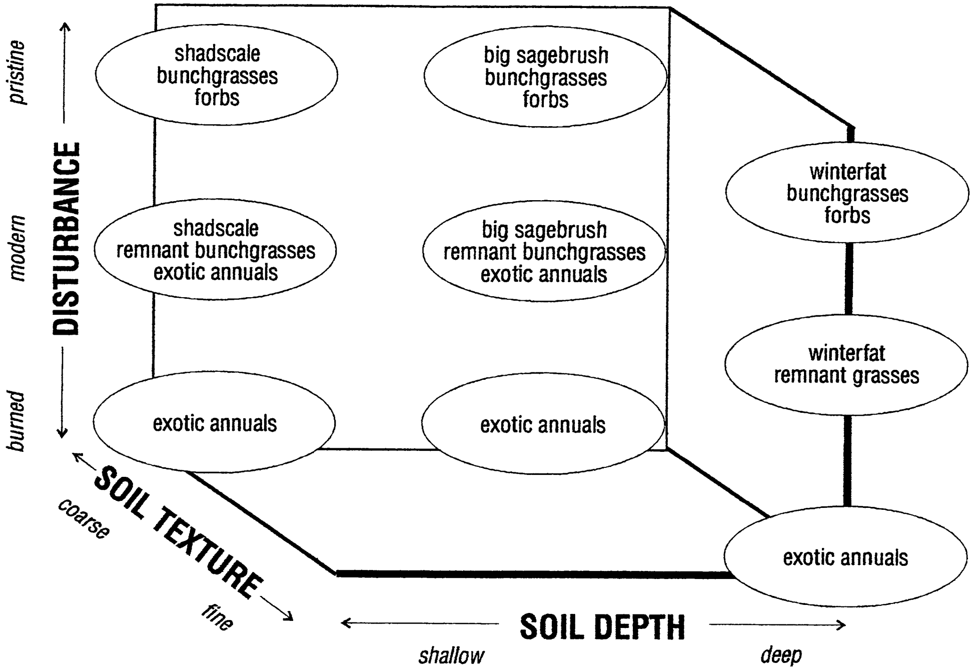

FIG. 1.—A conceptual model fo relationships between soil depth, soil texture, degree of disturbance, and vegetation types in the western Snake River Plains ecosystem. Pristine vegetation (top ovals) was degraded to the oval directly below it by injudicious cattle grazing and is being further degraded by wildfires to a variable mixture of exotic annuals. The combination of shallow soil and fine soil texture is rare in the study area and not shown

Although wildfires are a natural factor in this ecosystem, exotic annuals are highly flammable when dry in late summer, and their proliferation has changed the frequency and severity of wildfires (Wright, 1985). Wildfires now kill native shrubs and damage perennial bunchgrasses (Wright, 1985), which are replaced by communities dominated by exotic annuals, especially cheatgrass, tumblemustard (*Sisymbrium altissimum*), tansymustards (*Descurainia* spp.) and peppergrass (*Lepidium perfoliatum*). Exotic annuals are prone to burn again, further shortening and intensifying the burn cycle (Yensen, 1980), preventing return to native vegetation. Although native species can reestablish, the short burn cycle makes this unlikely (Whisenant, 1990). Thus, burned areas tend to become permanently dominated by exotic annuals and, in extreme cases, become cheatgrass moncultures (Yensen, 1980; Whisenant, 1990). Between 1980 and 1988, and especially in 1981–1983, wildfires burned more than 75,000 ha (31% of the total area) in the Snake River Birds of Prey Area, converting vast areas formerly dominated by big sagebrush, shadscale and winterfat to extensive stands of exotic annuals (Kochert and Pellant, 1986).

METHODS

Burrow counts.—In order to determine if ground squirrel populations had actually declined in 1986, an earlier data set was needed for comparison, and two were available. Smith and

Johnson (1985) provided estimates of annual variation in density from intensive live-trapping at five 1-ha sites located in close proximity. Nydegger and Smith (1986) used burrow counts as an index of ground squirrel density from transects throughout the Snake River Birds of Prey Area. Despite the indirectness of burrow counts, we believed that an index of ground squirrel density in a variety of vegetation types over a large area would be more representative than an intensive trapping program at only a few sites.

A significant correlation between densities of ground squirrels and active burrow entrances has been found for other ground squirrels such as *Spermophilus beecheyi* (Owings and Borchert, 1975) and *S. columbianus* (Weddell, 1989). Nydegger and Smith (1986) calibrated their technique using burrow entrance transects on Smith and Johnson's (1985) trapping grids in 1975–1979. When they compared burrow counts with live-trapping density estimates, they found a high, positive correlation ($r = 0.94$, $P = 0.002$ for the 4 yr combined) between the number of burrows and squirrel density (regression line: $Y = 0.09X - 0.04$).

Nydegger and Smith (1986) censused 190 transects stratified by vegetation type in 1982. Their transects were in relatively homogeneous vegetation and did not cross ecotones. We were able to relocate 54 of the transects censused in 1982 and recensused them in 1986, 1987, 1988 and 1989 to assess recent Townsend's ground squirrel population trends in the Snake River Birds of Prey Area.

Burrow entrances were censused using the 400 × 5-m belt transects at the end of the active season during June and July of 1982, 1986, 1987, 1988 and 1989. The observer walked systematically back and forth within the transect searching for all burrow entrances of Townsend's ground squirrels and badgers active that year.

One of us (DLQ) was involved in live trapping and burrow counts in both of the earlier studies (Smith and Johnson, 1985; Nydegger and Smith, 1986) and ensured that all observers used the same burrow-recognition criteria. Active burrow entrances have loose soil on all sides, particularly on the bottom, which makes them appear as though a brush had been passed through the opening. Claw marks, fecal pellets, and hair tufts may also be present. After a few days of disuse, soil in the burrow opening becomes hardened. Many openings do not persist over winter and those that do but are not used the following year appear very eroded (DLQ and EY, pers. observ.). Townsend's ground squirrel burrow entrances were larger than those used by other small mammals in the Snake River Birds of Prey Area except for Ord's (*Dipodomys ordii*) and chisel-toothed kangaroo rats (*D. microps*); however, kangaroo rat burrows usually open at a shallower angle and have characteristic tail drag marks. Badger "digs" included all types of excavations constructed by badgers except those showing signs of subsequent use by coyotes.

No relationship between the number of openings and the number of burrow systems was assumed. However, some tunnels have multiple entrances in close proximity (Alcorn, 1940; Reynolds and Wakkinen, 1987). If the size of the cluster varied with vegetation type, possibly to provide more escape routes in sparser vegetation, then this would bias the results. Consequently, in 1986 we also recorded the number of openings in each cluster. A cluster was operationally defined as a group of burrow openings <1 m apart.

Vegetation analysis.—Vegetation data were collected in June and July 1986 at 40 1-m^2 quadrats, one placed at the end of each 10-m interval along the transect (Daubenmire, 1959). Percent cover for each species in each quadrat was estimated to the nearest 1% using a rectangular 1-m^2 frame divided by cross wires into 10 sections. Relative cover and frequency were averaged to give importance values for each species on each transect (Cox, 1990). The original vegetation of transects that burned before 1986 was determined from an unpublished 1979 vegetation survey of the Snake River Birds of Prey Area (Boise District, U.S. Bureau of Land Management files).

Weather variables.—We attempted to determine if Townsend's ground squirrel population fluctuations were related to weather variables during the study. Five measures of winter severity were examined: duration of spring snow cover (days past 1 January), total days of snow cover, total heating degree days in November–January, number of days with low temperatures below 0 C, and number of days with high temperatures below 0 C. Three measures of precipitation during the year preceding the census were examined: September–October precipitation, November–April precipitation, and September–May precipitation. September–October precipitation, November–April precipitation, and September–May precipitation of 2 winters preceding the census also were examined.

Weather data were taken from National Oceanic and Atmospheric Administration monthly Idaho Climatological Data reports for the Kuna 2 NNE weather station (ca. 10 km N of the study area), except snow cover data that were from Boise Airport (ca. 20 km NW of the study area).

Data analysis.—We classified our transects using importance values of vascular plant species from our 1986 data. We employed nonmetric multidimensional scaling, a robust, nonparametric ordination method (Minchin, 1987), to identify the major floristic gradients. The analysis was conducted using PC-ORD (McCune, 1991) with all default settings as recommended, and the Bray-Curtis distance measure, which has a robust linear relationship with ecological distance (Faith *et al.,* 1987). The analysis was repeated using principal components analysis ordination scores as an alternative starting configuration to avoid local minima (Ludwig and Reynolds, 1988; McCune, 1991). Both analyses were similar and the latter is reported below. The transects were then clustered by two-way indicator species analysis (Gauch, 1982) using PC-ORD (McCune, 1991). All other data analyses were done with SYSTAT 5.0 (Wilkinson, 1990).

RESULTS

Burrow clusters.—Analysis of the 1986 burrow data showed that on all transects combined, 82.6% of the clusters consisted of single openings, 13.7% had two openings, 2.6% had three openings, 0.7% had four openings, 0.2% had five openings, and 0.1% had six openings. Cluster size did not vary significantly among vegetation types (χ^2 test of independence, $P > 0.05$). Consequently, a simple count of active burrow openings was used in all subsequent years.

Annual burrow entrance fluctuations.—The mean number of active burrow entrances on the 54 transects fluctuated 2.8-fold over the 5 yr ($\bar{x}$ = 193 b/ha in 1982 to 68 b/ha in 1988; 5-yr $\bar{x}$ = 112 b/ha, coefficient of variation [cv] = 50%). Mean burrow counts for the 54 transects were significantly different from the preceding year in all consecutive years (Wilcoxon matched-pairs signed-ranks tests, $P < 0.001$ in each case).

Vegetation patterns.—Five native shrub, five native bunchgrass, three native forb, and nine exotic annual species were recorded on the 54 transects. Six rare species (*Chrysothamnus viscidiflorus, Erodium cicutarium, Elymus cinereus, Crepis acuminata, Allium* sp. and *Salsola iberica* [=*kali*]) had importance values of <10 and occurred on <5 transects, and were omitted from further analyses.

Because of abrupt ecotones and the small species pool, we wished to determine if the transects could be grouped into a few discrete vegetation types. Using 1986 data, two-way indicator species analysis clustered the 54 stands into five groups (Table 1). "Winterfat" (10 unburned transects) was characterized by high importance values of winterfat and native bunchgrasses, especially Sandberg's bluegrass (*Poa secunda*) and low values of cheatgrass. These transects represent modern remnants of the pristine winterfat communities (Fig. 1). "Mixed" (10 transects) was characterized by significantly lower importance values of win-

TABLE 1.—Mean plant importance values for nine selected species in five vegetation types in the Snake River Birds of Prey Area. Lower case letters indicate pairs of values with significant differences (Mann-Whitney U-test) within each column; only indicated pairs were tested

Vegetation type	CELA[1]	ARTR	ATCO	POSE	SIHY	VUOC	BRTE	SIAL	DEPI
Winterfat	36.7[a]	0.5	0.2	18.4[a]	4.4[b]	9.7	5.4[b]	0.8	14.5
Mixed	19.6[a]	2.4	4.8	9.8[a]	10.5[b]	4.9	22.2[b]	9.5	10.1
Sagebrush	0.1	33.5	0.0	13.9	8.7	9.0	24.6	0.9	4.6
Exotic annuals	0.0	2.4	0.0	15.0	6.3	1.2	34.3	21.9	4.1
Shadscale	0.2	0.2	4.8	0.5	3.4	0.1	51.7	12.8	15.9

[a] $P < 0.01$
[b] $P < 0.001$
[1] Plant species acronyms: CELA, winterfat; ARTR, big sagebrush; ATCO, shadscale; POSE, Sandberg's bluegrass; SIHY, squirreltail; VUOC, six-weeks fescue; BRTE, cheatgrass; SIAL, tumblemustard; DEPI, pinnate tansymustard. See text for scientific names

terfat (Mann-Whitney U-test, $P < 0.005$) and Sandberg's bluegrass ($P = 0.005$), more squirreltail (*Sitanion hystrix*) ($P < 0.001$) and cheatgrass ($P < 0.001$), and higher percentages of other shrubs. The mixture of shrubs indicated that these transects were probably on intermediate soil types.

"Sagebrush" consisted of six unburned, sagebrush-dominated transects with moderate amounts of native grasses and cheatgrass. "Exotic annuals" consisted of nine burned and one unburned transect dominated by cheatgrass and tumblemustard, but with moderate to high amounts of remnant Sandberg's bluegrass. All of the exotic annual transects were originally dominated by big sagebrush.

"Shadscale" included 18 transects, 16 of which had burned since 1982 and were now dominated by exotic cheatgrass, pinnate tansymustard and tumblemustard. However, all were originally dominated by shadscale.

Five of the 54 transects had burned and become dominated by exotic annuals before the study began in 1982. Between 1982 and 1986, 21 transects burned; 16 in shadscale, five in sagebrush. In 1982–1983, by happenstance the large fires were in shadscale communities, and a disproportionate percentage (89%) of those transects burned. In 1987, one winterfat transect burned and two exotic-annual transects reburned. Thus, by 1989, 27 (50%) of the transects had burned.

Vegetation and burrow densities.—In all years, burrow densities differed significantly among vegetation types (Kruskal-Wallis tests, Fig. 2). Winterfat transects consistently had the highest burrow densities ($\bar{x} = 240$ b/ha), followed in sequence by mixed ($\bar{x} = 142$), sagebrush ($\bar{x} = 71$) and finally shadscale ($\bar{x} = 19$) transects. Exotic annual transects ($\bar{x} = 142$) had high burrow densities in some years (1982, $\bar{x} = 341$; 1987, $\bar{x} = 345$), but very low densities in 1986 ($\bar{x} = 43$) and 1988 ($\bar{x} = 28$).

Winterfat and big sagebrush communities were relatively stable; their highest densities were 1.85 (CV = 28%) and 2.1 (CV = 38%) times greater than their lowest densities, respectively. The mixed communities had slightly greater burrow density fluctuations (2.5-fold, CV = 43%), but were relatively stable compared to shadscale transects (8.5-fold, CV = 112%). Exotic annual transects were very unstable (12.4-fold, CV = 95%) (Fig. 2).

Winterfat and mixed were the only groups of transects with >1% winterfat, but differed significantly in the amounts of winterfat, native grasses and exotic annuals present (Table 1). Burrow densities were significantly lower in the mixed group than in winterfat (Fig. 2).

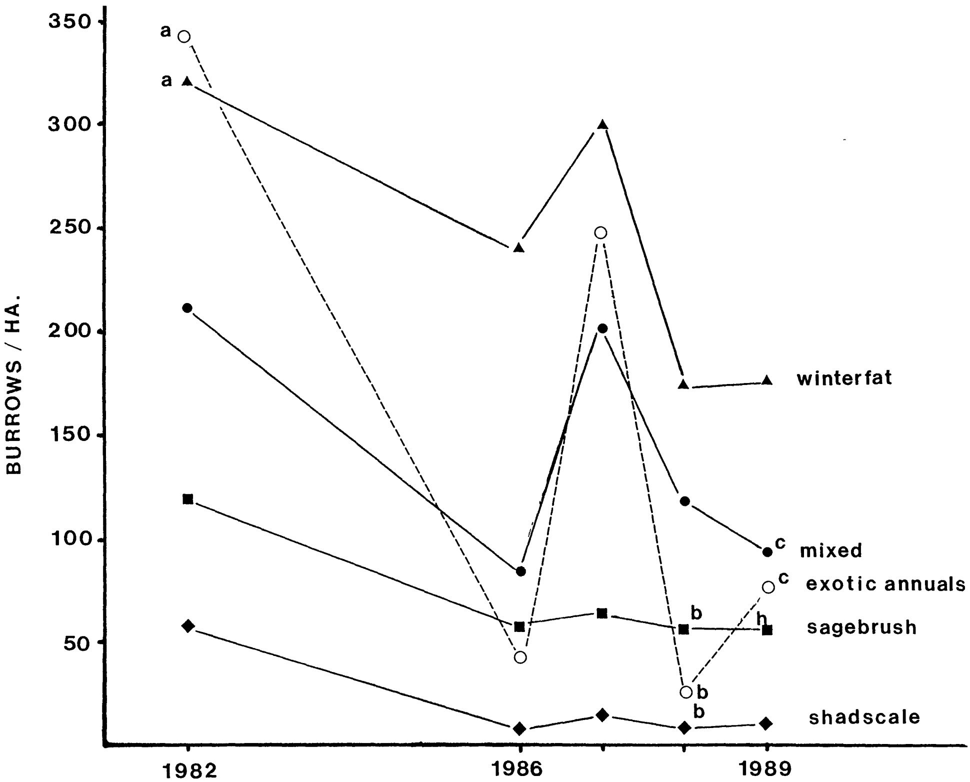

FIG. 2.—Annual fluctuations in Townsend's ground squirrel mean burrow densities in five vegetation types. All burrow densities within a given year were significantly different except those marked with a, b or c

Nonmetric multidimensional scaling (NMDS) revealed three underlying soil-vegetation axes with superimposed fire-related habitat changes (Table 2, *see* Fig. 3 for first two axes). Each axis correlated positively with one of the three major shrubs and negatively with exotic annuals.

Axis 1 distinguished winterfat-native bunchgrass communities (significant positive correlations with winterfat, six-weeks fescue [*Vulpia octoflora*] and Sandberg's bluegrass) from a set of species that dominate after wildfires (strong negative correlations with cheatgrass, tumblemustard [*Sisymbrium altissimum*] and peppergrass [*Lepidium perfoliatum*]). Other species correlated with this axis (Table 2) were spiny hopsage (*Grayia spinosa*), a shrub that frequently occurs with winterfat; prickly lettuce (*Lactuca serriola*), an introduced annual present in wet years such as 1986 (DLQ, pers. observ.); and introduced bur buttercup (*Ranunculus testiculatus*). In 1986, bur buttercup was in the explosive stage of invading the northern part of the study area (DLQ, pers. observ.) and has not been as abundant since.

Axis 2 apparently described a combined soil texture and disturbance gradient (Fig. 3). It distinguished sites with big sagebrush, Sandberg's bluegrass and squirreltail (generally on loams) from sites with pinnate tansymustard, native white forget-me-not (*Cryptantha*

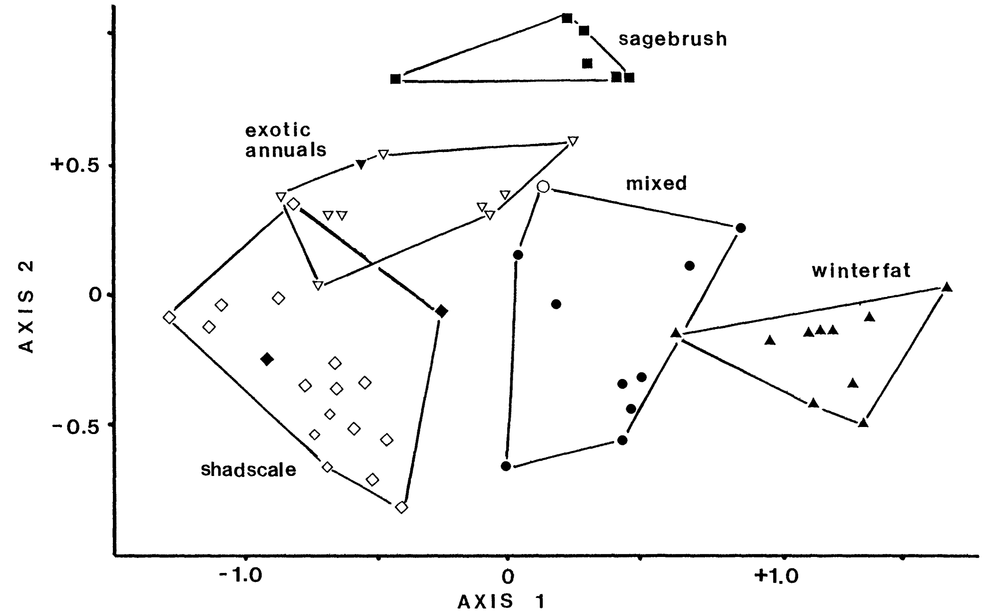

FIG. 3.—Nonmetric multidimensional scaling ordination of 54 transects. Axis 1 was a winterfat-native grass vs. exotic annuals gradient and was highly correlated with Townsend's ground squirrel densities. Solid symbols = unburned transects, open symbols = burned transects

interrupta) and winterfat (fine silts, Billings, 1949) (Table 2). Axis 3 described a gradient between shadscale communities and sites now dominated by exotic species (Table 2).

Using regression analysis, NMDS axis 1 was a highly significant predictor of 1986 burrow density ($F = 58.6$, $R^2_{adj.} = 0.521$, $P < 0.001$), whereas axis 2 was not a significant predictor, and axis 3 was negatively correlated ($F = 4.108$, $R^2_{adj.} = 0.055$, $P = 0.048$). Stepwise multiple regression did not substantially improve upon the simple regression ($F = 31.4$, $R^2_{adj.} = 0.534$, $P < 0.001$), indicating the relatively small contribution of axis 3 to the overall model. Moreover, using Spearman rank correlations, only axis 1 was significant ($r_s = 0.727$, $P < 0.001$). Thus, burrow densities seem to respond to a single plant-soil gradient.

Next, we investigated the relationships between 1986 burrow densities and importance values of individual plant species. There were significant positive correlations between burrow densities and importance values of Sandberg's bluegrass ($r_s = 0.69$, $P < 0.001$), six-weeks fescue ($r_s = 0.58$, $P < 0.001$) and winterfat ($r_s = 0.54$, $P < 0.001$) and significant negative correlations with cheatgrass ($r_s = -0.69$, $P < 0.001$), total exotic annuals ($r_s = -0.68$, $P < 0.001$), shadscale ($r_s = -0.43$, $P < 0.01$) and tumblemustard ($r_s = 0.40$, $P < 0.05$). Not surprisingly, all of these species were strongly positively or negatively correlated with axis 1.

It is possible that 1986 vegetation might influence 1987 rather than 1986 ground squirrel populations, because vegetation quality could affect overwinter survival. Consequently, we tested the 1986 vegetation data as a possible correlate of 1987 ground squirrel burrow densities. The results were similar; there were significant positive correlations (all $P < 0.001$) with importance values of Sandberg's bluegrass ($r_s = 0.71$), six-weeks fescue ($r_s =$

TABLE 2.—Pearson product-moment correlations of 16 common species with nonmetric multidimensional scaling ordination axes

Species	Axis 1	Axis 2	Axis 3
Winterfat	0.842**	−0.310*	−0.142
Big sagebrush	0.115	0.730***	0.215
Shadscale	−0.150	−0.181	0.522***
Spiny hopsage	0.412**	−0.077	0.085
Sandberg's bluegrass	0.602***	0.511***	−0.485***
Squirreltail	0.224	0.421**	0.498***
Indian ricegrass	0.051	−0.036	0.105
Six-weeks fescue	0.726***	0.148	0.101
Cheatgrass[1]	−0.894***	−0.106	0.293*
Tumblemustard[1]	−0.406**	0.035	−0.397**
Pinnate tansymustard[1]	0.057	−0.726***	−0.141
Peppergrass[1]	−0.272*	0.160	0.241
Bur buttercup[1]	0.521***	−0.008	−0.253
Desert wheatgrass[1]	−0.152	−0.162	−0.436***
Prickly lettuce[1]	−0.274*	0.188	−0.280*
White forget-me-not	0.235	−0.479***	0.080

* P < 0.05, ** P < 0.01, *** P < 0.001

[1] Introduced

0.50), and winterfat ($r_s = 0.48$), and significant negative correlations with total exotic annuals ($r_s = -0.565$), cheatgrass ($r = -0.528$), and shadscale ($r = -0.48$).

Weather variables and burrow densities.—In 1982 and 1986, precipitation during the previous winter (November through April) was abundant (210 and 231 mm, respectively), 1987 and 1988 were drought years (86 and 142 mm, respectively) and 1989 was near normal (186 mm).

Individual correlations of each of the 13 weather variables with ground squirrel burrow densities showed only two significant correlations. Townsend's ground squirrel b/ha was correlated with November–April precipitation of 2 winters prior to the census ($r = 0.88$, $P = 0.048$), although September–May precipitation of 2 winters prior was a better predictor ($r = 0.917$, $P = 0.029$). Because of the large number of variables in the analysis, a Spearman correlation matrix was produced, and Bonferroni adjusted probabilities were calculated (Wilkinson, 1991). Using this strict criterion, none of the correlations was significant.

To test whether winter–spring precipitation of 1.5 yr prior to the census might have predictive value, November–April and September–May precipitation data for 2 winters prior to the census were tested using the Townsend's ground squirrel population densities reported in Smith and Johnson (1985). However, these correlations were not significant ($r = 0.538$ and 0.412, respectively).

Epizootics.—The plague coccobacillus, *Yersinia pestis,* has been reported in Townsend's ground squirrels and badgers in the Snake River Birds of Prey Area (Messick *et al.,* 1983). If plague were responsible for the population fluctuations, it should spread rapidly over large areas with mortality rates of 98–100% (Cully, 1989). We tested this hypothesis by examining the pattern of increases and decreases on individual transects.

In 1986, burrow densities increased on five transects, while decreasing on 49. In 1987, burrow densities decreased on six transects while increasing on 48. In 1988, eight densities increased and 46 decreased, while in 1989, 18 decreased and 36 increased. There was nothing in the pattern of increases and decreases to suggest plague was sweeping across the area.

Badgers.—The number of active badger digs declined significantly from 1982 ($\bar{x}$ = 67 b/ha) to 1986 (20 b/ha) to 1987 (3 b/ha), then increased in 1988 (9 b/ha) and remained stable in 1989, roughly following a year behind Townsend's ground squirrel burrow densities (Fig. 2). Except for 1988–1989, numbers of badger b/ha in consecutive years were significantly different (Wilcoxon matched-pairs signed-ranks tests, all $P < 0.01$).

In all years, there were high positive correlations (Spearman rank correlations, $r_s = 0.513$ to 0.745, $P < 0.001$ in all cases) between the number of active ground squirrel burrows on a transect and the number of active badger digs. Transects with high ground squirrel burrow densities had high levels of badger activity, regardless of whether squirrel populations were increasing or decreasing.

DISCUSSION

Burrow count technique.—Although b/ha is an indirect measure of Townsend's ground squirrel densities, a count of active burrows provides a practical means of censusing ground squirrels at more sites and is independent of time of day, behavior and weather conditions.

Except for mothers with young, only a single squirrel would be expected in a burrow system (Michener, 1983). Townsend's ground squirrel burrows have one to many openings, and they use numerous auxiliary burrows in addition to their "home" or nest burrows. Consequently, there are many times more burrow openings than squirrels (Alcorn, 1940; Reynolds and Wakkinen, 1987; Yensen *et al.,* 1991). This would explain the low slope (0.09) of Nydegger and Smith's (1986) regression equation.

We converted our burrow count results from b/ha to ground squirrels/ha using Nydegger and Smith's regression equation and compared the reuslts to the densities reported by Smith and Johnson (1985). The ranges of the two data sets were very comparable. Smith and Johnson reported 7.6 to 18.6 vs. our 6.1 to 17.4 squirrels/ha. Thus, burrow counts yielded results of approximately the same magnitude as trapping.

One of us (EY, pers. observ.) has observed Columbian ground squirrels (*Spermophilus columbianus*) using large numbers of recently vacated burrows after the population was artificially reduced. If other ground squirrels use proportionally more burrows at low population densities (*i.e.,* the relationship between squirrels and burrows is nonlinear), the densities reported herein (Fig. 2) could be overestimated in sagebrush and shadscale vegetation types, and in low density years such as 1986. Nydegger and Smith's (1986: Fig. 1) scatterplot suggests the relationship is linear; if it were not, then our census results at low densities would be overestimates.

Causes of the population fluctuations.—The pattern of population increases and decreases on individual transects did not correspond to the usual pattern of plague epizootics. The only transects showing population extirpation between 1982 and 1986 (*e.g.,* 252 to 0 b/ha) were in burned shadscale communities. Moreover, the rapid recovery of Townsend's ground squirrels in 1987 was not characteristic of plague, making it an unlikely explanation for the population fluctuations. However, it is conceivable that another pathogen could have been responsible for the decline between 1982 and 1986. DLQ observed several sick ground squirrels in the study area in mid- to late May 1982.

If badger predation were driving the fluctuations, we would have expected to see an increase in badger density the year prior to a ground squirrel decrease. In fact, we saw the opposite pattern, so there is no evidence that badger predation was involved.

Smith and Johnson (1985) reported 72% overwinter mortality of Townsend's ground squirrels on their study plots. Overwinter mortality could be related to (a) winter severity or (b) amount of fat carried into hibernation. Ground squirrels may be food-limited (Dobson and Kjelgard, 1985a, b; Reynolds and Turkowski, 1972), which would affect fat deposition. Forage production is related to winter and spring precipitation (Piemeisel, 1938) in southwestern Idaho. If precipitation is related to amount of fat carried into hibernation, prior-year precipitation would be more important than precipitation in the year of the census. The failure to find significant correlations between weather variables and ground squirrel densities could result from having only 5 yr of data, or simply indicate that the relationship between ground squirrels and weather is complex.

Habitat alteration.—Regardless of why ground squirrel densities fluctuate, we found strong relationships between vegetation type and ground squirrel abundance and annual variability (Fig. 2). Our results and those of Nydegger and Smith (1986) both demonstrate that winterfat communities support high Townsend's ground squirrel populations. Likewise, Smith and Johnson's (1985) highest survival rates were at their study site with the most winterfat.

The nonmetric multidimensional scaling ordination and cluster analysis identified plant communities in the Snake River Birds of Prey Area that represent remnants of the three pristine shrub types (Fig. 1), an intermediate type ("mixed"), and a burned derivative of big sagebrush. There were no burned winterfat transects in 1986, and thus no winterfat derivative exotic annual type (Fig. 3). Interestingly, the burned and unburned shadscale transects still clustered together. This was due to the high percentage of exotic annuals in all of the shadscale transects (Table 1). The mix of exotic annuals differs slightly among derivatives of the three shrub types (Table 1).

Burrow densities were high in winterfat-bunchgrass communities and were negatively correlated with disturbance-related exotic species and shadscale. This conclusion was corroborated by individual correlations between plant importance values and ground squirrel densities.

Sandberg's bluegrass and squirreltail were the dominant native bunchgrasses. They are short-lived compared to other native bunchgrasses, but are the most grazing and fire-resistant of the native species and hence are the primary remnants of the bunchgrass flora (Yensen, 1980). Although 1986 was a wet year, few native forbs were recorded. Thus, the five vegetation types reported above represent degraded remnants of the original vegetation (Fig. 1).

Winterfat is highly palatable to domestic livestock (Smith, 1900; Mozingo, 1987) and ground squirrels (Yensen and Quinney, *in press*). Analysis of Townsend's ground squirrel diets in the Snake River Birds of Prey Area indicated that Townsend's ground squirrels relied heavily upon a very limited number of food plants, especially Sandberg's bluegrass, cheatgrass and winterfat (Yensen and Quinney, *in press*). Winterfat transects with high importance values of native perennial bunchgrasses, particularly Sandberg's bluegrass, should provide a perennial, dependable food source, and these transects had the highest burrow densities in this study. Exotic annual communities can be very productive during wet years, but may have very low productivity during drought years (Blaisdell, 1958). Although Townsend's ground squirrels eat cheatgrass, its erratic biomass fluctuations may explain the strong negative correlations between ground squirrel densities and cheatgrass; it is not a reliable food source.

Fires *per se* probably have no direct effect upon Townsend's ground squirrels because heat from the fire would penetrate only a few cm into the ground and fires occur later in the summer after the squirrels have entered estivation. However, fires drastically reduce the food plant biomass available to squirrels in the following spring, and replace perennial species with annual species, which have greater annual fluctuation in biomass.

Groves and Steenhof (1988) found that Townsend's ground squirrel populations were lower in burned than unburned study plots. However, shrub removal did not affect Uinta ground squirrel (*Spermophilus armatus*) population sizes, sex ratios or age structure, although it may decrease the diversity of food plants (Parmenter and MacMahon, 1983). Thus, the loss of shrubs *per se* may not be as critical to Townsend's ground squirrels as changes in annual stability of their food supply. With fewer forbs and bunchgrasses, exotic annual communities have lower plant species diversity than the pristine shrub communities (Fig. 1) they are replacing (Piemeisel, 1938), and thus less nutritional variety for ground squirrels.

The results of this study suggest that range fires affect Townsend's ground squirrel populations by substituting unstable and possibly less palatable food sources for native vegetation. Townsend's ground squirrel populations living in burned areas appear to be vulnerable to erratic fluctuations in food biomass and limited food plant diversity, and have resulting high-amplitude population fluctuations.

Recent workers (Pimm *et al.,* 1989) have considered populations with high amplitude fluctuations to be extinction-prone. Thus, local populations of Townsend's ground squirrels living in exotic annual-dominated communities should become increasingly vulnerable. These low density demes could be "rescued" from extirpation (Brown and Kodric-Brown, 1977) by dispersal from nearby high density areas, as long as the latter areas remain unburned, although overall squirrel density should decrease.

Widespread conversion of large tracts of desert shrub communities to exotic annual-dominated habitat could eventually eliminate winterfat-bunchgrass communities. This would leave the entire squirrel population increasingly extinction-prone, which does not bode well for the future of the predator guild that depends upon Townsend's ground squirrels in southwestern Idaho.

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