

## MOUNDS OF THE AMERICAN BADGER (*TAXIDEA TAXUS*): SIGNIFICANT FEATURES OF NORTH AMERICAN SHRUB-STEPPE ECOSYSTEMS

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In the western United States, American badgers (*Taxidea taxus*) excavate large volumes of soil and create fan-shaped mounds while foraging for fossorial rodents. Densities of 790 mounds/ha were recorded on the Snake River Plain, west-central Idaho. More mounds were recorded from unburned compared with burned sites, but no differences were found between sites dominated by sagebrush (*Artemisia tridentata wyomingensis*) and winterfat (*Krascheninnikovia lanata*). Mounds and diggings occupied an average of 5–8% of the landscape and the mass of mounded soil averaged 33.8 kg, equivalent to 26 t/ha. The surface cover of plants, cryptogams, and litter increased, and bare ground decreased, as mounds aged. Excavation holes were present at 96% of active and crusted mounds compared with 31% of older recovering mounds. Sites with a greater density of shrubs tended to have a greater density of both badger mounds and ground squirrel diggings. Additionally, increased density of badger mounds was associated with increases in the density of ground squirrel holes and scratchings. These results indicate that badger mounds are a significant landscape structure and that badger activity is likely to have major impacts on soil and ecosystem processes in shrub-steppe ecosystems.

Key words: American badger, badger digs, biopedturbation, mounding, shrubland, *Taxidea taxus*

Soil disturbance by animals (biopedturbation) contributes in a large way to the development of landscape patchiness in arid and semiarid environments. Burrowing, digging, and scratching by animals have profound effects on soil processes and properties such as soil texture, structure, fertility, bulk density, and porosity (Butler 1995; Kinlaw 1999; Reichman and Smith 1990; Whitford and Kay 1999). Animal digging also creates heterogeneity in the landscape by depositing patches of subsoil on the soil surface (Sherrod and Seastedt 2001). These patches of subsoil have higher levels of incident light and therefore higher surface temperatures (Cortinas and Seastedt 1996; Huntly and Inouye 1988), and are likely to support different plant communities with different levels of production.

The effects of digging are generally beneficial but can sometimes be deleterious. For example, in Australia, bedding sites of kangaroos (*Macropus*) in arid and semiarid areas create soils with higher levels of carbon, nitrogen, and sulfur (Eldridge and Rath 2002). In contrast, the occupation of large areas of Australia by the European rabbit (*Oryctolagus cuniculus*) has led to the proliferation of nutrient-poor patches (warrens)

colonized by Mediterranean weeds (Eldridge and Myers 1999; Eldridge and Simpson 2002). Prairie dogs (*Cynomys*) create distinct patches around their burrow entrances, altering physical and chemical properties of the soil for hundreds of years (Whicker and Detling 1988). Similarly, pocket gophers (*Geomys bursarius*) create mounds with significantly different soil textures and levels of nitrogen, phosphorus, and potassium than the surrounding soil matrix (Huntly and Inouye 1988). Inside the burrows, caches of excreta and uneaten food can create patches of higher nutrient availability. Tunnels increase the replenishment of moisture to the subsoil, influencing the productivity of perennial grasses (Rezsutek and Cameron 2000).

Animal activity also makes sediment available for subsequent erosion. In a study of soil excavation in the Ardennes, Luxembourg, voles (*Microtus*) and the common mole (*Talpa europaea*) played a significant role in colluviation despite the low levels of downslope soil movement (Imeson 1976). Activities of other animals such as grizzly bears (*Ursus arctos horribilis*), European badgers (*Meles meles*), pigs (*Sus scrofa*), and European rabbits provide sediment for mobilization by overland flow (Butler 1995; Eldridge and Myers 2001; Vroom et al. 1980). In the Negev Desert in Israel, porcupines (*Hystrix indica*—Alkon 1999) contribute sediment to the surface as they dig for bulbs. This sediment is mobilized by overland flow, and contributes to the buildup of soil in the lower parts of the catchment (Yair 1995; Yair and Rutin 1981).

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The point at which animals influence catchment-scale processes depends on the size of their population and the densities of their structures. Estimated rates of soil turnover vary in studies worldwide. On sandstone-derived soils in eastern Australia, combined soil movement by kangaroos (*Macropus*), bandicoots (*Isodon*), echidnas (*Tachyglossus aculeatus*), ants (*Camponotus intrepidus*), and termites (*Nasutitermes exitiosus*) amounted to only  $0.05 \text{ t ha}^{-1} \text{ year}^{-1}$  (Mitchell 1988). This value contrasts with values of 20–50  $\text{t ha}^{-1} \text{ year}^{-1}$  reported for vertebrates such as the common mole (Abatarov 1972; Imeson 1976).

In the western United States, American badgers (*Taxidea taxus*) are a major predator of ground squirrels (*Spermophilus*) and other ground-dwelling fauna such as burrowing owls (*Athene cunicularia*), which use the squirrels' burrow systems (Desmond et al. 2000). While preying on ground squirrels, badgers enlarge the small squirrel holes, producing a large pit and fan-shaped mound at the burrow entrance (Desmond et al. 2000; Green and Anthony 1989). My observations of the large density of these mounds suggest that badger diggings are likely to have marked impacts on the soil. The objective of this paper was to document basic attributes of mounds and diggings of the American badger. Specifically, I examined the size, mass, and volume of mounds, as well as the plant cover of mounds in relation to vegetation community and burning. I also examined relationships between the density of badger mounds and the density of ground squirrel scratchings and holes, which are surrogates for ground squirrel density (Yensen et al. 1992).

## MATERIALS AND METHODS

**The study site.**—The study was conducted within vegetation communities of mixed sagebrush shrub-steppe in the Snake River Birds of Prey National Conservation Area on the western Snake River Plain, about 40 km southwest of Boise, Idaho ( $43^{\circ}27'N$ ,  $116^{\circ}26'W$ ; 884–914 m above sea level). The soils in the area are predominantly fine, silty Xerollic Haplargids (Aridisols—Collett 1980) formed on loess and sedimentary deposits covering basalt lava flows (Hironaka et al. 1983). The soils are relatively high in silt and increase gradually in soil texture with depth. Clay levels are <5%, and silt ranges from 24% at the surface to 60% at 50 cm. Soil pH is slightly alkaline (7–8) with low levels of electrical conductivity (<1 dS/m). The climate is semiarid, with hot, dry summers and cool, wet winters. Annual precipitation ranges from 178 to 305 mm, with less than 35% of the moisture occurring between April and September (Hironaka et al. 1983). Mean daily temperatures range from  $-1^{\circ}\text{C}$  in January to  $24^{\circ}\text{C}$  in July. The topography of the area is generally flat, with small basalt outcrops or remnants of volcanic activity.

Two distinct shrub-steppe community types characterized by sagebrush and winterfat (*Krascheninnikovia lanata*) were chosen for the study. Wyoming big sagebrush (*Artemisia tridentata wyomingensis*) occurs as a dominant shrub over large areas at variable densities, with a perennial herbaceous understory of Sandberg's bluegrass (*Poa secunda*) and bottlebrush squirreltail (*Sitanion hystrix*). Burned sites were dominated by cheatgrass (*Bromus tectorum*) and scattered Russian thistle (*Salsola kali* var. *kali*), with occasional bluebunch wheatgrass (*Pseudoroegneria spicata*) and Thurber's needlegrass (*Achnatherum thurberianum*).

Mixed winterfat-big sagebrush communities occurred as intergrades in the area and also were selected for study. Understory species were

predominantly Sandberg's bluegrass and bottlebrush squirreltail, with a variable cover of cheatgrass. Burned winterfat communities sampled in this study were dominated by exotic cheatgrass, exotic Russian thistle, and occasionally forage Kochia (*Kochia prostrata*), which had been artificially seeded into some areas or had spread from seeded areas nearby. No monospecific stands of winterfat were examined.

**Field survey and measurements.**—A broad-scale survey of badger mounds and diggings was carried out at 20 sites across an area of approximately 300  $\text{km}^2$  in the Birds of Prey National Conservation Area west of Initial Point. Fieldwork was carried out from September to October 2002. Ten of the 20 sites were dominated by Wyoming big sagebrush, and 10 sites were dominated by winterfat. Five of the 10 sites in each vegetation community were burned and 5 were unburned. Sites had been burned approximately 5–10 years before the survey was carried out. Uncontrolled grazing by sheep and cattle since the late 19th century has resulted in the invasion of much of the western United States by annual Eurasian weeds, particularly cheatgrass (Mack 1981). These grasses have increased fine-fuel densities and reduced the interval between wildfire from once every 80–100 years to <10 years (Whisenant 1990). Frequent fires have eliminated sagebrush and other fire-sensitive shrubs, and the short intervals between fire means that recovery of native shrubs and forbs is poor or nonexistent (Wroblewski and Kauffman 2003). Large areas of *Artemisia* shrub-steppe have now been converted to annual grasslands that are structurally and compositionally different from unburned shrub-steppe (Anderson and Inouye 2001).

The 20 sites were selected a priori by examining vegetation maps and consulting local experts on the location of burned and unburned sites from each vegetation community. The sites were chosen to sample the variability of landscapes dominated by the 2 shrub communities while confining the study to a single soil type. At each of the 20 sites, a  $50 \times 10\text{-m}$  plot was established about 100 m from the main access track, but away from power lines, tracks, easements, and obvious areas of disturbance from off-road vehicles. All badger diggings and mounds within the plot were measured, provided that the point of excavation occurred within the boundaries of the plot.

Mounds typically consisted of a circular hole excavated by the badgers, around which the topsoil is piled in a fan-shaped deposit (Fig. 1). Each badger digging was classified as active, crusted, or recovering. Active mounds had been excavated within the past 2–3 weeks and comprised loose, powdery soil with no evidence of crusting. Crusted mounds showed signs of the development of a thin physical crust, and recovering mounds were dominated by an organic (biological) crust (cryptogamic crust) or were partially colonized by vascular plants. Field observations suggested that active mounds become crusted within 2 weeks to 2 months after excavation. Other evidence of animal activity also was recorded. Shallow diggings, scratchings, and tunnels of ground squirrels were counted, as well as badger diggings not associated with a mound. The following attributes of each mound were measured: diameter of the excavation hole, width of the fan at 2 locations, maximum length of the fan-shaped deposit, and maximum depth of the deposited material. In addition, percent cover by plants (by species), cryptogamic crusts (mosses, lichens, and cyanobacteria), bare soil, and litter were measured on each mound. At each site, density of sagebrush and winterfat shrubs was measured.

Bulk density ( $\text{Mg/m}^3$ ) was assessed to convert mound volumes to mass of soil. Bulk density was measured by using a soil corer of 47 mm diameter and 50 mm depth on each of the 3 surface types. Soil samples were oven-dried at  $105^{\circ}\text{C}$  for 24 h. Three subsamples were taken (and averaged) from each surface type ( $n = 15$ ). Litter accumulating in the excavated holes was assessed as being either shallow (<0.5 cm deep), deep (>0.5 cm deep), or absent.



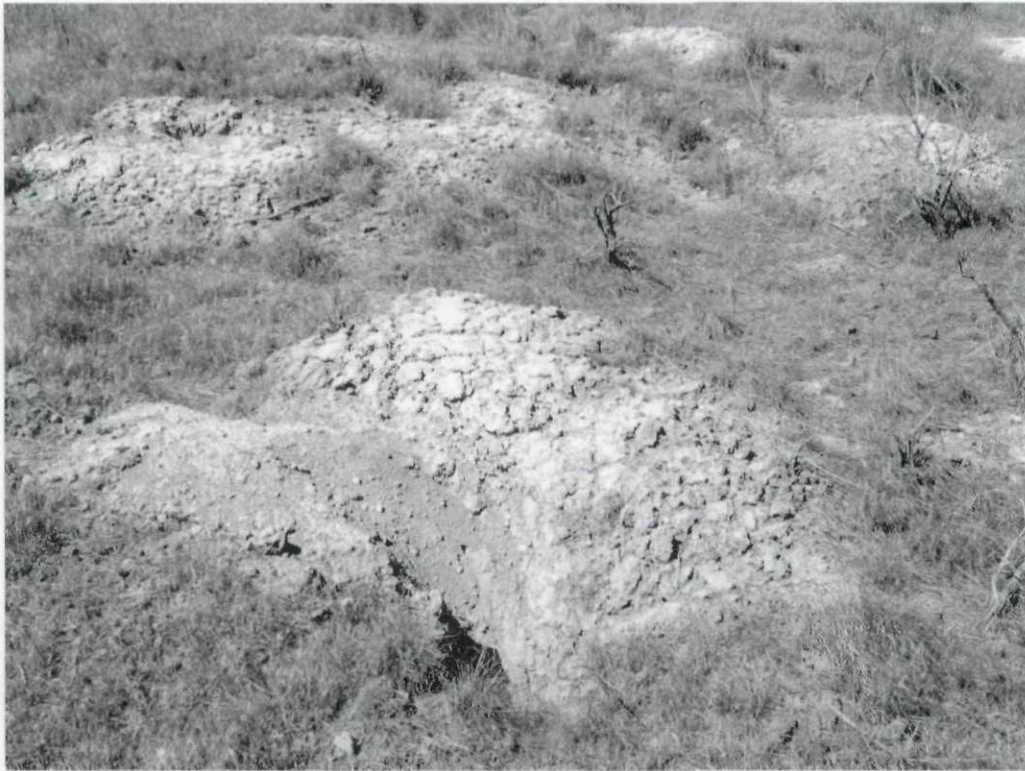


FIG. 1.—A typical badger mound and hole showing the fan-shaped accumulation of soil, in west-central Idaho, October 2002.

*Data analyses.*—Differences in mound morphology, in relation to both burning and vegetation community (and their interactions), were examined by using general linear models (Minitab 1997) after checking for homogeneity of variance with Levene's test. General linear models were required because the data were unbalanced, that is, not all mound types were present at all sites. The general linear model was a split-plot design with 2 error terms. The whole-plot stratum considered vegetation community and burning (and their interactions), and the subplot stratum partitioned mound type and its 2- and 3-way interactions with vegetation community and burning. Because individual mounds at a given site could not be considered true replicates in a statistical sense, site data were averaged across each of the 3 mound types before statistical analysis. Differences in means between vegetation community, levels of burning, mound types, and their interactions were compared by using least significant difference testing.

## RESULTS

The surface soil on recently excavated (active) mounds was massive and silty to the touch and had a fine granular appearance. Scattered nodules of calcrete and silica, transported by the badgers from the subsoil, were common close to the surface of active mounds and created a roughened mound surface. Field observations during wind storms indicated that the surface of active mounds is extremely erodible by wind due to the combination of a bare surface and the fine, massive soil material. However, shortly after rainfall, the surface forms a physical, raindrop-impacted crust, hastening the development of cyanobacterial crust, which ultimately develops a polygonal structure as the mounds progress from the crusted to the recovering stage. Mound recovery is associated with reduced

polygonal cracking, increased cover of plants (Fig. 2), generally short-lived grasses such as *Poa secunda*, and a change in the cover of cryptogamic communities from one dominated by cyanobacteria to one dominated by mosses and lichens.

The surface of the crusted mounds was compact and cemented, and typically comprised a thin, dispersed crust layer up to 2 mm thick (physical crust *sensu* Valentin [1991]). These crusts are often formed by the infilling of soil pores by silt. The only discernible microrelief on crusted mounds was some thin polygonal cracking. Recovering mounds were characterized by a variable cover of cryptogamic crusts, particularly cyanobacteria, short mosses (*Crossidium* and *Bryum argenteum*), lichens (*Aspicilia terrestris*, *Caloplaca tominii*, and *Placidium squamulosum*), and Sandberg's bluegrass. It was often difficult to separate recovering mound surfaces from nonmound, control surfaces because recovering mounds had little local relief (<8 cm high) and had many of the characteristics of control surfaces.

Across all 20 sites, mounds averaged  $964 \text{ mm} \pm 19 \text{ SE}$  long  $\times$   $770 \pm 14 \text{ mm}$  wide  $\times$   $84 \pm 2 \text{ mm}$  high. Mounds on burned sites were longer ( $1,067 \text{ mm}$ ,  $F = 8.26$ ,  $d.f. = 1, 16$ ,  $P = 0.008$ ) and wider ( $826 \text{ mm}$ ,  $F = 7.86$ ,  $d.f. = 1, 16$ ,  $P = 0.01$ ) than those on unburned sites ( $933 \text{ mm}$  long  $\times$   $746 \text{ mm}$  wide). The height of mounds showed a consistent decline with mound age ( $F = 5.79$ ,  $d.f. = 2, 24$ ,  $P = 0.009$ ; Table 1). Treatment by mound-type interactions for mound length ( $F = 4.15$ ,  $d.f. = 2, 24$ ,  $P = 0.028$ ) and width ( $F = 4.84$ ,  $d.f. = 2, 24$ ,  $P = 0.017$ ) indicated a decline in mound size with age on the burned sites, but an increase in size with age on the unburned sites. The vegetation community by mound-type interaction for mound width indicated that



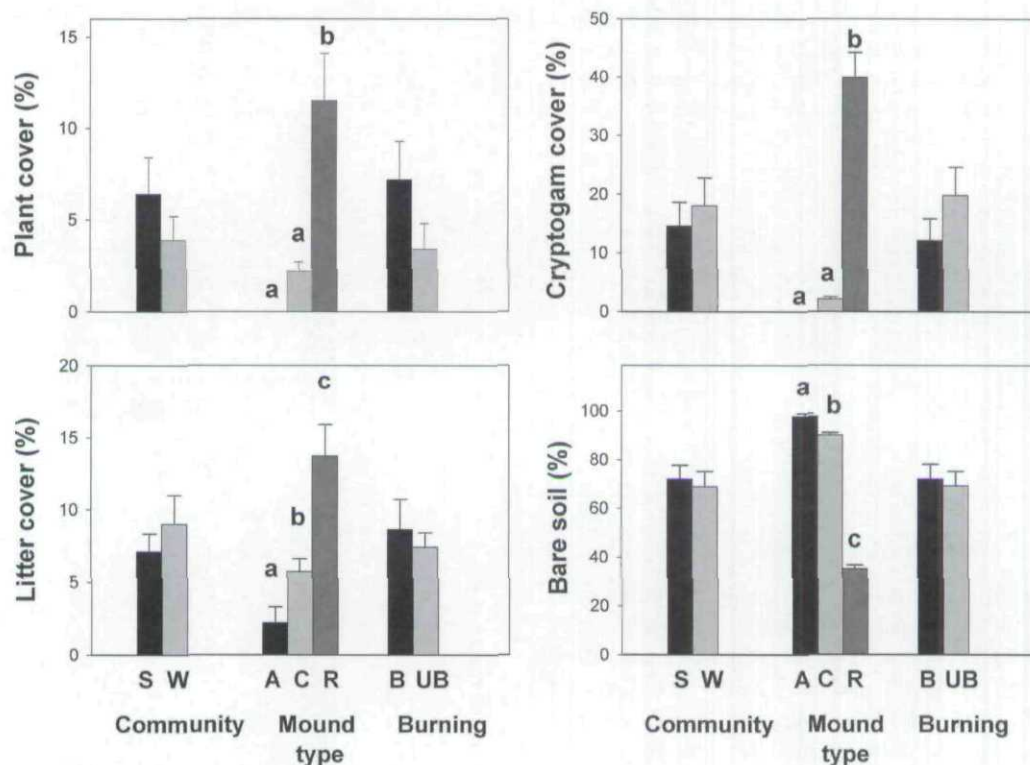


FIG. 2.—Cover of plants, cryptogams, litter, and bare soil in relation to vegetation community, mound type, and burning status, in west-central Idaho, September–October 2002. Community: S = sagebrush, W = winterfat. Mound type: A = active, C = crusted, R = recovering. Burning status: B = burned, UB = unburned. Different letters within a community, mound type, or burning status indicate a significant difference at  $P < 0.05$ . Lines above bars indicate SE. (Note: no plant cover or cryptogam cover for active mounds.)

mounds widened with age on the sagebrush sites (from 707 mm to 824 mm) but narrowed with age on the winterfat sites (from 1,084 mm to 796 mm,  $F = 6.82$ ,  $d.f. = 2, 24$ ,  $P = 0.005$ ).

A total of 790 mounds was recorded across the 20 sites, equal to a density of 790 mounds/ha. Similar densities were found on communities dominated by sagebrush (778 mounds/ha) and winterfat (802 mounds/ha; Fig. 3). Not all mound types were found at all sites. Active mounds were absent from 5 of the 10 burned (4 winterfat and 1 sagebrush) sites. Field observations indicate that the crusted mounds form about 0.5–2 months after their excavation. The measurements therefore indicate the absence of badger activity at these sites up to 2 months before field survey.

Averaged across vegetation communities, more mounds occurred on the unburned sites than on burned sites ( $F = 5.03$ ,  $d.f. = 2, 24$ ,  $P = 0.031$ ; Fig. 3). Crusted mounds were the most common across all vegetation communities and treatments, and active mounds were the least common ( $F = 29.1$ ,  $d.f. = 2, 24$ ,  $P < 0.001$ ; Fig. 3). The vegetation community by treatment interaction ( $F = 9.62$ ,  $d.f. = 1, 16$ ,  $P = 0.004$ ) indicated that although burning was associated with a reduced density of mounds at winterfat sites (608 and 996 mounds/ha on burned and unburned sites, respectively), burning had little effect at the sagebrush sites (824 and 732 mounds for burned and unburned sites, respectively).

Ninety-six percent of active and crusted mounds had holes compared with only 31% of recovering mounds ( $F = 758.7$ ,

$d.f. = 2, 24$ ,  $P < 0.001$ ). Hole diameter averaged  $163 \pm 3$  mm, and was not different between burning treatments, vegetation community, or mound types ( $P > 0.05$ ; Tables 1 and 2). The proportion of holes that trapped litter and organic matter increased as the mounds aged (Table 1). Bulk density values were similar on active, crusted, and recovering mounds ( $P > 0.05$ ), and averaged  $1.34 \text{ Mg/m}^3$  (range =  $1.19\text{--}1.42 \text{ Mg/m}^3$ ) across all mound types. Across all 20 sites, the mass of soil excavated by badgers averaged  $33.8 \pm 0.2$  kg per mound, equating to a total mass of 26.7 t/ha. Mounds and diggings occupied an average of 5–8% of the landscape.

No differences were found in plant cover, or cover of cryptogams, litter, or bare soil between mounds in sagebrush and winterfat communities, or between mounds at burned or unburned sites ( $P > 0.05$ ; Fig. 2). However, recovering mounds had greater plant cover, cryptogam cover, and litter cover, and consequently, less cover of bare ground compared with younger (active and crusted) mounds ( $P < 0.001$ ).

The density of squirrel holes and scratchings at a site was positively correlated with the density of shrubs ( $F = 12.68$ ,  $d.f. = 1, 18$ ,  $P = 0.002$ ,  $r^2 = 0.41$ ; Fig. 4A). Further, the density of badger mounds was correlated with shrub density ( $F = 8.10$ ,  $d.f. = 1, 18$ ,  $P = 0.011$ ,  $r^2 = 0.35$ ; Fig. 4B). Increased density of badger mounds was associated with increases in the density of squirrel holes and scratchings ( $r = 0.66$ ,  $n = 20$ ,  $P = 0.001$ ; Fig. 5).



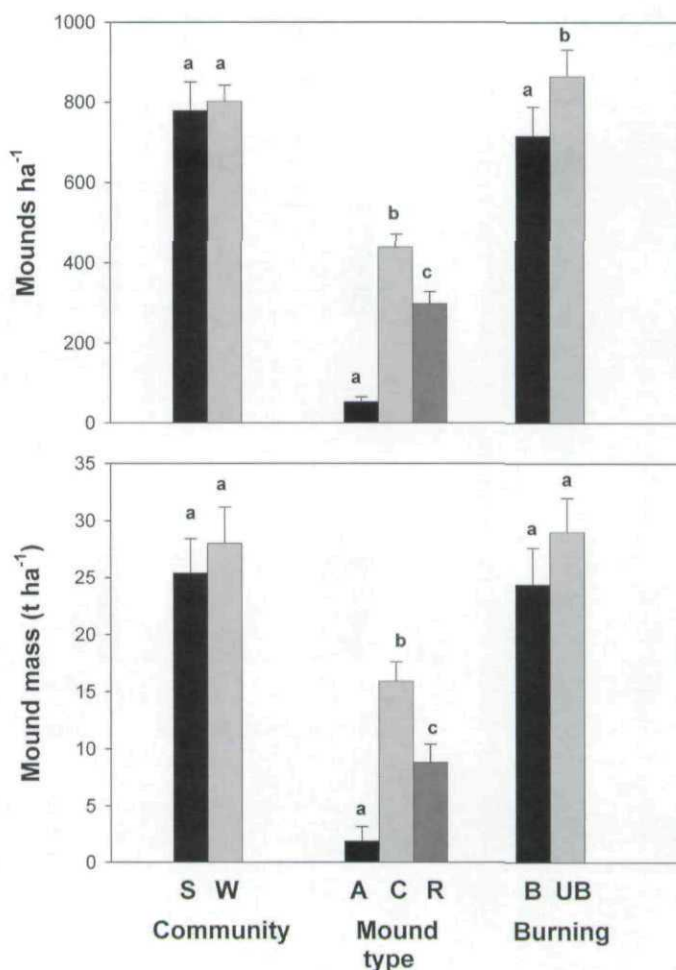
**TABLE 1.**—Dimensions and cover components for badger mounds by mound type for sites in west-central Idaho, September–October 2002. For each variable, different superscript letters within a vegetation community, mound type, or burning treatment indicate a significant difference at  $P < 0.05$ .

Variable	Mound type					
	Active		Crusted		Recovering	
	Mean	SE	Mean	SE	Mean	SE
Mound length (mm)	1,058 <sup>a</sup>	54	944 <sup>a</sup>	48	1,015 <sup>a</sup>	27
Mound width (mm)	786 <sup>a</sup>	76	758 <sup>a</sup>	36	810 <sup>a</sup>	22
Mound height (mm)	103 <sup>a</sup>	9	89 <sup>b</sup>	5	73 <sup>c</sup>	6
Hole diameter (mm)	175 <sup>a</sup>	9	166 <sup>a</sup>	5	143 <sup>a</sup>	10
Mounds with holes (%)	94.7 <sup>a</sup>	2.9	97.1 <sup>a</sup>	0.8	31.3 <sup>b</sup>	3.9
Holes with litter (%)	29.6 <sup>a</sup>	8.6	90.3 <sup>b</sup>	3.9	99.1 <sup>b</sup>	0.7
<i>n</i>	53		439		298	

## DISCUSSION

Biopedurbation by mammals is an important ecosystem process leading to the development of patchiness in essentially infertile landscapes (Boeken et al. 1995; Eldridge and Rath 2002; Kinlaw 1999; Whitford and Kay 1999). The present study has demonstrated that badger mounds, pits, and diggings are a substantial landscape element on fine-textured soils in west-central Idaho. These animal-moderated structures, constructed while foraging for fossorial animals (ground squirrels, burrowing owls, kangaroo rats, and mice), were relatively large ( $0.5\text{--}1.5\text{ m}^2$ ) and therefore conspicuous at a landscape scale. Very few mammals, apart from some fossorial rodents from China (Hongo et al. 1993), Chile (Contreras et al. 1993), and Argentina (Whitford and Kay 1999), construct such conspicuous structures on such a broad scale. In the present study, densities of 53 active mounds/ha are within the range of figures reported for similar areas of west-central Idaho (range 3–67 active mounds/ha—Yensen et al. 1992). I measured all mounds regardless of their age. Because of the difficulty of distinguishing between low, vegetated recovering mounds and nonmound (control) surfaces, the cover of mounds (5–8% of the landscape) is doubtless an underestimate of the true coverage. It is probable that badgers have a greater impact on soil disturbance (Fig. 2).

Badgers are regular inhabitants of the shrub–steppe ecosystem, and although not strictly shrub–steppe obligates, are nonetheless habitat-selective (Vander Haegen et al. 2001). The distribution of badgers is indirectly linked to shrub–steppe vegetation due to their preferences for small and mesoscale animals that inhabit shrub–steppe ecosystems (Messick and Hornocker 1981). A detailed study of the behavioral ecology of badgers in the Snake River Plain indicated that they have relatively large home ranges ( $1.6\text{--}2.0\text{ km}^2$ ) and disperse distances in excess of 100 km (Messick and Hornocker 1981). Few data are available on the impact of badgers on soil processes (e.g., Hole 1981; Voslamber and Veen 1985; Whitford and Kay 1999; Yensen et al. 1992), and no data are available on the number of mounds dug by a single badger in any one year. However, estimates of 3.2–5 badgers/ $\text{km}^2$  (Messick and Hornocker 1981) indicate that conservatively, each badger constructs between 1,100 and 1,700 mounds/year, given that 7% of mounds are active.



**FIG. 3.**—Density of badger mounds (mounds/ha) and mass of mound soil (t/ha) in relation to vegetation community, mound type, and burning status, in west-central Idaho, September–October 2002. Community: S = sagebrush, W = winterfat. Mound type: A = active, C = crusted, R = recovering. Burning status: B = burned, UB = unburned. Different letters within a community, mound type, or burning status indicate a significant difference at  $P < 0.05$ . Lines above bars indicate SE.

Although no data are available on the length of time that badger mounds persist, examination of empirical data relating the area of animal disturbance to the longevity of their diggings for a range of fossorial mammals suggests that mounds persist for about 7–10 years (Whitford and Kay 1999). As indicated previously, field observations suggest that the surface of badger mounds crusts over rapidly, and that this process is hastened by even small amounts of rainfall or dew. Colonization of mounds by plants is thought to occur over a 2- to 3-year period (Platt 1975). The relatively high density of older crusted mounds in the present study is an indication of cumulative activity over the past 6–9 months. Although this may seem at odds with the figure of 7–10 years before mounds are indistinguishable from the general soil surface, mounds can probably persist for many years as slightly raised hummocks of vegetated soil above the level of the surrounding landscape. Indeed, slight rises, low undulations, and hummocks are common over much of the shrub–steppe landscape, a consequence of former digging sites.



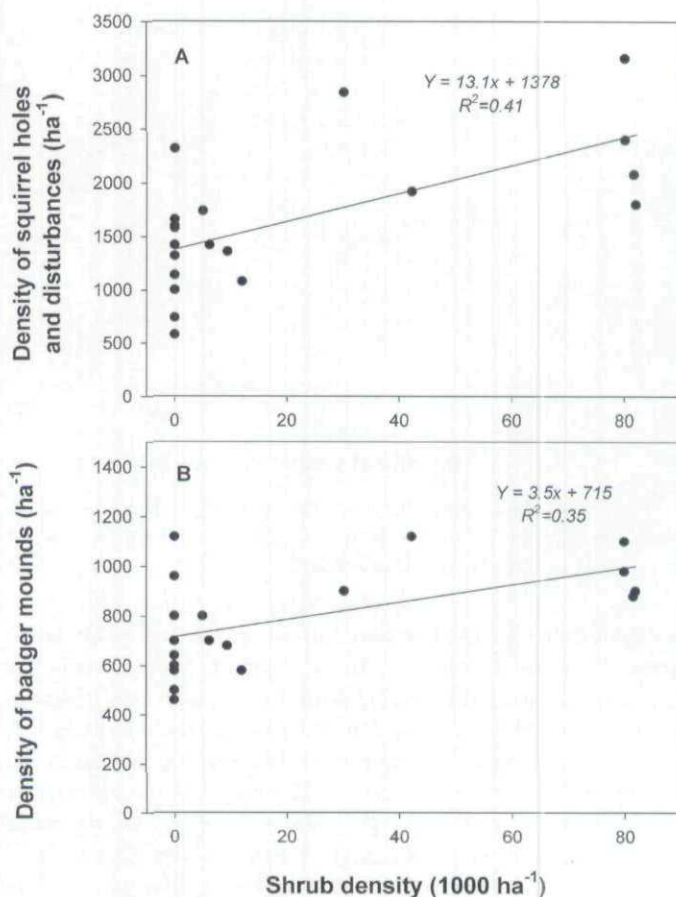
**TABLE 2.**—Dimensions and cover components for badger mounds by vegetation community and burning treatment for sites in west-central Idaho, September–October 2002. For each variable, different superscript letters within a vegetation community, mound type, or burning treatment indicate a significant difference at  $P < 0.05$ .

Variable	Vegetation community				Burning treatment			
	Sagebrush		Winterfat		Burned		Unburned	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Mound length (mm)	973 <sup>a</sup>	62	1,026 <sup>a</sup>	51	1,067 <sup>a</sup>	70	933 <sup>b</sup>	42
Mound width (mm)	746 <sup>a</sup>	31	829 <sup>b</sup>	34	826 <sup>a</sup>	36	746 <sup>b</sup>	30
Mound height (mm)	86 <sup>a</sup>	6	87 <sup>a</sup>	5	82 <sup>a</sup>	5	90 <sup>a</sup>	5
Hole diameter (mm)	159 <sup>a</sup>	8	160 <sup>a</sup>	6	148 <sup>a</sup>	9	170 <sup>a</sup>	5
Mounds with holes (%)	72.6 <sup>a</sup>	6.6	69.6 <sup>a</sup>	6.9	68.6 <sup>a</sup>	7.6	73.6 <sup>a</sup>	5.9
Holes with litter (%)	72.0 <sup>a</sup>	5.2	76.4 <sup>a</sup>	5.8	68.8 <sup>a</sup>	6.3	79.6 <sup>a</sup>	4.4
n	389		401		358		432	

These older mounds often have been described as fossil mounds (E. Yensen, pers. comm.).

The present study identified differences in badger mound density in relation to burning and vegetation community (Table 2). These differences are likely due in large part to the distribution and abundance of ground squirrels (Vander Haegen et al. 2001), the badgers' principal prey items (Messick and Hornocker 1981), and other prey such as deer mice (*Peromyscus maniculatus*), reptiles (e.g., gopher snake [*Pituophis melanoleucus*]), and invertebrates (Messick and Hornocker 1981). Populations of Piute ground squirrels (*Spermophilus mollis*) are highly cyclic, and are known to be lower in burned areas (Groves and Steenhof 1988) because burning reduces the availability of food for squirrels. In shrub-steppe ecosystems, fire suppresses spring plant production and converts relatively stable perennial production into an annual-based system, which has greater variation in production (Yensen et al. 1992). During some years, ground squirrels can survive at sites with sparse shrub cover, but prefer cover levels of 10–20%. The optimal landscape is one where shrubs exist in a mixture of burned and unburned patches, providing a mosaic of successional stages and therefore forage requirements (Vander Haegen et al. 2001).

Apart from slightly wider mounds on the winterfat sites, no substantial differences were found between sites dominated by *Artemisia* or those dominated by *Krascheninnikovia* (Table 2). If badgers are preying predominantly on ground squirrels (70%), principally the Piute ground squirrel (*S. mollis*, formerly *S. townsendii mollis*) as reported by Messick and Hornocker (1981), then mound density would likely have been greater in *Krascheninnikovia*-dominated sites, which are known to support higher populations of ground squirrels (Nydegger and Smith 1986; Yensen et al. 1992). Instead, densities of mounds were slightly greater in *Krascheninnikovia*-dominated sites, but the differences were not significant, and certainly not of the magnitude reported by Nydegger and Smith (1986) or Yensen et al. (1992). A possible reason for the lack of difference between *Artemisia* and *Krascheninnikovia* sites is that the study was undertaken when populations of *S. mollis* were high, with individuals occupying all available habitat, thereby negating any possible habitat differences (E. Yensen, pers. comm.).



**FIG. 4.**—Relationships between shrub density ( $\text{ha}^{-1}$ ) and A) density of squirrel holes and disturbances and B) density of badger mounds ( $\text{ha}^{-1}$ ), in west-central Idaho, September–October 2002.

Despite the lack of an effect of vegetation type, landscape structure is nonetheless important for badgers and their fossorial prey. Examination of the data suggests that reductions in shrub cover are associated with reduced densities of ground squirrels (Fig. 4A) and therefore badger diggings (Fig. 4B). It is likely that badger digging creates feedback effects on shrub recruitment and survival or alters the ability of shrublands to carry a wildfire, thereby affecting ground squirrel habitat and abundance of the badgers' principle prey source. Knowledge of the 3-way linkage between shrubs, ground squirrels, and badgers is critical to our understanding of functional shrub-steppe ecosystems. Links between soil processes and recruitment and survival of shrub-steppe plants, are the subject of current research in the Snake River Plain.

Badgers in the present study moved approximately  $20 \text{ m}^3$  of soil per hectare over a 7- to 10-year period. Soil removal by badgers is of a similar order of magnitude to that of the European rabbit, which is reported to move 2–63  $\text{m}^3$  of soil per hectare (Butler 1995), although turnover rates have not been reported. Other fossorial animals such as southern hairy-nosed wombats (*Lasiorhinus latifrons*) construct large mounds ranging in volume from 16 to 55  $\text{m}^3$  (Steele and Temple-Smith 1998) but at substantially lower densities of 0.1–0.2 mounds/ha (Loffler and Margules 1980). Animals of smaller body size such as



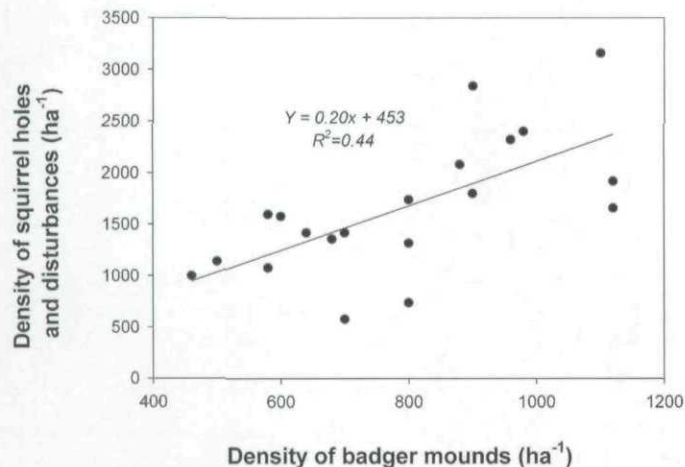


FIG. 5.—Relationships between the density of badger mounds ( $\text{ha}^{-1}$ ) and density of squirrel holes and disturbances ( $\text{ha}^{-1}$ ), in west-central Idaho, September–October 2002.

ground squirrels, kangaroo rats, and pocket gophers are known to move substantial volumes of soil in areas where foraging is concentrated (e.g., Price 1971; Whitford and Kay 1999). Studies in wooded slopes in the Ardennes in Belgium attributed a low rate of only 4.4 kg of excavated soil per hectare to the activity of European badgers (*M. meles*) during a 6-month period (Voslamber and Veen 1985). This activity would have corresponded to active diggings, which amounted to 1.9 t of soil per hectare in the present study (Fig. 3). Given that active mounds had been constructed in the past few months, and assuming a conservative estimate that 20% of crusted mounds are less than 12 months old, then a cautious estimate of mound turnover rates is  $5.1 \text{ t ha}^{-1} \text{ year}^{-1}$ .

Scratchings, diggings, and mound excavation influence a range of soil physical processes such as infiltration of water (Cox 1987; Hole 1981), aeration, bulk density, and porosity (Heth 1991; Laundré and Reynolds 1993). They also influence the chemistry of surrounding soil (see Eldridge and Rath 2002; Whitford and Kay 1999). Mounds, their holes, and associated scratchings also tend to trap essential resources such as organic matter, soil, litter, and water. Examination of data from the present study demonstrates that holes associated with mounds are effective traps for litter. As shown in studies of the diggings of other medium- and large-sized animals (Dean and Milton 1991a, 1991b; Gutterman 2001), this is likely to lead to enhanced levels of carbon and nitrogen in the holes, promoting the development of fertile patches for vascular plants (Eldridge and Rath 2002). Litter trapped under soil in the holes also may promote fungal growth, further enhancing soil nutrients and the breakdown of organic material. The extent to which increased nutrients in the holes influence landscape-level nutrient loads is the subject of current research.

This study demonstrated that activity by badgers while foraging for fossorial animals produces extensive soil disturbance that initiates dramatic changes in landscape structure. From a geomorphological perspective, badger activities are a dominant process in the production of available sediment in shrub-steppe ecosystems. In the short-term, badger mounds may

appear to be unstable landscape elements providing a hostile environment for vascular plants. However, they rapidly form a surface crust and are likely to contribute to landscape heterogeneity through impacts on water flows and soil nutrients. The holes excavated by badgers become sinks for soil, seeds, and litter and may provide habitat for unknown vertebrates and invertebrates.

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