

THE BIOGEOGRAPHY OF SMALL MAMMALS OF FRAGMENTED SAGEBRUSH-STEPPE LANDSCAPES

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We sampled small mammals of fragmented sagebrush steppe on the Snake River Plain, Idaho, and compared the effects of habitat isolation on their diversity, abundance, and species composition in 2 landscapes, kipukas, which are patches of sagebrush-steppe habitat that were isolated by late-Pleistocene and early-Holocene lava flows, and remnant patches of sagebrush steppe that remain within recently developed agricultural areas. Species richness decreased with increasing isolation in both lava and agricultural landscapes, and *Peromyscus maniculatus* (deer mouse) was the only species found on kipukas that were isolated by more than 400–800 m, suggesting that many native sagebrush-steppe species may decline or disappear from fragmented sagebrush steppe. Density of small mammals increased with isolation on the agricultural patches, but decreased with isolation on kipukas; however, increased densities were entirely due to *P. maniculatus*. Diversity of small mammals on kipukas was highly correlated with absolute and proportional abundance of shrubs, probable indicators of sagebrush-steppe vegetation. Additionally, *Bromus tectorum* (cheatgrass) may play a role in the low diversity and density of mammals on kipukas, because both diversity and density were lower where cheatgrass was present than where it was absent.

Key words: habitat fragmentation, Idaho, island biogeography, isolation, kipuka, matrix habitat, sagebrush steppe

Since MacArthur and Wilson (1967) proposed a mechanistic framework for diversity of insular habitats (the MacArthur–Wilson model), the effects of isolation on the biodiversity of habitat fragments has received much study (e.g., Brown 1971; Debinski and Holt 2000; Saunders et al. 1991). The MacArthur–Wilson model assumed that islands that were more distant from sources of dispersing individuals would have lower immigration rates, resulting in lower diversity. The model also assumed that island size would affect biodiversity, with smaller islands having higher rates of local extinction, resulting in lower diversity. These ideas have been extended to insular patches of habitat, for which the intervening matrix of other habitats can promote or reduce dispersal success, modulating isolation and so influencing diversity (Lomolino 1994, 2000; Ricketts and Morris 2001; Vandermeer and Carvajal 2001; Witt and Huntly 2001). Additionally, isolation can affect the densities of species within habitat patches. Low immigration rates can lead to lower (Brown and Kodric-Brown

1977; Soulé and Simberloff 1986) or higher (Adler and Levins 1994; Lomolino 1984) density on more isolated patches.

Study of the populations of habitat fragments is increasingly important to conservation practice, because the world's habitats are increasingly fragmented by human land use (Bolger et al. 1997; Saunders et al. 1991). In agricultural regions, of which sagebrush steppe is becoming an example (Knick and Rotenberry 1995, 1997), native vegetation is found only in discrete patches within a matrix of agricultural lands (McIntyre and Hobbs 1999). Of the 10.3 million hectares of sagebrush steppe that historically were found in Idaho (West 1983), approximately 3.5 million hectares have been cleared for agricultural purposes (Lipske 2000). Agricultural practices also have led to the spread of the nonnative grass, *Bromus tectorum* (cheatgrass—D'Antonio and Vitousek 1992), which has increased fire frequency and further exacerbated fragmentation of sagebrush steppe (Klemmenson and Smith 1964; Melgoza et al. 1990; Knick and Rotenberry 1997).

We examined the small mammal fauna of isolated sagebrush-steppe fragments in 2 landscapes of the Snake River Plain, Idaho, that differed in land-use history to determine the effects of habitat isolation on the diversity, abundance, and species composition of small mammals of sagebrush steppe. The lava flows on the Snake River Plain in south-central Idaho provide the opportunity to compare habitat patches that were

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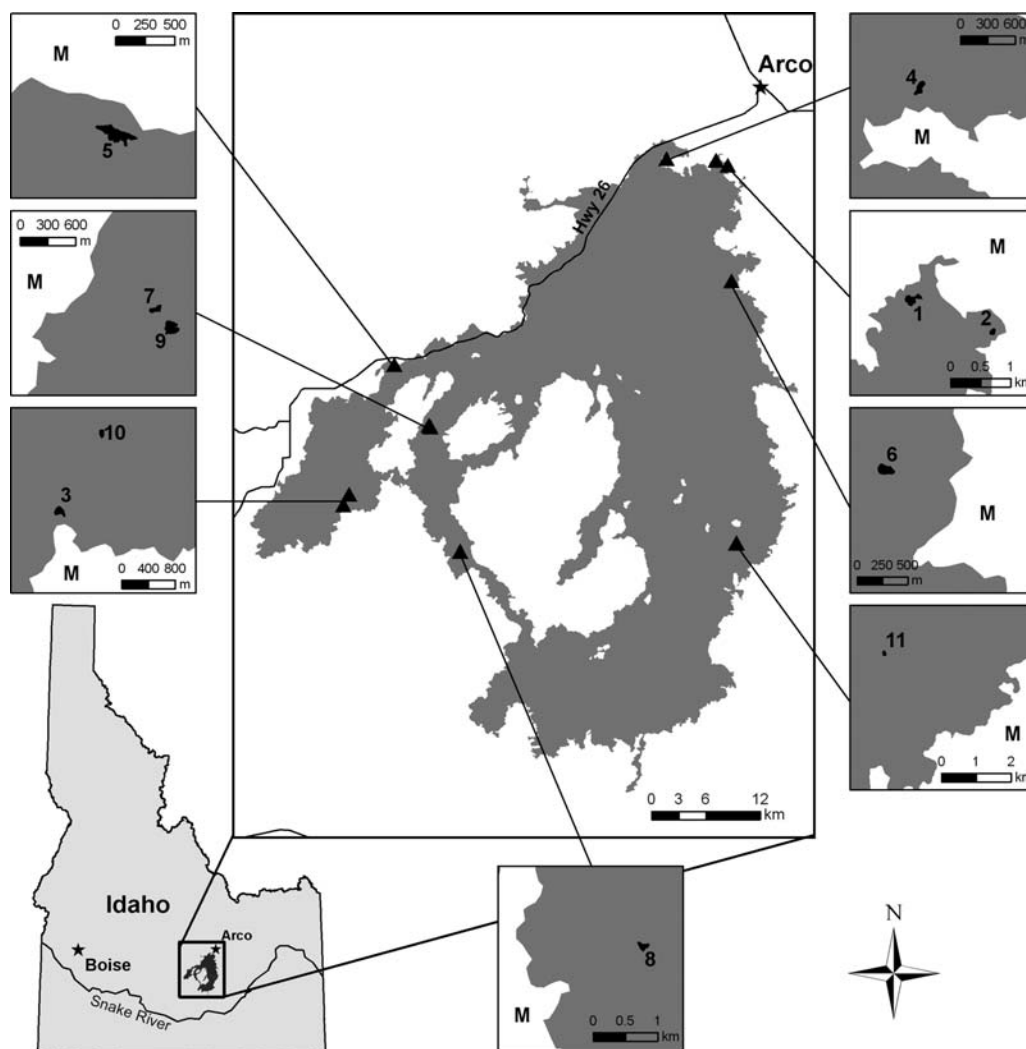


FIG. 1.—Craters of the Moon Lava Field, Idaho. The 8 insets show locations of the kipukas from which small mammals were sampled and the nearest sagebrush-steppe mainland (M). Kipukas are remnant patches of sagebrush steppe that are surrounded by lava rock formed from late-Pleistocene and early-Holocene lava flows; shaded areas represent this lava matrix. Arco is at 43.63°N latitude, 113.30°W longitude.

formed long ago by physical processes and are relatively free of recent land-use impacts with habitat patches that have been created by recent intensified land use by humans. The lava flows produced kipukas, small islands of habitat that are formed when molten lava flows around rather than covering areas that then become isolated patches with remnant soils and vegetation. The kipukas of the eastern Snake River Plain are patches of sagebrush steppe that were isolated by volcanic activity in the Great Rift volcanic zone and that are now surrounded by sparsely vegetated lava rock. These areas have not been farmed or grazed and thus are believed to retain native sagebrush-steppe habitat that has been minimally influenced by human land-use practices. Recent agricultural development also has produced remnant sagebrush-steppe patches embedded in a matrix of vegetation (crops) that is highly altered by humans and that would be expected to have diverged considerably from historical sagebrush-steppe habitat. We hypothesized that species richness on both agricultural patches and kipukas would decline with increasing

isolation, consistent with the theory of island biogeography (MacArthur and Wilson 1967); kipukas would retain higher-quality native sagebrush-steppe habitat and thus would have higher species richness at low isolation; species richness would decline more sharply with isolation on kipukas, which have a longer history of isolation as well as a potentially harsher matrix habitat (lava versus crops); and diversity and abundance of small mammals would be correlated with habitat characteristics, which would suggest habitat elements important to small mammals.

MATERIALS AND METHODS

Kipukas were located within the Craters of the Moon National Monument at the northern edge of the eastern Snake River Plain in Idaho (Fig. 1). The Craters of the Moon Lava Flow ranges in age from 2,100 to 15,000 years ago (Kuntz et al. 1988). Mean elevation of the lava flow is 1,526.5 m $\pm$ 88.6 SD, precipitation (Arco, Idaho) averages 247 mm/year (but was only 186 mm during the year preceding this study; Idaho State Climate Services, Moscow, Idaho),

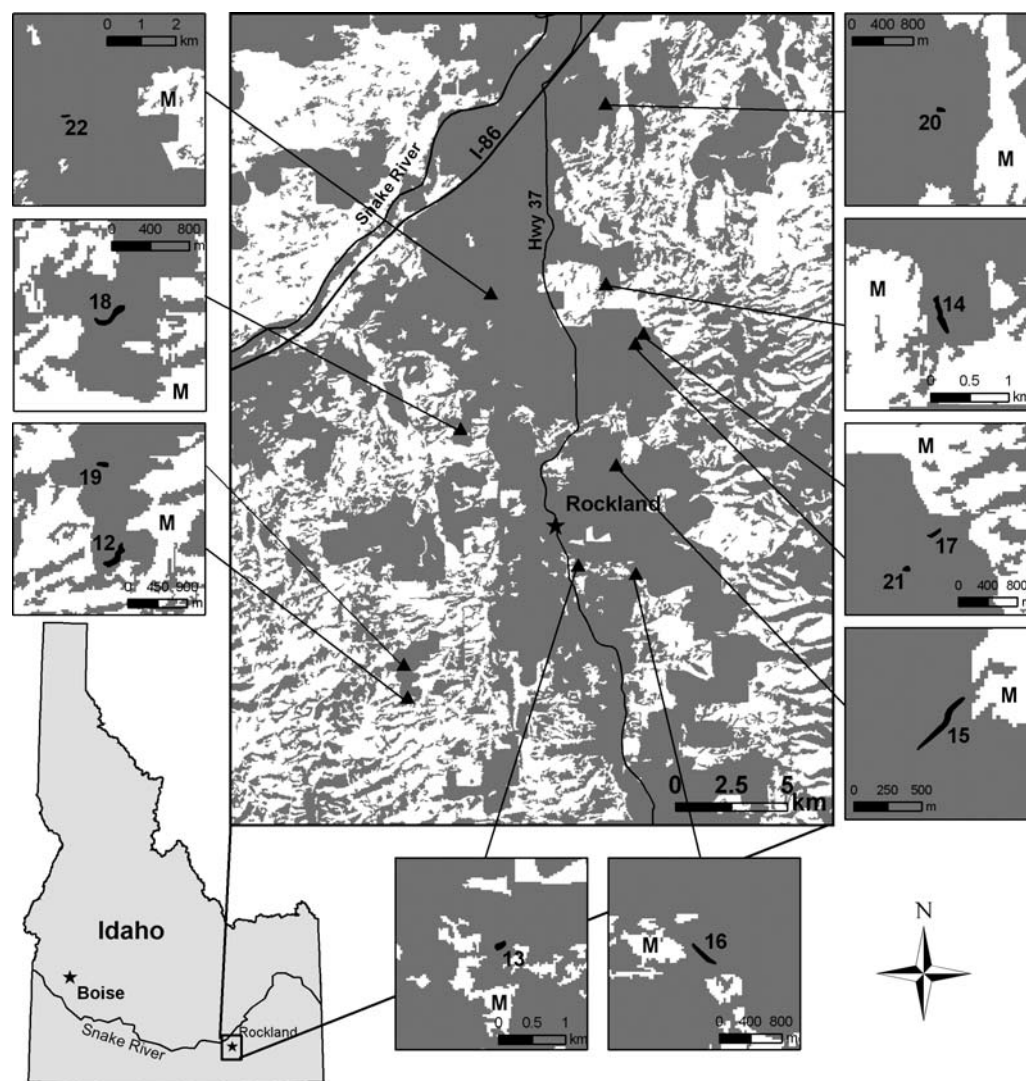


FIG. 2.—Rockland Valley, Idaho. The 9 insets show locations of agricultural patches (sagebrush steppe surrounded by agricultural lands) from which small mammals were sampled and the nearest sagebrush-steppe mainland (M). Shaded areas represent the agricultural matrix. Rockland is at 42.57°N latitude, 112.88°W longitude.

and mean daily minimum and maximum temperatures are 2.36°C and 22.35°C in summer and −11.55°C and 3.53°C in winter, respectively (Western Regional Climate Center, Reno, Nevada). Vegetation of kipukas is characterized by *Artemisia tridentata* (big sagebrush), *A. tripartita* (tri-tip sagebrush), *Purshia tridentata* (bitterbrush), and grasses (*Poa* and *Stipa*), and the surrounding lava flows are relatively barren, with sparse areas of *A. tridentata*, *Chamaebatiaria millefolium* (desert sweet), and *P. tridentata*.

We also located patches of sagebrush steppe that had been isolated by development of agriculture in the Rockland Valley on the southern edge of the Snake River Plain (Fig. 2). Agricultural development began in 1883 in this area, and arable land was fully settled by 1910 (D. Glascock, pers. comm.). The region is used primarily for wheat production, but areas with rocky substrate or high relief are not developed; thus, remnant sagebrush-steppe habitat remains within a primarily agricultural landscape. Mean elevation of the valley is $1,541.5 \pm 90.7$ m, precipitation averages 287 mm/year (but was only 166 mm during the year preceding this study; Idaho State Climate Services, Moscow, Idaho), mean daily minimum and maximum temperatures are 6.81°C and 23.32°C in summer and −5.47°C and

4.53°C in winter, respectively (Western Regional Climate Center, Reno, Nevada).

Within each landscape we sampled 11 habitat patches, chosen to represent a broad range of isolation while minimizing variation in area (Figs. 1 and 2). Kipukas ranged in isolation from 39 to 1,867 m distant from extensive sagebrush steppe that surrounds the lava flows, and agricultural patches were 84–1,243 m distant from sagebrush steppe surrounding agricultural areas; kipuka sizes ranged from 0.42 to 1.99 ha and agricultural patches from 0.35 to 3.04 ha.

Patches were selected and their isolation and area determined from global information system (GIS) databases constructed for the Craters of the Moon Lava Flow and Rockland Valley using ArcView (ESRI, Redlands, California). We identified patches on United States Geological Survey digital orthophoto quarter-quadrangles and digital raster graphics obtained from the Idaho State University GIS Training and Research Center and digitized them into the GIS. We identified 420 kipukas within the Craters of the Moon Lava Flow with a mean isolation of 1,003.80 m (range 8.1–6,898.51 m) and a mean area of 9.71 ha (range 0.009–924.3 ha) and 116 agricultural patches with a mean isolation of 183.80 m (range 15.0–1,433.00 m) and a mean

area of 1.29 ha (range 0.019–7.569 ha). We measured isolation as the shortest straight-line distance from a kipuka to the nearest large tract of continuous sagebrush steppe outside of the lava flow (i.e., the sagebrush-steppe “mainland”). Because of difficulty discriminating sagebrush steppe on digital orthophoto quarter-quadrangles in the Rockland Valley, we used ArcInfo (ESRI) to identify regions of sagebrush cover > 10 ha on the Idaho Gap Analysis land cover classification map (Homer 1998) and measured the isolation of agricultural patches as the distance between the agricultural patch and the nearest area of sagebrush steppe > 10 ha.

We trapped small mammals on agricultural patches and kipukas between late May and late June 2001, using a trapping grid of 25 trap stations located a minimum of 10 m from any patch edge, with trap stations spaced at 10-m intervals, and 2 Sherman live traps (23 × 8 × 9 cm; H. B. Sherman Traps, Inc., Tallahassee, Florida) at each station baited with rolled oats. We set traps before sunset and checked them each morning after sunrise for 3 consecutive days on each patch, with order of trapping randomized amongst groups of patches. Captured animals were weighed, sexed, checked for reproductive condition, tagged with a uniquely numbered Monel fingerling tag (National Band and Tag Co., Newport, Kentucky), and released. We calculated species richness (the total number of species caught within a trapping period), Simpson's index ($1/\sum p_i^2$, a measure that incorporates evenness as well as the number of species [Krebs 1989]), and density (individuals per hectare, using the Peterson method [Krebs 1989]) for each patch. Trapping and ear-tagging procedures followed guidelines established by the American Society of Mammalogists (Animal Care and Use Committee 1998) and were approved by the Animal Welfare Committee of Idaho State University.

We sampled vegetation and other ground cover on each patch using point-frame interception (Floyd and Anderson 1982). We centered a 50-m transect at the approximate center of each trap grid and ran 10-m transects perpendicular to this and on alternating sides from 2 randomly selected points within each 10-m section of the transect. We used a 1 × 0.5-m point frame with 36 points to sample vegetation at the 1-, 3-, 5-, 7-, and 9-m marks along each 10-m transect, for a total of 50 samples and 1,800 sample points on each kipuka or agricultural patch. We calculated species richness, as well as cover of bare ground, dead shrub, rock, litter, and total vegetation, and both cover and proportional cover of shrubs, forbs, cheatgrass, and native grasses.

We tested for relationships of species richness, Simpson's index, or density of small mammals with area or isolation within each habitat (kipuka or agricultural patch) and compared these relationships between kipukas and agricultural patches with multiple regression, using habitat (kipuka or agricultural patch, coded as a dummy variable), isolation or area, and the interaction between habitat and isolation or area as predictor variables. In this latter analysis, a significant habitat response indicates that intercepts of the regressions differ between habitats, and a significant interaction response indicates that slopes of the regressions differ between the 2 habitats. We also used this technique to analyze the density-isolation relationship for *Peromyscus maniculatus* (deer mouse), the most abundant species in our samples, and for the pooled density of the other species.

We tested for nestedness of species occurrence on both kipukas and agricultural patches using the Atmar and Patterson procedure (nestedness temperature calculator—Atmar and Patterson 1995). Nestedness, the pattern where the species of less species-rich assemblages tend to be subsets of those comprising more species-rich assemblages, is expected to result from ordered extinctions, which may occur if species are differentially lost from habitat fragments by

extinction, differentially supplied or replaced by immigration, or a combination of the 2 processes. The Atmar and Patterson procedure computes a comparative metric, *T*, which is lower for more strongly nested faunas (Atmar and Patterson 1993).

We tested for correlations between diversity or density and vegetational and other habitat characteristics within each landscape using Pearson correlation analysis, and then used multiple stepwise regression (forward method, *P* to enter = 0.10, *P* to remove = 0.15) to select a set of habitat variables (from plant species richness, total percentage plant cover, shrub cover, native grass cover, and cheatgrass cover) that was best associated with diversity or density. Abundance and diversity of vegetation often are strong predictors of occurrence or abundance of small mammals (Dueser and Porter 1986; Dueser and Shugart 1978; Ellison and van Riper 1998; Huntly and Inouye 1987; Peles and Barrett 1996). Cheatgrass has been identified as playing a role in degradation of sagebrush steppe (D'Antonio and Vitousek 1992), so we also compared density and species richness of the 6 kipukas on which cheatgrass was present with that of the 5 kipukas that lacked cheatgrass using a *t*-test with unequal variances.

RESULTS

We captured 56 small mammals on kipukas and 158 on agricultural patches during 3,300 trap nights. Five species (*P. maniculatus*, *Tamias minimus* [least chipmunk], *Reithrodontomys megalotis* [western harvest mouse], *Perognathus parvus* [Great Basin pocket mouse], and *Neotoma cinerea* [bushy-tailed woodrat]) were present on kipukas, and 7 species (*P. maniculatus*, *P. parvus*, *R. megalotis*, *T. minimus*, *Microtus montanus* [montane vole], *Zapus princeps* [western jumping mouse], and *Lemmys curtatus* [sagebrush vole]) were present on agricultural patches (Table 1).

Species richness of small mammals was lower on kipukas (average 1.55, range 0–4) than on agricultural patches (average 2.73, range 1–4; $t = 2.389$, *d.f.* = 20, $P = 0.027$; Table 1). Species richness decreased with isolation on both kipukas and agricultural patches, and neither the slope nor the intercept of the relationship differed significantly between the 2 patch types (Table 2; Fig. 3). Simple linear regressions suggested that the relationship between species richness (SR) and isolation was stronger on kipukas ($\log(\text{SR} + 1) = 1.061 - 0.281 \log \text{isolation}$; $r^2 = 0.693$, *d.f.* = 10, $P = 0.018$) and more variable for agricultural patches ($\log(\text{SR} + 1) = 1.082 - 0.270 \log \text{isolation}$; $r^2 = 0.291$, *d.f.* = 10, $P = 0.087$). Additionally, the pattern of species occurrence in relation to patch isolation was more nested on kipukas ($T = 1.47$) in comparison to the agricultural patches ($T = 17.06$). Patch isolation and area were uncorrelated in the sample of kipukas (Pearson's $r = -0.386$, $P = 0.241$) but were correlated in the sample of agricultural patches ($r = -0.711$, $P = 0.014$); however, neither species richness nor Simpson's index was significantly related to patch area (Table 3).

The mean density of small mammals also was lower on kipukas (38.4 animals/ha, range 0–131.25 animals/ha) than on agricultural patches (102.1 animals/ha, range 46.25–184.15 animals/ha; $t = -3.291$, *d.f.* = 20, $P = 0.004$; Table 1). A study conducted in a nearby large tract of ungrazed sagebrush steppe (Reynolds 1980) reported mean density of 3.71

TABLE 1.—Occurrence of small mammals on kipukas, remnant patches of sagebrush steppe that are surrounded by lava rock, and agricultural patches, remnants of sagebrush steppe surrounded by agricultural lands. Patches are listed in order of isolation from large contiguous patches of shrub-steppe habitat, and table values are the number of individuals captured. A total of 9 species of small mammals was captured from the 2 patch types, including *Peromyscus maniculatus*, *Tamias minimus*, *Microtus montanus*, *Reithrodontomys megalotis*, *Perognathus parvus*, *Zapus princeps*, *Lemmus curtatus*, and *Neotoma cinerea*.

Patch	Isolation (m)	Area (ha)	<i>P. maniculatus</i>	<i>T. minimus</i>	<i>M. montanus</i>	<i>R. megalotis</i>	<i>P. parvus</i>	<i>Z. princeps</i>	<i>L. curtatus</i>	<i>N. cinerea</i>
Kipukas										
1	39	1.95	6	3						
2	65	0.44	4	12		2				1
3	92	1.05	5							
4	162	0.70	2	3		1	1			
5	215	1.99	2							
6	422	1.04	5	5						
7	801	0.42	3							
8	925	0.91								
9	1,031	1.33	1							
10	1,121	0.44	1							
11	1,867	0.63								
Agricultural patches										
12	83	3.04	1	4	5			1		
13	141	2.23	7	1			2			
14	182	2.28	10		1	1				
15	193	1.29	11		3	2				
16	241	1.30	7		3					
17	282	0.51	9		2					
18	339	1.43	13			1				
19	422	0.69	10		1		2		1	
20	626	0.35	3			1	2			
21	799	0.35	28		1	1				
22	1,243	0.39	21							

animals/100 trap nights, similar to our finding of 3.52 animals/100 trap nights on the kipukas, but much lower than the 9.39 animals/100 trap nights we found on agricultural patches. Density of all species other than *P. maniculatus*, which was the most abundant species in both Reynolds' and our samples, was similar: mean density in 100 trap nights was 1.7 for kipukas, 2.12 for agricultural patches, and 1.11 for the large tract of ungrazed sagebrush steppe.

Density of small mammals decreased with isolation of kipukas ($y = -0.962x + 3.66$), but increased with isolation of agricultural patches ($y = 0.236x + 1.38$), and both the slope and intercept of the relationship differed significantly between the 2 landscapes (Table 4; Fig. 3C). Density of small mammals on kipukas decreased strongly with isolation (simple linear regression: $\log(\text{density} + 1) = 3.662 - 0.963 \log \text{isolation}$; $r^2 = 0.577$, $d.f. = 10$, $P = 0.007$), but density was not significantly related to isolation on agricultural patches ($\log(\text{density} + 1) = 1.372 + 0.238 \log \text{isolation}$; $r^2 = 0.15$, $d.f. = 10$, $P = 0.239$). In both landscapes, density was unrelated to area (Table 3). The relationship of density to isolation reflected the pattern of abundance of *P. maniculatus*, which increased with isolation on agricultural patches ($\log(\text{density} + 1) = 0.777 \log \text{isolation} - 0.169$) and decreased with isolation on kipukas ($\log(\text{density} + 1) = -0.718 \log \text{isolation} + 2.88$); the densities of other small mammals declined similarly with increasing isolation in both landscapes (Table 4; Fig. 4).

Habitat characteristics predicted the diversity and density of small mammals of kipukas, but not those of agricultural

patches. Both species richness and Simpson's index of small mammals on kipukas were positively correlated with proportional abundance of shrubs and percentage bare ground and negatively correlated with proportional and absolute abun-

TABLE 2.—Effects of isolation from large contiguous tracts of sagebrush steppe on species richness (model $r^2 = 0.586$, $F = 8.481$, $d.f. = 3$, 18 , $P = 0.001$), Simpson's index (model $r^2 = 0.392$, $F = 3.439$, $d.f. = 3$, 16 , $P = 0.042$), and density of small mammals (model $r^2 = 0.720$, $F = 14.175$, $d.f. = 3$, 18 , $P < 0.001$) of 2 habitats (sagebrush-steppe patches surrounded by lava rock [kipukas] and those surrounded by agricultural lands), as shown by multiple regressions (overall model fit and coefficient [B], standard error of coefficient [SE], test statistic [t], and probability level [P] for each tested model parameter).

	<i>B</i>	<i>SE</i>	<i>t</i>	<i>P</i>
Species richness				
Constant	1.061	0.207	5.121	<0.001
Habitat	-0.064	0.391	-0.164	0.871
Log(isolation)	-0.281	0.080	-3.506	0.003
Habitat $\times$ log(isolation)	0.106	0.155	0.683	0.503
Simpson's index				
Constant	0.557	0.206	2.701	0.016
Habitat	0.309	0.360	0.857	0.404
Log(isolation)	-0.173	0.084	-2.046	0.058
Habitat $\times$ log(isolation)	-0.094	0.145	-0.648	0.526
Density				
Constant	3.662	0.542	6.753	<0.001
Habitat	-2.279	1.025	-2.224	0.039
Log(isolation)	-0.963	0.210	-4.582	<0.001
Habitat $\times$ log(isolation)	1.199	0.405	2.962	0.008

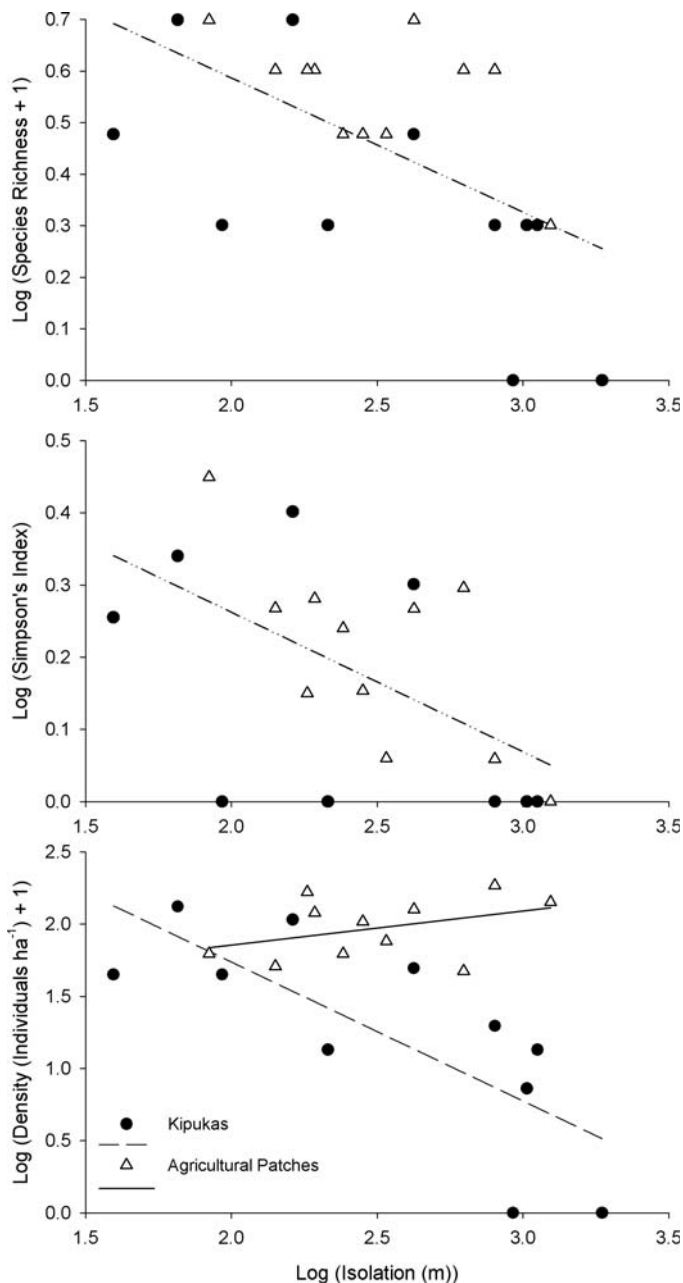


FIG. 3.—Effect of isolation from large contiguous tracts of sagebrush steppe on diversity, as indicated by species richness and Simpson's index, and density of small mammals of sagebrush-steppe patches surrounded by lava rock (kipukas) and those within agricultural lands (agricultural patches) in southeastern Idaho. All 3 measures varied significantly with isolation.

dance of cheatgrass. Density also was positively associated with proportional shrub abundance and bare ground, but was only weakly related to cheatgrass (Table 5). In contrast, there were no significant correlations of diversity of small mammals of agricultural patches with any of the measured habitat characteristics (all $P > 0.19$ for species richness, all $P > 0.42$ for Simpson's index), and density was only marginally correlated with proportional abundance of forbs ($P = 0.07$) and absolute abundance of forbs or of rock ($P = 0.11$; all other $P > 0.21$; Table 5).

TABLE 3.—Effect of area of habitat patches (kipukas, remnant sagebrush steppe surrounded by lava rock, and agricultural patches, remnant sagebrush steppe surrounded by agricultural lands) on species richness (model $r^2 = 0.285$, $F = 2.392$, $df = 3, 18$, $P = 0.102$), Simpson's index (model $r^2 = 0.136$, $F = 0.842$, $df = 3, 16$, $P = 0.491$), and density of small mammals (0.353 , $F = 3.275$, $df = 3, 18$, $P = 0.045$), as shown by multiple regressions (overall model fit and coefficient [B], standard error of coefficient [SE], test statistic [t], and probability level [P] for each tested model parameter).

	B	SE	t	P
Species richness				
Constant	0.346	0.059	0.583	<0.001
Habitat	0.214	0.082	2.595	0.018
Log(isolation)	-0.690	0.245	-0.281	0.782
Habitat $\times$ log(isolation)	0.191	0.299	0.639	0.531
Simpson's index				
Constant	0.141	0.052	2.707	0.016
Habitat	0.064	0.070	0.913	0.375
Log(isolation)	-0.056	0.201	-0.279	0.784
Habitat $\times$ log(isolation)	0.240	0.244	0.981	0.341
Density				
Constant	1.225	0.174	7.023	<0.001
Habitat	0.744	0.242	3.07	0.007
Log(isolation)	-0.124	0.720	-0.172	0.865
Habitat $\times$ log(isolation)	-0.055	0.880	-0.063	0.951

Stepwise multiple regressions showed a similar difference in habitat predictors between kipukas and agricultural patches. For kipukas, species richness of small mammals was strongly associated with abundance of shrubs and total cover, and Simpson's index was negatively associated with abundances of cheatgrass and native grasses (Table 6). For agricultural patches, no habitat measures were significant predictors of diversity or density.

Finally, diversity and abundance of small mammals differed between kipukas that were free of cheatgrass and those where cheatgrass was present. Species richness ($\bar{X} = 2.6 \pm 1.75$ SE without cheatgrass compared to 0.67 ± 0.21 with cheatgrass, $t = 2.405$, $df = 4.765$, $P = 0.064$), Simpson's index (1.9 ± 0.45 SE compared to 1 ± 0 , $t = 3.121$, $df = 7$, $P = 0.016$), and density (68.4 animals/ha ± 21.81 SE compared to 13.54 ± 6.73 animals/ha, $t = 3.040$, $df = 4.987$, $P = 0.029$) all were significantly lower where cheatgrass was present.

DISCUSSION

Species richness of small mammals decreased with increasing isolation of habitat patches in both lava and agricultural landscapes. We found only *P. maniculatus* on kipukas that were isolated by more than 422–800 m, and 3 (*R. megalotis*, *P. parvus*, and *N. cinerea*) of the 5 species found on kipukas were found only on those isolated by less than 200 m. These patterns suggest that isolation limits immigration to kipukas. On agricultural patches, only 4 (*P. maniculatus*, *M. montanus*, *R. megalotis*, and *P. parvus*) of the 7 total species were found at isolation >300 m, and only *P. maniculatus* was found at isolation >800 m (Table 1). Only

TABLE 4.—Effect of patch isolation on density of *Peromyscus maniculatus* (model $r^2 = 0.687$, $F = 13.149$, $d.f. = 3, 18$, $P < 0.001$) and all other small mammals (model $r^2 = 0.495$, $F = 5.889$, $d.f. = 3, 18$, $P = 0.006$) in 2 habitats (sagebrush-steppe patches surrounded by lava rock [kipukas] and those surrounded by agricultural lands), as shown by multiple regressions (overall model fit and coefficient [B], standard error of coefficient [SE], test statistic [t], and probability level [P] for each tested model parameter).

	B	SE	t	P
<i>Peromyscus maniculatus</i>				
Constant	2.871	0.514	5.582	<0.001
Habitat	-3.033	0.972	-3.122	0.006
Log(isolation)	-0.714	0.199	-3.583	0.002
Habitat $\times$ log(isolation)	1.490	0.284	3.881	0.001
Other Species				
Constant	2.681	0.846	3.169	0.005
Habitat	1.310	1.598	0.819	0.423
Log(isolation)	0.839	0.328	-2.560	0.020
Habitat $\times$ log(isolation)	-0.272	0.631	-0.430	0.672

Z. princeps, which was represented in our sample by a single animal, and *T. striatus* were restricted to patches of low isolation. These patterns suggest that colonization is less limited by isolation in the agricultural landscape.

We found no differences in the richness–isolation relationship between agricultural patches and kipukas, which were similar in both total diversity and rate of decline of diversity with isolation (Table 2; Fig. 3). Thus, the apparent difference in diversity between agricultural patches and kipukas was largely a consequence of the somewhat higher average isolation of kipukas in the sample.

Although the decline in diversity with increasing isolation did not differ between agricultural islands and kipukas, the species composition of the 2 landscapes presented evidence that agricultural and lava-flow landscapes differentially affected small mammals. The total number of species was greater within the agricultural landscape (Table 1), and several species were found in only 1 landscape. The rocky and sparsely vegetated lava matrix may be a greater barrier to some species that were found on agricultural patches but not kipukas; for instance, *M. montanus* and *Z. princeps* are herbivores and tend to occupy mesic habitats with high cover (Getz 1985; Walker 1975), and *L. curtatus* occurs in habitats dominated by sagebrush and with loose soils (Carroll and Genoways 1980). However, another species probably benefited from the lava matrix. We captured *N. cinerea*, which typically builds dens in or around rocky areas (Smith 1997), only within the kipuka-lava landscape.

Additionally, the pattern of occurrence of species on sagebrush-steppe patches within the lava versus agricultural landscapes suggested that the small mammal faunas of kipukas were more strongly influenced by isolation than were those of agricultural areas. Species found on kipukas had a much more nested pattern of occurrence, as indexed by the Atmar and Patterson metric, T . Most species were present on kipukas of low isolation, and the species that were less frequently

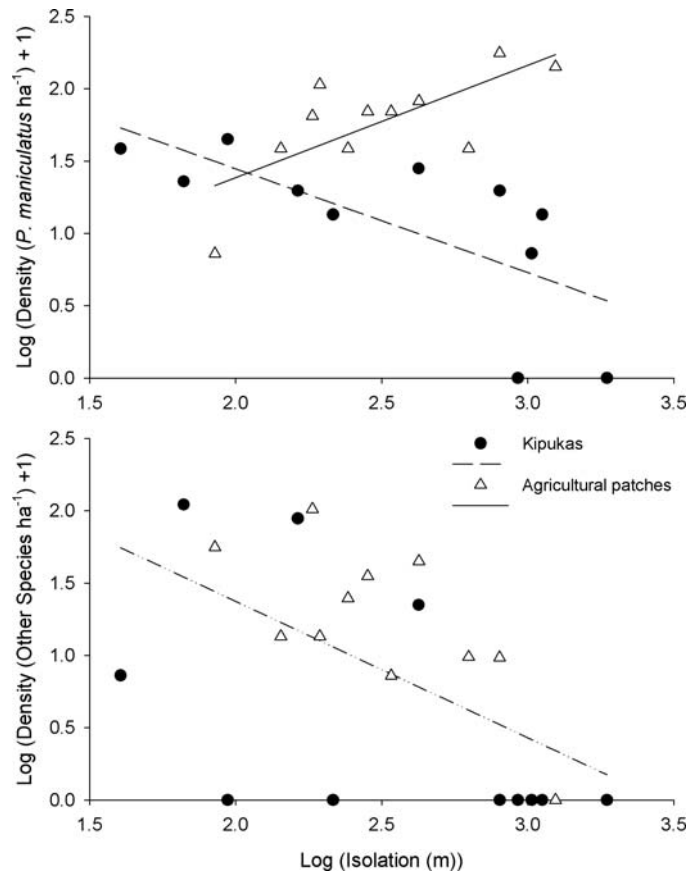


FIG. 4.—Effect of isolation from extensive sagebrush-steppe habitat on the density of small mammals of kipukas (sagebrush-steppe patches surrounded by lava rock) and agricultural patches (sagebrush patches within agricultural lands). Density of *Peromyscus maniculatus* increased with isolation of agricultural patches, but decreased with isolation of kipukas, whereas the combined density of all other small mammal species decreased with isolation in both agricultural patches and kipukas.

present tended to be present on less isolated patches; however, for agricultural patches, occurrence was not regularly associated with isolation, and 2 of the less common species were found on 1 or more of the most isolated patches (Table 1).

Several species that might be expected to occur in sagebrush steppe were absent from both of the sets of habitat patches that we sampled. Reynolds (1980) provides a list of species of small mammals from a large area of continuous sagebrush steppe near our study sites. In rank order of abundance, he found *P. maniculatus*, *T. minimus*, *Onychomys leucogaster* (northern grasshopper mouse), *R. megalotis*, *Spermophilus townsendii* (Townsend's ground squirrel), *P. parvus*, *Dipodomys ordii* (Ord's kangaroo rat), *L. curtatus*, and *M. montanus*. We did not capture *O. leucogaster*, *D. ordii*, or *S. townsendii* in either landscape. *O. leucogaster* is carnivorous and has a large home range (McCarty 1978), which may make it especially vulnerable to extirpation from habitat fragments. Both *D. ordii* and *S. townsendii* are larger than most of the species we captured, and both inhabit burrows (Garrison and

TABLE 5.—Relationship between habitat characteristics and species richness, Simpson's index, and density of small mammals of kipukas (sagebrush-steppe patches surrounded by lava) and agricultural patches (sagebrush steppe surrounded by agricultural lands), as shown by Pearson correlation analysis (Pearson correlation coefficient [r] and probability level [P] for each tested correlation).

Variables	$\bar{X} \pm SD$	Species richness		Simpson's index		Density	
		r	P	r	P	r	P
Kipukas							
Cover	45.7 $\pm$ 9.22	-0.363	0.27	-0.256	0.505	-0.399	0.22
Bare ground	18.8 $\pm$ 13.50	0.664	0.03	0.671	0.048	0.576	0.06
Dead shrub	6.3 $\pm$ 2.63	0.294	0.38	0.348	0.358	0.451	0.16
Rock	12.1 $\pm$ 16.80	-0.435	0.18	-0.514	0.157	-0.385	0.24
Litter	16.0 $\pm$ 4.58	0.405	0.22	0.396	0.292	0.435	0.18
Plant richness	12.8 $\pm$ 2.93	0.527	0.10	0.387	0.303	0.451	0.16
Absolute shrub	26.1 $\pm$ 8.87	0.526	0.096	0.472	0.2	0.46	0.154
Proportional shrub	57.58 $\pm$ 19.11	0.787	<0.01	0.658	0.054	0.746	<0.01
Absolute forb	6.4 $\pm$ 4.31	-0.217	0.521	0.028	0.943	-0.303	0.365
Proportional forb	14.37 $\pm$ 10.60	-0.12	0.73	0.111	0.776	-0.194	0.57
Absolute cheatgrass	7.8 $\pm$ 9.32	-0.592	0.055	-0.682	0.043	-0.494	0.122
Proportional cheatgrass	16.40 $\pm$ 19.06	-0.571	0.07	-0.675	0.046	-0.454	0.16
Absolute native grasses	5.1 $\pm$ 3.75	-0.437	0.179	-0.359	0.343	-0.5	0.117
Proportional native grasses	11.06 $\pm$ 7.83	-0.398	0.23	-0.296	0.439	-0.461	0.15
Agricultural patches							
Cover	58.0 $\pm$ 13.5	0.091	0.79	0.147	0.666	0.114	0.74
Bare ground	11.0 $\pm$ 14.99	0.041	0.91	-0.123	0.718	-0.232	0.49
Dead shrub	3.0 $\pm$ 3.04	0.175	0.61	-0.039	0.91	-0.288	0.39
Rock	0.6 $\pm$ 1.27	0.297	0.38	-0.124	0.716	0.504	0.11
Litter	26.45 $\pm$ 9.55	-0.305	0.36	-0.046	0.892	0.189	0.58
Plant richness	18.9 $\pm$ 7.10	0.089	0.8	-0.013	0.969	0.22	0.52
Absolute shrub	28.2 $\pm$ 13.65	0.291	0.385	0.267	0.427	0.055	0.872
Proportional shrub	47.9 $\pm$ 18.00	0.307	0.36	0.216	0.524	0.028	0.94
Absolute forb	15.7 $\pm$ 13.77	0.141	0.678	-0.143	0.675	0.506	0.112
Proportional forb	14.4 $\pm$ 10.60	0.193	0.57	-0.162	0.633	0.571	0.07
Absolute cheatgrass	10.3 $\pm$ 14.45	-0.058	0.866	-0.011	0.975	-0.301	0.368
Proportional cheatgrass	17.7 $\pm$ 23.75	0.003	0.99	0.047	0.89	-0.405	0.21
Absolute native grasses	9.7 $\pm$ 9.01	-0.37	0.263	-0.068	0.841	0.09	0.793
Proportional native grasses	18.7 $\pm$ 20.11	-0.43	0.19	-0.166	0.625	0.08	0.82

Best 1990; Rickart 1987), traits that may make them also more likely to disappear from habitat patches and less likely to recolonize across either lava fields or intensively used agricultural land.

Diversity of small mammals on agricultural patches was not predicted by habitat characteristics, whereas diversity of small mammals on kipukas was highly correlated with shrub cover and total vegetational cover. Both the difference in time since agricultural patches and kipukas became isolated from larger sagebrush-steppe tracts and the difference between cropland and lava flows as alternative habitat for small mammals might contribute to the differences in association of diversity with habitat characteristics. Kipukas have been isolated for 2,000 years or more, so the presence of a species on a kipuka suggests that adequate resources are available to support a viable population or at least to allow persistence of a population that is periodically replenished by immigration. Agricultural patches became isolated during the past 90–120 years, and species may still be disappearing from patches within which they cannot persist over the longer term, given current immigration and extinction rates. The higher total number of species (7) sampled over the 11 agricultural patches, as compared with the total of only 5 on the 11

kipukas, 1 of which (*N. cinerea*) is likely representative of the lava matrix rather than the sagebrush-steppe habitat of the kipukas, is consistent with the hypothesis that local extinctions are occurring at rates that cannot be offset by current immigration rates. Extinctions in agricultural patches may not yet be fully realized, and immigration rates likely are higher across the agricultural matrix. The small mammal populations of agricultural patches might even in part depend on the surrounding cropland matrix, which also would be consistent with the weaker relationship of diversity to isolation of agricultural patches.

Total density of small mammals increased with isolation on the agricultural patches and decreased with isolation on kipukas. However, this difference was due to 1 species, *P. maniculatus* (Fig. 4), which can inhabit wheat fields (Kaufman and Kaufman 1990) and was likely resident in the agricultural matrix as well as the sagebrush-steppe patches. The density of all other species decreased with isolation, presumably reflecting lower immigration rates and higher vulnerability to local extirpation for most small mammals on isolated patches of sagebrush steppe in both landscapes.

Finally, cheatgrass may play a role in the low diversity and density of mammals that we found on kipukas. Both diversity

TABLE 6.—Effects of habitat characteristics on species richness (model $r^2 = 0.767$, $F = 13.151$, $d.f. = 2, 8$, $P = 0.003$) and Simpson's index (model $r^2 = 0.789$, $F = 11.190$, $d.f. = 2, 6$, $P = 0.009$) of the small mammals of kipukas, patches of sagebrush-steppe surrounded by lava rock, as determined using forward stepwise regression (standard error of coefficient [SE], test statistic [t], and probability level [P] for each tested model parameter).

	Coefficient	SE	t	P
Species richness				
Constant	2.255	1.201	1.878	<0.097
Shrub	0.143	0.131	4.667	0.002
Total cover	-0.099	0.027	-3.738	0.006
Simpson's index				
Constant	2.370	0.230	10.319	<0.001
Cheatgrass	-0.061	0.014	-4.327	0.005
Native grasses	-0.097	0.32	-3.028	0.023

and density were lower on kipukas that had cheatgrass, and absolute and relative covers of cheatgrass were the only variables that showed significant ($P < 0.05$) pairwise correlations with Simpson's index for kipukas (Table 5). Additionally, cheatgrass cover was explanatory in the stepwise regression of Simpson's index and habitat characteristics, with Simpson's index lower where cheatgrass was more abundant. Unfortunately, presence of cheatgrass was confounded with isolation in our data set, so the independent effects of these 2 factors could not be separately estimated.

Our findings have implications for the conservation of small mammals within the sagebrush-steppe ecosystem. Species richness decreased with isolation in both kipukas and agricultural remnants of sagebrush steppe. The decrease in species richness was stronger for the older kipukas than for the more recently isolated agricultural patches, the total number of species found was smaller for kipukas than for agricultural patches, and *P. maniculatus* was the only species found on kipukas isolated by more than 400–800 m. If these results typify effects of long-term isolation, many native sagebrush-steppe species may be at risk of extirpation as sagebrush steppe becomes ever more fragmented. Further, the small mammal fauna of kipukas tended to be nested, with most species present in the least isolated kipukas and only *P. maniculatus* present on the most isolated, and the diversity of small mammals was strongly related to habitat characteristics of kipukas, whereas habitat parameters were not good predictors of diversity of small mammals on agricultural patches. These patterns suggest that the older kipukas retain reduced communities based on their current habitat conditions, whereas the more recently formed agricultural patches either were not truly isolated by croplands, which many of the small mammals may inhabit, or will undergo future loss of species as their communities become limited by habitat area and the decreased colonization that is expected as a consequence of fragmentation from more extensive sagebrush steppe. Additionally, kipukas that had cheatgrass, which degrades sagebrush steppe, had significantly lower diversity and abundance of small mammals than did kipukas without cheatgrass.

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