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Eugene W. Schupp, *Utah State University*



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LAGOMORPHS AND THE DISPERSAL OF SEEDS INTO COMMUNITIES DOMINATED BY EXOTIC ANNUAL WEEDS

Eugene W. Schupp^{1,2}, Hoyt J. Heaton^{1,3}, and José M. Gómez^{1,4}

ABSTRACT.—Large areas of western rangeland are presently dominated by alien annual weeds such as *Bromus tectorum* (cheatgrass). These communities resist succession to perennial communities primarily because the annuals are competitively superior to establishing perennial seedlings and they promote fires that favor weeds over perennials. Succession may be further slowed, however, by low rates of seed dispersal into annual grasslands. We investigated the role of lagomorphs (*Sylvilagus nuttallii*, Nuttall's cottontail; *S. audubonii*, desert cottontail; and *Lepus californicus*, black-tailed jackrabbit) in seed dispersal across an ecotone between an open juniper woodland and an annual grassland. We collected pellets along five 100 × 2-m transects parallel to the ecotone: 50 m into woodland, border, and 20 m, 50 m, and 100 m into grassland. We searched pellets for juniper seeds visually and for any other species through germination from crushed pellets after cold, moist stratification. Pellets were not evenly distributed across transects, but there was no trend with respect to position of transect. *Juniperus osteosperma* (Utah juniper) was the most abundant seed. Both the number of juniper seeds and the proportion of pellets with juniper seeds decreased steadily from a high in woodland to absence at 100 m into grassland. Only 2 dicot seedlings emerged from pellets, 1 *Salsola pestifer* and 1 unknown that died prior to identification. Consequently, there was little seed movement into the grassland; 72% of all seeds were collected from either woodland or border transects. Lagomorphs apparently do not effectively replenish the native perennial seed pool of cheatgrass-dominated disturbances at Dugway.

Key words: *Juniperus osteosperma*, seed dispersal, lagomorphs, *Bromus tectorum*, range restoration, degraded rangeland.

Overgrazing, fires, and other disturbances from human activities have degraded extensive areas of native vegetation in the Intermountain region of the western USA, leading to the domination of many rangelands by alien annual weeds such as *Bromus tectorum* (cheatgrass), *Taeniatherum asperum* (medusahead), and *Salsola pestifer* (Russian thistle; Billings 1990, Young 1994). Over 1.3 million ha are completely dominated by *B. tectorum* or *T. asperum* and 30.8 million ha more are infested or susceptible to invasion (Pellant and Hall 1994). Once established, these annual grasslands largely resist succession to native rangelands because the weeds are highly competitive with establishing perennials (Monsen 1994, Pyke and Novak 1994, Young 1994), and because of the initiation of a "cheatgrass-wildfire" cycle wherein annual weeds promote fire that favors the further spread of weeds and thus of more fires (Billings 1990, Whisenant 1990, Peters and Bunting 1994).

Although competition and increased fire frequencies make it difficult for native species to reestablish, given enough time between fires at least some native species such as *Sitanion hystrix* (bottlebrush squirreltail; Hironaka and Sindelar 1973) and *Agropyron smithii* (western wheatgrass; Monsen 1994) appear able to invade these weed communities. In addition to competition and repeated fires, then, succession to native perennial rangelands may be partly limited by low seed availability due to depletion of the native seed bank over time (Pyke 1994, L.D. Humphrey and E.W. Schupp unpublished data) and potentially low levels of dispersal into the annual grasslands.

Lagomorphs, however, may effectively disperse seeds from native rangelands into annual grasslands. They range widely, feeding in shrubland, woodland, and grassland (Smith 1948, Kundaali and Reynolds 1972, Westoby and Wagner 1973, McAdoo et al. 1987, Zeveloff 1988, Smith 1990) and, in the process, disperse viable

¹Department of Rangeland Resources, and The Ecology Center, Utah State University, Logan, UT 84322, USA.

²Address correspondence to this author at Department of Rangeland Resources, Utah State University, Logan, UT 84322-5230.

³Present address: Department of Botany and Plant Sciences, University of California, Riverside, CA 92507.

⁴Present address: Departamento de Biología Animal y Ecología, Facultad de Ciencias, Universidad de Granada, E-18071 Granada, Spain.

seeds (1) of grasses and forbs consumed incidentally while feeding on foliage (Welch 1985, Zedler and Black 1992, Malo and Suárez 1995, Malo et al. 1995) and (2) of fleshy-fruited plants whose fruits are intentionally consumed (Smith 1948, D'Antonio 1990, Schupp et al. 1996, 1997).

The objective of this study was to examine the role of lagomorphs in the dispersal of seeds across an ecotone between a relict open juniper woodland and a burned area dominated by exotic annual weeds. We were especially concerned with (1) the diversity and quantity of native and exotic seeds found in pellets and (2) the spatial pattern of native seed deposition in the grassland relative to distance from the woodland.

STUDY SITE

The study site is an open juniper woodland and adjacent annual grassland on the U.S. Army Dugway Proving Grounds, Tooele County, Utah, USA ($\approx 40^{\circ}15'N$, $112^{\circ}50'W$), at an elevation of ≈ 1460 m, roughly where old Lake Bonneville sand dunes meet the lower slopes of the Cedar Mountains. The climate is arid, with mean annual precipitation of 19.2 cm (Bagley 1991). Aerial photographs show that wildfire converted a shrubland adjacent to the woodland into an annual grassland sometime between 1978 and 1985 (R. Johnson personal communication). The burn was seeded with *Agropyron cristatum*/*A. desertorum* (crested wheatgrass) and *Kochia prostrata* (prostrate kochia) after the fire, but the seeding was not very successful and densities of these exotic perennials are low. Native perennials such as the grasses *Oryzopsis hymenoides* (Indian ricegrass) and *Sporobolus cryptandrus* (sand dropseed) and the forbs *Sphaeralcea munroana* (Munroe's globemallow) and *Oenothera pallida* (pale evening primrose) are also present at low densities. The overwhelmingly dominant species, however, are exotic annual weeds, mostly *B. tectorum* with variable quantities of *S. pestifer* and *Sisymbrium altissimum* (tumbling mustard).

Vegetation within the adjacent woodland consists of scattered large *Juniperus osteosperma* (Utah juniper) with a well-developed shrub understory of predominantly *Atriplex canescens* (four-wing saltbush) and *Sarcobatus vermiculatus* (greasewood), and a diverse herbaceous layer including *Erysimum asperum* (wallflower), *Eriogonum* spp. (buckwheats), and

the native perennials listed from the burn. All annual weeds from the burn are also found in low densities scattered through the adjacent woodland. The lagomorphs *Sylvilagus nuttallii* (Nuttall's cottontail), *S. audubonii* (desert cottontail), and *Lepus californicus* (black-tailed jackrabbit) are present at the site.

METHODS

In February 1995 we placed a transect 100 m long \times 2 m wide in the annual grassland directly adjacent to the border of the juniper woodland (transect = 0), successive transects at 20 m (+20), 50 m (+50), and 100 m (+100) into the grassland, and a final transect 50 m into the woodland (-50). All transects were parallel to the border. After clearing *S. pestifer* skeletons with a pitchfork, we collected all intact lagomorph feces (pellets) encountered in each transect. After completing collections, we realized that we had used a more thorough technique on the +100 m transect, pulling up cheatgrass to expose pellets trapped within clumps of vegetation or within the upper few cm of soil. Consequently, we re-collected remaining transects with the same thoroughness.

Decomposition of lagomorph pellets in arid environments is slow. In west Texas, Flinders and Crawford (1977) estimated time for complete decomposition to be 4.4 yr for *L. californicus* pellets and 9.5 yr for *S. audubonii* pellets. Consequently, these collections represent long-term patterns of deposition, suggesting the results are, at least for this single site, relatively robust. Accumulations are not so long term, however, that collections from the annual grassland (≥ 10 yr old) would be biased by inclusion of significant numbers of relict pellets deposited in the former shrubland.

Pellets were kept in plastic bags in a refrigerator until processing. Because larger pellets are more likely to contain seeds than small pellets (E.W. Schupp, M. Fuentes, and J.M. Gómez unpublished data), we randomly selected 25 pellets/transect and measured length to the nearest 0.1 mm with dial calipers to compare pellet size across transects. We then processed the entire sample from each transect by cleaning the surface of each pellet with a stiff camel hair brush to dislodge any seeds clinging to the surface and then crushing all pellets to search for the relatively large and

obvious seeds of juniper and the shrubs. We did not open juniper seeds to determine percent filled because the only cone crop available for dispersal in the 2 yr preceding this study had <1% filled seeds when mature (E.W. Schupp unpublished data). Because lagomorphs do not appear to discriminate among cones based on seed filling (E.W. Schupp, M. Fuentes, and J.M. Gómez unpublished data), results should also be representative of years with high levels of filled seeds.

Due to the difficulty of locating small seeds in fibrous remains of pellets, we searched for the presence of species other than juniper with germination tests. After breaking pellets apart further, we spread them on wet washed sand in 0.25 × 0.50-m plastic nursery trays, wet the pellet materials, covered them with plastic lids to prevent drying, and placed them in a refrigerator at ≈3–4°C from 16 June to 28 August 1995 (73 d). On 28 August we placed the trays in a growth chamber with a 24-h cycle of 12 h light at 15°C and 12 h dark at 10°C. After 5 wk we increased temperatures to 20°C and 15°C, respectively, but terminated the experiment after 3 d because temperature began fluctuating wildly. While the experiment was in progress, we misted pellet material daily and transplanted emerging seedlings to small pots to grow until identified.

We used chi-square goodness of fit tests to analyze distributions of pellets and seeds across transects with an expectation that they would be evenly distributed, and a likelihood ratio chi-square test of a 2 × 5 contingency table to analyze for differences among transects in proportions of pellets with and without seeds. Spearman rank correlations tested for trends

in number of pellets, number of seeds, and proportions of pellets with seeds as functions of distance from the woodland transect. We analyzed differences among transects in pellet size (length) with one-way ANOVA followed by a Tukey HSD post-hoc test to determine which transects differed; because a normal probability plot suggested the data were normally distributed and a Bartlett's test ($\chi^2_{[4]} = 6.122$, $P = 0.190$) demonstrated homogeneity of group variances, we used untransformed data. Analyses were performed with SYSTAT 5.0 (Wilkinson 1990).

RESULTS

We collected a total of 8425 pellets from the 1000 m² sampled. Pellets were not evenly distributed across transects ($\chi^2_{[4]} = 797.97$, $P \ll 0.0001$). There was, however, no relationship between number of pellets and distance from the woodland transect ($r_s = 0.200$, $n = 5$, $P > 0.5$). The greatest number of pellets was found at +20 m, and the least at +100 m (Table 1).

Pellet size, as measured by length, differed significantly among transects ($F_{[4,120]} = 11.8$, $P < 0.001$). The difference was due entirely to the -50 transect having larger pellets than all other transects, which did not differ from each other (Table 1).

Fifty-seven pellets (0.7%) contained a total of 61 whole and apparently undamaged juniper seeds; 1 contained 3 seeds, 2 contained 2 seeds, and the remainder contained a single seed. An additional 17 pellets contained broken seeds or seeds separated along the seam joining the 2 halves of the seed coat. No other large-

TABLE 1. Number of pellets, mean pellet length (mm), number of pellets with whole seeds, proportion of pellets with whole seeds, and number of whole seeds by transect. For pellet length, values followed by the same letter are not significantly different at $P < 0.05$ based on a Tukey HSD test.

Transect	Pellets				
	Number	Length [mean (s)]	Number with seeds	Proportion with seeds	Number of seeds
WOODLAND					
-50	1588	11.1 (1.3) a	25	0.0157	28
ECOTONE					
0	1436	9.8 (1.4) b	16	0.0111	16
GRASSLAND					
+20	2597	9.5 (1.1) b	11	0.0042	12
+50	1777	9.0 (0.9) b	5	0.0028	5
+100	1027	9.7 (1.0) b	0	0.0000	0

seeded species were found in the pellets. Considering only whole seeds, a 2×5 contingency table analysis showed the proportion of pellets containing seeds differed among transects (likelihood ratio $\chi^2_{[4]} = 38.44$, $P < 0.001$; Table 1). Similarly, a chi-square analysis showed that numbers of whole seeds were not evenly distributed across transects ($\chi^2_{[4]} = 38.10$, $P < 0.001$; Table 1). In contrast to the number of pellets, both the proportion of pellets with seeds and the number of seeds decreased steadily with increasing distance from the woodland ($r_s = -1.00$, $n = 5$, $P = 0.05$ in both cases; Table 1). Analyses using all seeds (whole + broken) yielded virtually identical results.

Only 2 seedlings emerged from the rabbit pellet fragments during germination tests. After 7 d 1 *S. pestifer* emerged from the +20 transect material and after 35 d 1 unidentified dicot emerged from the +100 transect material but died before growing to an identifiable size.

DISCUSSION

Although the lack of replication across sites makes it difficult to generalize results beyond our site, the fact that our samples represent relatively long-term accumulations of pellets strengthens interpretations for this site. Our results strongly suggest that lagomorphs do not effectively disperse seeds of native species into weed-infested communities at Dugway. Consequently, they appear to contribute little to replenishing the native seed bank in these degraded areas.

Though not abundant, the most frequently encountered seed was that of juniper. This supports the growing realization that lagomorphs are involved in seed dispersal of fleshy-fruited species in general (D'Antonio 1990, Nogales et al. 1995), and of junipers in particular. They have been recorded dispersing *J. pinchoti* and *J. ashei* in Texas and Oklahoma (Smith 1948), *J. osteosperma* in Utah (this study, Schupp et al. 1996), *J. occidentalis* in Oregon (Schupp et al. 1997), and *J. phoenicea* in southwestern Spain (Muñoz-Reinoso 1993). Although the European rabbit (*Oryctolagus cuniculus*) breaks many juniper seeds (Muñoz-Reinoso 1993), the large number of damaged seeds in this study was not found in Oregon (Schupp et al. 1997) or at 2 other Dugway sites only a few km from the present site (Schupp et al. 1996). Many of these broken

seeds were apparently old unfilled ones beginning to split along the seam after several years in a pellet.

The percentage of pellets with juniper seeds in this study was considerably lower than the 4–7% reported for the 2 nearby woodland sites (Schupp et al. 1996). This is probably a function of irregular fruiting of *J. osteosperma*; while pellet collections for the previous study corresponded to a period of heavy fruitfall, the present study includes pellets deposited over many years, encompassing years with both heavy and light fruit production. Even if more seeds were dispersed, however, few would be dispersed much beyond the boundary of the woodland; 72% of all seeds were found in either the woodland transect or directly along the border, and the number of seeds dropped off rapidly to zero at 100 m.

Reasons for this pattern of dispersal are uncertain. Based on pellet counts, *L. californicus* use of seeded grasslands has been documented to decrease with distance from native shrubland, although in 2 of 3 sites the decrease was not evident within the 100-m range we consider in this study (Westoby and Wagner 1973, McAdoo et al. 1987). Similarly, numbers of pellets, and thus presumably activity, did not decrease with distance from woodland in this study—overall decreased lagomorph activity with distance cannot alone explain the detected pattern of juniper seed deposition. Variation in pellet size also cannot fully explain the pattern. Larger pellets are more likely to contain juniper seeds (E.W. Schupp, M. Fuentes, and J.M. Gómez unpublished data) and pellets were larger in the woodland, but pellet size did not change from 0 to +100 while the number of juniper seeds dropped rapidly. It is possible that the lagomorph species differ in both the importance of juniper in the diet and in habitat use such that the species dispersing the most juniper seeds is (are) also least likely to forage out into the grassland. We have no data on abundances of the 3 species nor species-specific data on either juniper feeding or foraging location, but known differences between *Sylvilagus* spp. and *L. californicus* in habitat preference and predator-escape strategies (Zaveloff 1988) suggest *Sylvilagus* spp. might be less likely to venture into the grassland. If they also disperse more juniper seeds than *L. californicus*, the pattern of dispersal is easily explained. Since *L. californicus* is a larger

species, however, it should produce the larger pellets. If so, the distribution of pellet size across transects and the generally greater occurrence of seeds in larger pellets argue that it is in fact *L. californicus* that is least likely to forage away from the woodland and most likely to disperse juniper seeds. Although this is contrary to expectations based on habitat affinities, it could explain the pattern of dispersal. A final possible explanation is that gut passage is rapid relative to the rate at which lagomorphs move out into the grassland, and that although they continue to move and feed, they void most juniper seeds near the woodland. No data exist for evaluating this possibility.

We were especially surprised by the low number and diversity of other species in pellets. In southern California, Zedler and Black (1992) germinated 10 herbaceous species from *Sylvilagus* spp. pellets at a rate of ≈ 87 seedlings per 1000 pellets. In central Spain, Malo and Suárez (1995) germinated 2034 seeds of 52 herbaceous species from 312 g of *O. cuniculus* pellets, equivalent to ≈ 2200 of our pellets. More similar to our results, Welch (1985) found fairly low levels of emergence of 8 species from hare (*Lepus europaeus* and *L. timidus*) and rabbit (*O. cuniculus*) pellets in Scotland. Part of the difference is likely due to methods. Other studies used repeated collections of fresh pellets (up to several months old), while ours was a single collection of pellets spanning at least several years of age; repeated collections of newly deposited pellets may have yielded greater numbers of emerging seedlings at our site. Additionally, our germination experiments ended after 38 d. Nonetheless, the nearly total lack of seedling emergence from 8425 pellets is striking; lagomorph dispersal of herbaceous species at Dugway is apparently an unusual event.

One last observation is worth noting. The peak in pellet density at +20 was associated with 2 relict shrubs, 1 on and the other adjacent to the transect. Pellets were extremely abundant in the vicinity of these shrubs, which is compatible with the notion that jackrabbit activity in open habitats is concentrated in the vicinity of protective shrubs (Longland 1991). In other systems where lagomorphs may be more important in dispersing seeds of native species, their use in restoration of open grassland may be enhanced by first planting scattered shrubs throughout the grassland to pro-

vide cover from predators. These shrubs may then become foci for lagomorph-mediated invasion of native species.

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