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DISPERSAL OF *JUNIPERUS OCCIDENTALIS* (WESTERN JUNIPER) SEEDS BY FRUGIVOROUS MAMMALS ON JUNIPER MOUNTAIN, SOUTHEASTERN OREGON

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Juniperus occidentalis Hooker var. *occidentalis* (western juniper, Cupressaceae) covers more than 1 million ha (Miller and Wigand 1994) from south central Washington through eastern Oregon to northeastern California and southwestern Idaho (Adams 1993). Like many other junipers in the West, *J. occidentalis* has undergone extensive recent population expansions, increasing in density and invading downslope into shrub-grasslands. Most believe this juniper expansion has been driven by a combination of climate change, severe overgrazing, and reduced fire frequency (Burkhardt and Tisdale 1976, Eddleman 1987, Miller and Wigand 1994, Miller and Rose 1995; but see Lanner 1977).

The rate and pattern of expansion can be fully understood only with knowledge of seed dispersal, however (Schupp and Fuentes 1995); yet few quantitative studies of dispersal exist for junipers in general (e.g., Livingston 1972, Salomonson 1978, Holthuijzen et al. 1987, Jordano 1993, Chavez-Ramirez and Slack 1994, Santos and Tellería 1994), and none for *J. occidentalis*. Especially lacking are studies of endozoochorous dispersal by frugivorous mammals (but see Chavez-Ramirez and Slack 1993, Muñoz-Reinoso 1993, Schupp et al. 1996). In fact, seed dispersal ecology of temperate frugivorous mammals in general has been all but ignored (Willson 1993).

With the linked objectives of increasing our knowledge of juniper dispersal in particular and seed dispersal by temperate frugivorous mammals in general, we quantitatively describe mammalian endozoochorous seed dispersal of *J. occidentalis* on Juniper Mountain, southeastern Oregon, USA. We discuss results in the context of disperser effectiveness, where effectiveness is the product of the quantity of seed dispersed and the quality of dispersal given each seed; that is, the number of seeds dispersed multiplied by the probability a dispersed seed produces a new adult (Schupp 1993). Although a complete evaluation is premature, our data address aspects of both major components of effectiveness, thus providing a useful framework.

Juniperus occidentalis is a monoecious or dioecious tree found mostly on dry, rocky slopes from 1500 to 3000 m elevation. The 5- to 10-mm diameter fleshy, resinous seed cones mature in their 2nd fall and contain 2–3 seeds, each 2–4 mm long (Adams 1993). At least 12 species of birds feed on *J. occidentalis* cones and disperse seeds; coyotes (*Canis latrans*) are the only frugivorous mammals reported dispersing the seeds (Gabrielson and Jewett 1940, Maser and Gashwiler 1978, R. F. Miller personal communication, L. E. Eddleman personal communication).

Juniper Mountain is a relatively isolated mountain rising to 2036 m along the border of Harney and Lake counties, Oregon, USA (≈42°55′ N, 119°55′ W). Most of the mountain is covered with *J. occidentalis* woodland that is expanding into surrounding sagebrush steppe of Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*) and mixed perennial bunchgrasses. We collected mammal feces at 5

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of 6 permanent plots for a study of *J. occidentalis* physiology and genetics by R. Tausch and R. Nowak. The 2 sites with an eastern aspect are 1600E (1601 m elevation) and 2000E (1994 m); the 3 with a western aspect are 1650W (1653 m), 1800W (1801 m), and 2000W (1987 m). Partial collections were made at 2 other sites; coyote feces at ≈1650 m on the east side (camp) and deer pellets near the summit at ≈2000 m (summit).

We made field collections 22–23 May 1994. Based on the presence of seeds and dried ripe fruits on the ground, we are confident a reasonably abundant cone crop was produced in the season preceding sampling. At each site we spent 1.5–2 h collecting feces of *Sylvilagus nuttallii* (Nuttall's cottontail), *Odocoileus hemionus* (mule deer), *Cervus elaphus* (elk), and *C. latrans* (coyote). We did not use defined plots, but most feces were collected within a 50-m radius; the goal was to quantify frequency of seed occurrence more than density. We slowly walked the area, carefully searching for relatively recent feces. Based on our experience in west central Utah, we believe most feces were from the preceding fall through early spring. For each site we combined all *S. nuttallii* pellets into a single sample and individually bagged ungulate pellet groups and *C. latrans* feces. We returned feces to the laboratory, where they were refrigerated until processing. This involved moistening in plastic bags to soften (5–15 min) before breaking them apart to carefully search for whole juniper seeds and fragments of broken ones.

Seeds were very rare in mammal feces (Table 1), and no patterns were evident across elevation or aspect. On a per site basis, dispersal by *S. nuttallii* was most frequent; seeds were found at 4 of 5 sites, followed by *C. latrans* (3/6), *O. hemionus* (2/6), and *C. elaphus* (0/2). On a per pellet (feces) or pellet group basis, *C. latrans* was the most frequent seed disperser; 13.8% of feces contained seeds. The next highest frequency was an order of magnitude lower; 1.2% of *O. hemionus* pellet groups contained seeds. Similarly, we found 437 seeds in *C. latrans* feces compared to only 8, 6, and 0 in *S. nuttallii, O. hemionus*, and *C. elaphus* feces, respectively.

Seeds dispersed by *C. latrans* tended to be deposited with many conspecifics, while seeds dispersed by the other mammals tended to be deposited singly. The 4 *C. latrans* seed-containing feces had 1, 59, 175, and 202 seeds. In contrast, pellets of *S. nuttallii* and *O. hemionus* never contained more than 1 seed, and pellet groups of the latter contained no more than 4 seeds.

Although we have no data on the effects of gut passage on seed viability, most seeds were apparently undamaged—only a single seed in an *S. nuttallii* scat had been broken. Due to the size and hardness of juniper seeds, it is unlikely any were destroyed to the extent they were missed.

Results of this study provide new insight into dispersal of *J. occidentalis* and add support to a growing perception of taxonomic patterns of seed dispersal by north temperate mammals. While rabbits (Smith 1948, Schupp et al. 1996) and deer (Martin et al. 1951) were known to eat fruits and disperse seeds of junipers, the most recent compilation of *J. occidentalis* fruit use (Maser and Gashwiler 1978) lists *C. latrans* as the only mammal dispersing seeds endozoochorously. Although we add *O. hemionus* and *S. nuttallii* to the list, these species disperse very few seeds. With respect to the quantitative component of disperser effectiveness, it appears that only *C. latrans* may be important.

Considering the qualitative component of effectiveness, our data address aspects of both the quality of treatment in the mouth and gut and the quality of deposition (sensu Schupp 1993). The preliminary interpretation is that all species may provide high-quality treatment; virtually all seeds were passed intact without evidence of damage. Very low rates of juniper seed damage by carnivores (Herrera 1989, Chavez-Ramirez and Slack 1993) and lagomorphs (Schupp et al. 1996) have been previously reported and may be a common result. Note, however, that the European rabbit *Oryctolagus cuniculus* feeding on fleshy fruits in Spain (Muñoz-Reinoso 1993) and the Canary Islands (Nogales et al. 1995) breaks seeds and reduces germination of surviving seeds. Carnivores, which often pass seeds with most of the pulp attached, may be less likely to reduce viability and may even increase germination rate (Bustamante et al. 1992).

In contrast, the quality of deposition may be relatively low, especially for *C. latrans*, which deposited large numbers of seeds in individual

TABLE 1. Numbers and frequencies of *Juniperus occidentalis* seeds in defecations of 4 mammal species in southeastern Oregon. See site descriptions in the text. NA = not applicable for that site.

Species	Collection site							Total
	1600E	1650W	Camp	1800W	2000E	2000W	Summit	
Sylvilagus nuttallii								
No. pellets	970	121	NA	228	359	368	NA	2046
No. (prop.) with seeds	1 (.0010)	0 (.0000)	NA	2 (.0088)	2 (.0056)	3 (.0082)	NA	8 (.0039)
No. seeds	1	0	NA	2	2	3[a]	NA	8
Odocoileus hemionus								
No. pellet groups	50	24	NA	40	26	14	16	170
No. (prop.) with seeds	1 (.0200)	0 (.0000)	NA	0 (.0000)	0 (.0000)	1 (.0714)	0 (.0000)	2 (.0118)
No. pellets	5459	2394	NA	4387	2911	1887	2376	19,414
No. (prop.) with seeds	2 (.0004)	0 (.0000)	NA	0 (.0000)	0 (.0000)	4 (.0021)	0 (.0000)	6 (.0003)
No. seeds	2	0	NA	0	0	4	0	6
Cervus elaphus								
No. pellet groups	0	0	NA	0	2	2	NA	4
No. (prop.) with seeds	0 (.0000)	0 (.0000)	NA	0 (.0000)	0 (.0000)	0 (.0000)	NA	0 (.0000)
No. pellets	0	0	NA	0	256	302	NA	558
No. (prop.) with seeds	0 (.0000)	0 (.0000)	NA	0 (.0000)	0 (.0000)	0 (.0000)	NA	0 (.0000)
No. seeds	0	0	NA	0	0	0	NA	0
Canis latrans								
No. scats	6	3	9	3	6	2	NA	29
No. (prop.) with seeds	2 (.3333)	0 (.0000)	1 (.1111)	0 (.0000)	1 (.1667)	0 (.0000)	NA	4 (.1379)
No. seeds	261	0	175	0	1	0	NA	437

[a]Includes 1 broken seed.

defecations. Seed clumping may greatly reduce dispersal success by increasing density-dependent seed predation and competition during establishment (Howe 1989, Chavez-Ramirez and Slack 1993, Schupp 1993). In addition, all species probably deposit few seeds in the most suitable microhabitats. While successful *J. occidentalis* establishment is apparently most likely beneath shrubs (Burkhardt and Tisdale 1976, Miller and Rose 1995), carnivores (Bustamante et al. 1992, Chavez-Ramirez and Slack 1993), lagomorphs (Schupp et al. 1996), and ungulates (E. W. Schupp, J. M. Gómez, and M. Fuentes, unpublished data) tend to defecate and deposit seeds disproportionately often in open interspaces.

Mammals, with the possible exception of *C. latrans*, do not appear to be very effective dispersers of *J. occidentalis*. While these mammals have some role in juniper expansion, it appears to be minor unless rodents harvest seeds from feces and cache them preferentially beneath shrubs. We cannot evaluate the existence and/or importance of such an interaction between phase I and phase II dispersal (sensu Chambers and MacMahon 1994) at this time.

From the perspective of mammalian frugivory in general, our results support Willson's (1993) suggestion that *C. latrans* is one of the most highly frugivorous north temperate mammals and is, along with several other Carnivora, likely to be among the quantitatively most important mammalian dispersers of fleshy-fruited plants in the region. In contrast, lagomorphs and ungulates have been viewed mostly as dispersers of nonfleshy grass and forb seeds consumed incidentally while feeding on foliage (e.g., Welch 1985, Zedler and Black 1992, Malo and Suárez 1995). There is a growing realization, however, that lagomorphs are frugivorous and potentially important dispersers of some fleshy-fruited species (e.g., Smith 1948, D'Antonio 1990, Muñoz-Reinoso 1993, Nogales et al. 1995, Schupp et al. 1996), and that ungulates may occasionally consume large numbers of fleshy fruits, although they may often destroy seeds rather than disperse them (Sargent 1990, Englund 1993).

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LITERATURE CITED

ADAMS, R. P. 1993. *Juniperus.* Pages 412–420 *in* Flora of North America Editorial Committee, editors, Flora of North America north of Mexico. Volume 2. Oxford University Press, New York. 475 pp.

BURKHARDT, J. W., AND E. W. TISDALE. 1976. Causes of juniper invasion in southwestern Idaho. Ecology 76: 472–484.

BUSTAMANTE, R. O., J. A. SIMONETTI, AND J. E. MELLA. 1992. Are foxes legitimate and efficient dispersers? A field test. Acta Oecologica 13: 203–208.

CHAMBERS, J. C., AND J. A. MACMAHON. 1994. A day in the life of a seed: movements and fates of seeds and their implications for natural and managed systems. Annual Review of Ecology and Systematics 25: 263–292.

CHAVEZ-RAMIREZ, F., AND R. D. SLACK. 1993. Carnivore fruit use and seed dispersal of two selected plant species of the Edwards Plateau, Texas. Southwestern Naturalist 38: 141–145.

______. 1994. Effects of avian foraging and post-foraging behavior on seed dispersal patterns of Ashe juniper. Oikos 71: 40–46.

D'ANTONIO, C. M. 1990. Seed production and dispersal in the non-native, invasive succulent *Carpobrotus edulis* (Aizoaceae) in coastal strand communities of central California. Journal of Applied Ecology 27: 693–702.

EDDLEMAN, L. E. 1987. Establishment and stand development of western juniper in central Oregon. Pages 255–259 *in* R. L. Everett, editor, Proceedings—pinyon-juniper conference. USFS General Technical Report INT-215.

ENGLUND, R. 1993. Fruit removal in *Viburnum opulus*: copious seed predation and sporadic massive seed dispersal in a temperate shrub. Oikos 67: 503–510.

GABRIELSON, I. N., AND S. G. JEWETT. 1940. Birds of Oregon. Oregon State College, Corvallis. 650 pp.

HERRERA, C. M. 1989. Frugivory and seed dispersal by carnivorous mammals, and associated fruit characteristics, in undisturbed Mediterranean habitats. Oikos 55: 250–262.

HOLTHUIJZEN, A. M. A., T. L. SHARIK, AND J. D. FRASER. 1987. Dispersal of eastern red cedar (*Juniperus virginiana*) into pastures: an overview. Canadian Journal of Botany 65: 1092–1095.

HOWE, H. F. 1989. Scatter- and clump-dispersal and seedling demography: hypothesis and implications. Oecologia 79: 417–426.

JORDANO, P. 1993. Geographical ecology and variation of plant-seed disperser interactions: southern Spanish junipers and frugivorous thrushes. Vegetatio 107/108: 85–104.

LANNER, R. M. 1977. The eradication of pinyon-juniper woodland. Has the program a legitimate purpose? Western Wildlands 3: 12–17.

LIVINGSTON, R. B. 1972. Influence of birds, stones and soil on the establishment of pasture juniper, *Juniperus communis*, and red cedar, *J. virginiana* in New England pastures. Ecology 53: 1141–1147.

MALO, J. E., AND F. SUÁREZ. 1995. Herbivorous mammals as seed dispersers in a Mediterranean dehesa. Oecologia 104: 246–255.

MARTIN, A. C., H. S. ZIM, AND A. L. NELSON. 1951. American wildlife and plants. McGraw-Hill Book Co., Inc., New York. 500 pp.

MASER, C., AND J. S. GASHWILER. 1978. Interrelationships of wildlife and western juniper. Pages 37–82 *in* Proceedings of the western juniper ecology and management workshop. USFS General Technical Report PNW-74.

MILLER, R. F., AND J. A. ROSE. 1995. Historic expansion of *Juniperus occidentalis* (western juniper) in southeastern Oregon. Great Basin Naturalist 55: 37–45.

MILLER, R. F., AND P. E. WIGAND. 1994. Holocene changes in semiarid pinyon-juniper woodlands. Responses to climate, fire and human activities in the U.S. Great Basin. BioScience 44: 465–474.

MUÑOZ-REINOSO, J. C. 1993. Consumo de gálbulos de sabina (*Juniperus phoenicea* ssp. *turbinata* Guss, 1891) y dispersión de semillas por el conejo (*Oryctolagus cuniculus* L.) en el Parque Nacional de Doñana. Doñana, Acta Vertebrata 20: 49–58.

NOGALES, M., A. VALIDO, AND F. M. MEDINA. 1995. Frugivory of *Plocama pendula* (Rubiaceae) by the rabbit (*Oryctolagus cuniculus*) in xerophytic zones of Tenerife (Canary Islands). Acta Oecologica 16: 585–591.

SALOMONSON, M. G. 1978. Adaptations for animal dispersal of one-seed juniper seeds. Oecologia 32: 333–339.

SANTOS, T., AND J. L. TELLERÍA. 1994. Influence of forest fragmentation on seed consumption and dispersal of Spanish juniper *Juniperus thurifera.* Biological Conservation. 70: 129–134.

SARGENT, S. 1990. Neighborhood effects on fruit removal by birds: a field experiment with *Viburnum dentatum* (Caprifoliaceae). Ecology 71: 1289–1298.

SCHUPP, E. W. 1993. Quantity, quality and the effectiveness of seed dispersal by animals. Vegetatio 107/108: 15–29.

SCHUPP, E. W., AND M. FUENTES. 1995. Spatial patterns of seed dispersal and the unification of plant population ecology. Écoscience 2: 267–275.

SCHUPP, E. W., M. FUENTES, AND J. M. GÓMEZ. 1996. Dispersal of Utah juniper (*Juniperus osteosperma*) seeds by lagomorphs. Pages 496–497 *in* N. E. West, editor, Proceedings of the fifth international rangeland congress. Volume I. Society for Range Management, Denver, CO.

SMITH, H. N. 1948. Rabbits spread cedar menace. Cattleman 35: 97–98.

WELCH, D. 1985. Studies in the grazing of heather moorland in north-east Scotland. IV. Seed dispersal and plant establishment in dung. Journal of Applied Ecology 22: 461–472.

WILLSON, M. F. 1993. Mammals as seed-dispersal mutualists in North America. Oikos 67: 159–176.

ZEDLER, P. H., AND C. BLACK. 1992. Seed dispersal by a generalized herbivore: rabbits as dispersal vectors in a semiarid California vernal pool landscape. American Midland Naturalist 128: 1–10.

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