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BIOGEOGRAPHIC AND CONSERVATION IMPLICATIONS OF LATE QUATERNARY PYGMY RABBITS (*BRACHYLAGUS IDAHOENSIS*) IN EASTERN WASHINGTON

R. Lee Lyman[1]

ABSTRACT.—Five implications of a biogeographic model of pygmy rabbits (*Brachylagus idahoensis*) in eastern Washington proposed in 1991 are confirmed by 11 new late-Quaternary records. Pygmy rabbits from eastern Oregon colonized eastern Washington during the late Pleistocene and occupied their largest range during the middle and late Holocene. Disjunction of the eastern Washington population from that in eastern Oregon occurred during at least the late Holocene. Nineteenth-century cattle grazing and 20th-century agricultural practices reduced habitat preferred by pygmy rabbits. Conservation of the small remaining population of pygmy rabbits will necessitate altered land use practices.

Key words: agriculture, biogeography, Brachylagus idahoensis, *conservation, grazing, pygmy rabbit, Washington.*

Populations of pygmy rabbits (*Brachylagus idahoensis*) in eastern Washington are isolated from conspecific populations in southeastern Oregon, Nevada, and portions of adjacent states (Fig. 1). Lyman (1991) outlined a hypothetical biogeographic model for the populations in eastern Washington based on 8 prehistoric records. I have refined that model in light of 11 new prehistoric records of this diminutive leporid from the area.

Based on available data, Lyman (1991) hypothesized that (1) pygmy rabbits colonized eastern Washington from Great Basin populations in eastern Oregon during the late Pleistocene; (2) eastern Washington populations became disjunct from Great Basin populations at the end of the Pleistocene, ca. 10,000 radiocarbon years before present (RCYBP); (3) pygmy rabbits occupied much of the Columbia Basin in eastern Washington prior to about 5500 RCYBP when sagebrush-dominated steppe habitats were at their maximum extent coincident with a period of greater-than-modern aridity; (4) after 4500–4000 RCYBP the range of pygmy rabbits shrank as the range of big sagebrush (*Artemisia tridentata*) decreased, commensurate with increased effective moisture; and (5) agricultural practices over the last 100–150 years exacerbated the depletion of sagebrush range and further depleted populations, thus creating the current range of pygmy rabbits in eastern Washington.

MATERIALS AND METHODS

Records reported by Lyman (1991) were reviewed, and documents that appeared since 1990 were examined for evidence of prehistoric mammalian faunal remains in eastern Washington. All but 2 of the 19 records of pygmy rabbits derive from archaeological contexts (Table 1). McAllister (1995) believes that 1 of those 2 from the Juniper Dunes Preserve comprises remains of Nuttall's cottontail (*Sylvilagus nuttallii*) that were originally misidentified. McAllister (1995) could not relocate the specimens on which the original identifications were based, so this record plays no role in analysis. For comparative purposes, 20th-century records of pygmy rabbits were compiled from McAllister and Allen (1993), McAllister (1995), and Johnson and Cassidy (1997).

I noted locations of all sites producing prehistoric remains of pygmy rabbits (Fig. 2), frequency of pygmy rabbit remains, and evidence for determining the age of remains. All remains of pygmy rabbits are dated to the time of sediment deposition, indicated by radiocarbon ages (all ages reported here are in RCYBP) determined from charcoal within the sediments or stratigraphically associated, temporally diagnostic artifacts. Given that pygmy rabbits burrow (Weiss and Verts 1984), indicated ages may comprise maximum ages of remains. Many prehistoric pygmy rabbit specimens

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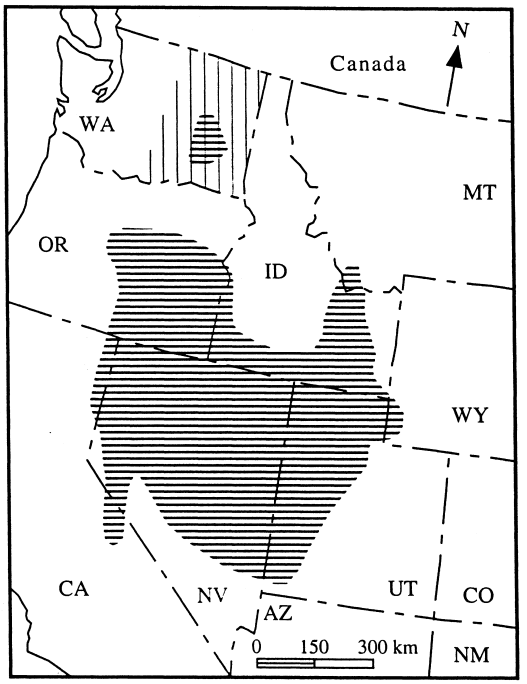

Fig. 1. Historic distribution of pygmy rabbit (horizontal hatching; after Lyman 1991). Vertical hatching shows area of Figure 2.

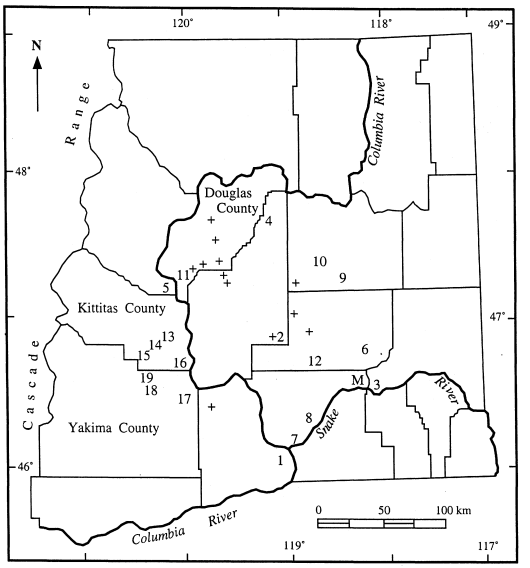

Fig. 2. Map of eastern Washington showing locations of 20th-century records of pygmy rabbits (+; from Johnson and Cassidy 1997, McAllister 1995, McAllister and Allen 1993) and prehistoric sites (numbers) that have produced remains of pygmy rabbits. County lines shown for reference. Numbers correspond to Table 1; M = Marmes Rockshelter.

examined, however, are stained and weathered to the same degree as associated bones of taxa believed to have been deposited at the same time as dated charcoal or artifacts. Pygmy rabbits have relatively small home ranges (Katzner and Parker 1997), and all examined remains of this species display no evidence that predators transported them far (Lyman 1994). I therefore assume that location of their recovery is within a few kilometers of where the individuals lived. Frequencies of all mammalian remains discussed are given as the number of identified specimens (NISP).

BIOGEOGRAPHIC HISTORY

The record from 45BN265 (Table 1:1) does not refute the 1st implication that pygmy rabbits were in the process of colonizing eastern Washington during the late Pleistocene (Fig. 1); this record is 1 of only 2 positive pieces of evidence. The single specimen of pygmy rabbit from site 45KT1362 (Table 1:16) dates between 10,700 and 10,000 RCYBP. It comprises the 2nd piece of positive evidence for the 1st implication because it suggests that pygmy rabbits had begun colonizing eastern Washington at the end of the Pleistocene. Remains of pygmy rabbits do not exist among 756 specimens identified to mammalian genus or species recovered from Marmes Rockshelter (45FR50) floodplain sediments (Caulk 1988, Gustafson and Wegener 1998). These sediments were deposited between 9500 and 10,500 RCYBP. If pygmy rabbits were not present there (Fig. 2) at this time, then their colonization of central Washington was not complete—the maximum range of their distribution had not yet been attained—at the end of the Pleistocene. Although the sample is small (NISP = 427), faunal remains of middle-Holocene age (8000 to 4000 RCYBP) from Marmes Rockshelter also do not include specimens of pygmy rabbit (Gustafson 1972). The single specimen from 45WT134 (Table 1:3), just east of Marmes Rockshelter, indicates that this taxon was in the general area at the end of the middle Holocene (ca. 4000 RCYBP).

Together with the record from 45GR97 (Table 1:2) dating to 8700 RCYBP, the 45BN265 (Table 1:1) and 45KT1362 (Table 1:16) records suggest pygmy rabbits were distributed across

TABLE 1. Prehistoric records of pygmy rabbits (*Brachylagus idahoensis*) in eastern Washington.

Site[a]	Age (RCYBP)	Reference
1. 45BN265	100,000–13,000	Rensberger et al. 1984
2. 45GR97	8700	Irwin and Moody 1978
3. 45WT134	4200–1000	Lyman 1990
4. 45GR445	2400–2150	Lyman n.d.
5. 45CH302	2500–150	Lyman unpublished data
6. 45AD2	<3000	Deaver and Greene 1978
7. 45FR5	1000–200	Olson 1983
8. Juniper Dunes Preserve	<3000	Miller 1977[b]
9. 45LI150	<5500	Lyman unpublished data
10. 45LI206	1500–500	Lyman unpublished data
11. 45DO331	3000–900	Lyman 1995
12. 45AD104	1900	Lyman 1993
13. 45KT980	2300	Lyman 1998a, 1998b
14. 45KT1003	3000–1700	Lyman 1998b
15. 45KT338	1200	Flenniken et al. 1997, Lyman unpublished data
16. 45KT1362	10,700–10,000	Lyman unpublished data
17. 45YA641	unknown	Lyman unpublished data
18. 45YA579	1700	Flenniken et al. 1997, Lyman unpublished data
19. 45YA533	7400, 2300	Flenniken et al. 1997

[a]Site number corresponds to map location in Figure 2.
[b]Specimen was likely misidentified; data omitted from analysis here.

at least a portion of their maximum range in eastern Washington during the early Holocene (ca. 10,000–8000 RCYBP). Determination of the full extent of their range must await recovery of additional materials of late-Pleistocene and early-Holocene age. Remains of pygmy rabbits from site 45YA533 (Table 1:19) may be as much as 7400 years old, although their age is unclear (Flenniken et al. 1997). Most pygmy rabbit remains from 45LI150 (Table 1:9) were deposited by raptors (Lyman unpublished data). Because these remains were recovered from depositional contexts stratigraphically above ages of 5500 RCYBP, they must be younger. If these remains date between 5500 and 4000 RCYBP, they indicate pygmy rabbits occurred in the central Columbia Basin near the end of the middle Holocene and they confirm the 3rd implication—that pygmy rabbits had their widest distribution in eastern Washington during the middle Holocene.

Given the lack of records for prehistoric pygmy rabbits along the Lower Columbia River during the Holocene, the 2nd implication—that eastern Washington populations became disjunct from those in the northern Great Basin at the end of the Pleistocene—cannot be refuted. Circumstantial evidence, i.e., archaeological samples in the McNary Reservoir area that do not include remains of pygmy rabbit (Burtchard 1981, Cole 1968, Lyman unpublished data), suggests that the disjunction was in place during the late Holocene (last 4000 RCYBP).

All other records of pygmy rabbits date to the last 3000 RCYBP (Table 1). If in fact pygmy rabbit range was decreasing after about 4000 RCYBP, then perhaps that range was larger than suggested by Figure 2. For example, records from eastern Kittitas County and northeastern Yakima County indicate pygmy rabbits occupied a range approximately 50 km west of their historically documented range during the late Holocene. It can be conjectured on this basis that their remains eventually will be found in central Yakima County.

IMPLICATIONS FOR CONSERVATION

Pygmy rabbits occupy stands of big sagebrush. They feed extensively on these plants and also use them for cover to avoid predation (Green and Flinders 1980a, 1980b, Gabler et al. 2001). Paleoenvironmental data from eastern Washington indicate that sagebrush was dense across much of the central Columbia Basin during the middle Holocene, and that between about 4000 and 2000 RCYBP, a dense understory of grass existed (Chatters 1995, 1998). The density of grass decreased after 2000 RCYBP as climatic conditions took on modern characteristics. This suggests that pygmy rabbits may

have occurred in locations during the last 2000 years where they have not been historically documented.

Katzner and Parker (1997) suggest that grazing has caused some loss of preferred pygmy rabbit habitat. Grazing by cattle and sheep in eastern Washington began in the mid-19th century, and "by the beginning of the 1870s, the intermountain country of the Pacific Northwest had become pretty generally a cattleman's country" (Oliphant 1947:220). No systematic census data on cattle numbers are available, but a single estimate from the 1880s suggested 20,000 head in Yakima Valley (Oliphant 1932). The Yakima River valley of Yakima County was used as winter range and the Kittitas River valley of Kittitas County as summer range (Oliphant 1947). Range deterioration was already apparent in the 1880s (Buechner 1953). It took the form of overgrazing, reducing or eliminating native grasses in various areas and reducing vegetation cover (Daubenmire 1940, Daubenmire and Colwell 1942); reduced vegetation altered erosion (Young 1943). Prior to the introduction of tractors, wheat farmers used horses to pull farm equipment. Once farmers adopted the tractor, shortly after the beginning of the 20th century, many work horses were turned out to pasture and contributed to overgrazing (Chohlis 1952).

Many cattle died during harsh winters and prompted the initiation of artificial feeding at the end of the 19th century (Oliphant 1932). Cattle consume significantly more grass than browse in local shrub-steppe habitats (Uresk and Rickard 1976, Hanley and Hanley 1982). When concentrations of cattle were high in eastern Washington, sagebrush "suffered heavily from breakage" (Daubenmire 1970:13). Harsh winters there may have forced cattle to consume even more browse, resulting in marked destruction of sagebrush. With the replacement of horses by tractors, more acreage was tilled, some of which had previously been cattle and horse pasture (Oliphant 1948, Chohlis 1952).

Pygmy rabbits also require deep (≥50 cm), friable sediment, often with high sand content, in which to dig burrows (Weiss and Verts 1984, Gabler et al. 2001). It is well documented that cattle grazing causes increased compaction of sediment (Chanasky and Naeth 1995). In some cases the bulk density of sediment increases as much as 20% (McCarty and Mazurak 1976). Data reported by Weiss and Verts (1984) indicate that surface sediment "strength" ($kg \cdot cm^{-2}$ necessary to penetrate) was significantly lower in loci occupied by pygmy rabbits than in unoccupied loci. Therefore, compaction of sediment by grazing cattle likely decreased the suitability of sediment for pygmy rabbits. If use of an area by grazing cattle also decreased the abundance of sagebrush, then cattle would have had a significant influence on pygmy rabbit habitat. Alterations to local floras by 19th-century grazing practices were followed by tillage, which ultimately resulted in less sagebrush. In addition, when irrigation began in the early 20th century, sagebrush was eradicated by herbicides and fire and replaced by fields and grasslands (Buechner 1953).

Comparison of 20th-century records of pygmy rabbits (McAllister and Allen 1993, McAllister 1995, Johnson and Cassidy 1997) with prehistoric records, irrespective of age, suggests reduction of pygmy rabbit range (Fig. 2). The 1st formal surveys and collections of local mammals took place in the early 20th century (Dice 1919, Couch 1928, Taylor and Shaw 1929, Svihla and Svihla 1940, Larrison 1944, Booth 1947, Dalquest 1948, Johnson et al. 1950). Any historic distribution map of pygmy rabbits is, therefore, at least partially a function of 19th-century agricultural practices. The 5th implication of Lyman's (1991) model—that agricultural practices depleted pygmy rabbit range via habitat destruction—seems to be borne out.

CONCLUSION

Lyman's (1991) biogeographic model has implications for modern management of the pygmy rabbit. The extant population of pygmy rabbits in eastern Washington is restricted to central Douglas County (McAllister 1995). Holocene climatic change and modern agricultural practices especially have significantly depleted habitat suitable for this leporid and reduced the size and range of the extant population. To maintain the isolated and unique gene pool represented by the extant population of pygmy rabbits in eastern Washington, steps must be taken to alter modern land-modification activities.

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