PREBLE'S MEADOW JUMPING MOUSE (*Zapus hudsonius preblei*) IN WYOMING: STATUS REPORT, JULY 2003

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INTRODUCTION

The management of Preble's meadow jumping mouse (*Zapus hudsonius prebeli*) is a high priority for natural resource professionals in southeast Wyoming and north-central Colorado. It is currently listed as Threatened under the U.S. Endangered Species Act (ESA; USDI 1998), and discrete units of critical habitat necessary for the subspecies' recovery will soon be designated by the USDI Fish and Wildlife Service (USFWS; USDI 2003). New land use regulations designed to enhance recovery within critical habitat units have the potential to alter traditional uses of natural resources throughout the subspecies' range.

Clearly the main scientific controversy surrounding the conservation and management of jumping mice in southeast Wyoming is whether or not the species meadow jumping mouse, *Z. hudsonius*, and the subspecies Preble's meadow jumping mouse, *Z. h. preblei*, are distinct and valid taxa here. Unfortunately there are no straightforward criteria with which to evaluate the validity of within-genera taxa. It has long been recognized that biological diversity at this level exists as a continuum, with gradations (as opposed to quanta) of difference between individuals, populations, and races. The traditional taxonomic system forces the identification of artificially discrete units along that continuum. In this context, no single trait can adequately partition the continuum, necessitating a "weight of evidence" approach that considers multiple traits (e.g., morphology, genetics) to define within-genera taxa (DeWeerdt 2002).

This report is a to-date summary of scientific information on the morphology, genetics, ecology, and biogeography of *Zapus* in southeast Wyoming, and is organized in a way that should inform "weight of evidence" evaluations of species and subspecies occupying the region. It is intended as an update of a similar report completed in July 2001 (Beauvais 2001), and is one of several reports on rare plants, rare animals, and important vegetation communities produced by the Wyoming Natural Diversity Database (WYNDD). This research and service unit of the University of Wyoming serves as a central clearinghouse of scientific information on the biota of Wyoming, and distributes this information to all interested parties in order to facilitate appropriate management of natural resources.

BACKGROUND KNOWLEDGE OF *Zapus*

Genus *Zapus* - North America supports 2 genera of jumping mice: *Napeozapus* and *Zapus*. Only the latter occurs in the state and vicinity of Wyoming (Hall 1981, Whitaker 1999a, Whitaker 1999b, Cranford 1999, Gannon 1999; Figure 1). A similar genus, *Eozapus*, occupies eastern Asia (Krutzsch 1954).

Species *Zapus hudsonius* - The genus *Zapus* includes 3 species. Two of these, the western jumping mouse, *Z. princeps*, and the meadow jumping mouse, *Z. hudsonius*, occur within the state and vicinity of Wyoming (Figure 1; Figure 2). The more common and westerly-distributed *Z. princeps* generally occurs along streams and in mesic upland vegetation in montane and subalpine zones, occasionally ranging into foothills and even prairie zones along stream courses. The more easterly-distributed *Z. hudsonius* is rarer in this region, occurs in riparian zones in prairie and foothills environments, and occasionally ranges into montane areas along stream courses (Quimby 1951, Krutzsch 1954, Long 1965, Armstrong 1972, Whitaker 1972, Hall 1981, Clark and Stromberg 1987, Fitzgerald et. al. 1994, Cranford 1999, Whitaker 1999a).

Subspecies *Zapus hudsonius preblei* - E.A. Preble made the first scientific collection of *Z. hudsonius* in this region at a site near present day Loveland, Colorado, in 1899 (Preble 1899). Early specimens of *Z. hudsonius* from southeast Wyoming and northern Colorado were classified as *Z. h. campestris* (e.g., Warren 1910, Cary 1911). This trinomial is currently reserved for the Bear Lodge meadow jumping mouse, a separate subspecies now thought to occur only in the

Black Hills region (Whitaker 1999a; Figure 2). Krutzsch (1954) first described the subspecies *Z. h. preblei* in southeast Wyoming and northern Colorado.

Mammalogists currently recognize 5 subspecies of *Z. hudsonius* in the vicinity of Wyoming (Whitaker 1999a, Hafner et al. 1981, Morrison 1992; Figure 2). Only *Z. h. preblei* and *Z. h. campestris* are thought to occur in the state (southeast and northeast corners, respectively). Three subspecies (*Z. h. intermedius*, *Z. h. campestris*, *Z. h. pallidus*) are regarded as contiguous (i.e., interbreed regularly along the boundaries of their respective distributions) and essentially represent the westernmost extent of the continuous distribution of *Z. hudsonius* in the United States (Hall 1981, Whitaker 1999a). The remaining 2 subspecies, *Z. h. preblei* and *Z. h. luteus*, are thought to be Pleistocene relicts completely isolated from each other and other *Z. hudsonius* subspecies (Hafner et al. 1981, Jones 1981, Morrison 1992, Hafner 1997; Figure 1, Figure 2).

CURRENT MANAGEMENT AND CONSERVATION STATUS

Concern over the viability and persistence of *Z. h. preblei* began as early as September 1985 when the USFWS placed the taxon in Category 2 status, which indicated that at that time a proposal to list under the ESA may have been appropriate but conclusive biological information to support such a proposal did not yet exist. This was followed by 20 other official USFWS decisions over the next 18 years, as documented in the Federal Register (see: https://ecos.fws.gov/species_profile/SpeciesProfile?spcode=A0C2). These decisions include the Final Rule to list as Threatened in May 1998 (USDI 1998), Proposed Special Regulations in August 2001, and Notice of Availability of a Draft Habitat Conservation Plan in February 2003 (USDI 2003).

The current status of *Z. h. preblei* as Threatened under the ESA precludes it from receiving other special designations from federal land management agencies in Wyoming, such as the USDA Forest Service (Region 2) and the USDI Bureau of Land Management (Wyoming State Office). Although each of these agencies maintains a Sensitive Species list to help guide management actions (e.g., USDA Forest Service 1994, USDI Bureau of Land Management 2001), each list specifically excludes taxa already listed under ESA because those taxa are automatic and pre-determined management priorities.

Zoologists at WYNDD have ranked *Z. h. preblei* as G5 T2 S1, with a Wyoming Contribution Score of Very High. Importantly, these designations are predicated on the

assumption that the subspecies is valid, identifiable, and distributed throughout lowland riparian systems in north-central Colorado and southeast Wyoming as currently understood by the USFWS:

G5 = The full species *Z. hudsonius* is demonstrably widespread, abundant, and secure with a very low probability of extinction from its entire range.

T2 = The subspecies *Z. h. preblei* is rare and imperiled with a high probability of extinction from its entire range.

S1 = The subspecies *Z. h. preblei* is rare and imperiled with a very high probability of extinction from the state of Wyoming.

Wyoming Contribution Very High = The subspecies *Z. h. preblei* is a native, resident taxon with a small continental range and a high percentage of that range within the state of Wyoming; thus Wyoming populations of *Z. h. preblei* contribute very highly to the rangewide persistence of the taxon.

Hafner et al. (1998) classified *Z. h. preblei* as "Endangered" under the system used by the International Union for Conservation of Nature and Natural Resources.

MORPHOLOGY

Morphology: Genus *Zapus* - The following generally describes individuals of both *Z. hudsonius* and *Z. princeps*. A small rodent with hind legs much longer than forelegs. The tail is longer than the body, sparsely haired, and darker above than below. Eyes are midway between the nose and the ear. Ears are dark but edged with white. There are 18 teeth, with upper incisors having distinct grooves on their outer faces. Cheek pouches are absent. Fur on the back is yellow olive-brown with scattered, long, black-tipped hairs which create a faint dorsal stripe. The sides are light yellow-brown, and the belly is white to light buff. Young tend to have softer, lighter fur than adults. Adult pelage appears rather coarse (Long 1965, Armstrong 1972, Clark and Stromberg 1987, Fitzgerald et al. 1994, USDI 2002).

The general appearance of jumping mice is relatively unique; it is difficult to confuse them with other rodents in Wyoming. The extremely long tail and large hind feet are especially good characters for recognizing jumping mice. Woodland jumping mice (*Napeozapus insignis*) are very similar in appearance, but do not occur within ca. 500 mi of Wyoming (Figure 1).

Morphology: Species *Zapus hudsonius* - The following dimensions are in addition to the above description of individuals in the genus *Zapus*. Adult measurements: total length 180-220 mm; head and body length <89 mm; tail 115-136 mm; hind foot 28-31 mm; ear 11-16 mm; weight 12-22 g (Clark and Stromberg 1987, Compton and Hugie 1993). In addition, incisive foramina <4.6 mm; palatal breadth at last molariform tooth <4.2 mm; condylobasal length usually <20.3 mm; and maxillary toothrow usually <3.7 mm (Whitaker 1972).

When specimens from distant sites are compared, known *Z. hudsonius* are on average smaller in several gross body dimensions than known *Z. princeps* (e.g., Hall 1981, Jones 1981, Schorr 2001). For several years it was thought that total body length and other gross dimensions were reliable indicators of species identity within the suspected range of *Z. h. preblei* (e.g., Clark and Stromberg 1987). However, it has since become clear that there is substantial overlap in these measurements between purported *Z. hudsonius* and purported *Z. princeps* from this region. This, coupled with essentially indistinguishable pelage and body shape, has lead most mammalogists in the region to conclude that no external morphological character can be used to classify specimens from here into 2 distinct taxa.

Using multivariate analysis techniques, Conner and Shenk (2001) compared precisely-measured skull dimensions of *Zapus* specimens from low elevations (purported *Z. hudsonius*) to those of *Zapus* specimens from high elevations (purported *Z. princeps*) in northcentral Colorado and southeast Wyoming. At a sub-millimeter scale, low-elevation skulls were significantly and consistently smaller than those from high elevations. Also, known *Z. hudsonius* typically possess an anterior median tooth fold (Kilngener 1963), and many of the low-elevation *Zapus* with small skulls identified by Conner and Shenk (2001) also had this character. These results support the contention that there are 2 *Zapus* taxa in the region that are separated by skull size and elevation in a manner predicted by general knowledge of *Z. princeps* and *Z. hudsonius*.

However, some data suggests that this separation is less apparent in the North Platte and extreme northern South Platte river basins than in areas to the south. Conner and Shenk (2001)

documented a steady decline in the size of high-elevation *Zapus* skulls when moving north from Colorado into southern Wyoming; i.e., although still statistically significant, the elevation-dependent difference in skull dimensions was less in Wyoming than in Colorado. Furthermore, some *Zapus* specimens recently captured at mid-elevations (ca. 7200') in the North Platte River basin in Wyoming have large skulls, suggesting *Z. princeps*, but also possess an anterior median tooth fold, suggesting *Z. hudsonius*. Preliminary analyses of other recently-captured specimens from southeast Wyoming indicate that individuals with large skulls and no tooth folds (suggesting *Z. princeps*) were captured within a few meters of individuals with small skulls and present tooth folds (suggesting *Z. hudsonius*; C. Meaney and C. Jones, personal communication; Denver Museum of Nature and Science).

Morphology: Subpecies *Zapus hudsonius preblei* - Compared to *Z. h. campestris* and *Z. h. pallidus*, *Z. h. preblei* is described as slightly smaller and duller in color, with a less distinct dorsal band and fewer black-tipped hairs (Krutzsch 1954).

As discussed above, there are no external morphological characters that can reliably classify specimens of *Zapus* from southeast Wyoming to species. Therefore, for live specimens that cannot be resolved to species, it is unreasonable to expect external morphology to reliably indicate subspecies; i.e., uncertainty at the species level would propagate to the subspecies level.

Even for prepared specimens tentatively classified as *Z. hudsonius*, external morphology is likely to be an inexact indicator of subspecies because distinctions at this level are qualitative and usually require subjective evaluation; e.g., ochraceous upper parts for *Z. h. preblei* versus "brighter ochraceous (and more blackish) upper parts" for *Z. h. campestris* (Long 1965). Although some *Zapus* from Wyoming and surrounding states may match the description of a particular subspecies quite well, most are likely to span the descriptions of 2 or more of the 5 subspecies in the region. This is probably especially true in and near areas where the subspecies co-occur and interbreed (e.g., the contact zone between *Z. h. campestris*, *Z. h. pallidus*, and *Z. h. intermedius* in northwest South Dakota; Figure 2).

Krutzsch (1954) first established the subspecies *Z. h. preblei* in southeast Wyoming and northcentral Colorado based on comparisons of precisely-measured body dimensions of prepared museum specimens. In a subsequent re-analysis using a larger sample of specimens, Jones (1981) concluded that although *Z. hudsonius* in this area were geographically isolated, there was

insufficient morphological evidence to support their subspecific status, or indeed the subspecific status of any *Z. hudsonius* population.

GENETICS

Genetics: Genus *Zapus* - At this time there is no significant debate among mammalogists over the validity of the genus *Zapus*. It is generally accepted as a distinct and biologically-meaningful taxon and thus its genetic distinction from similar genera will not be fully explored here. It is assumed that *Napeozapus* is the genus most closely allied with *Zapus*, and thus would show the most similar genetic patterns. As discussed above, *Napeozapus* does not occur within ca. 500 mi of Wyoming (Figure 1).

Genetics: Species *Zapus hudsonius* - Genetic analyses have shown *Z. hudsonius* to be a unique and identifiable species that is relatively easily distinguished from similar species, especially when specimens from distant sites are compared. Hafner et al. (1981) used to genetic analyses to identify and distinguish *Z. hudsonius* from nearby *Z. princeps* in Arizona and New Mexico. Wunder and Harrington (1996; as cited in Schorr 2001) were similarly successful in using genetic patterns to resolve *Z. hudsonius* from *Z. princeps* in the South Platte River Basin in Colorado.

Riggs et al. (1997) used mitochondrial DNA to analyze the genetics of *Zapus* along the Southern Rocky Mountain front in Colorado and southeast Wyoming. Their main conclusion was that *Zapus* specimens from low elevations that were suspected to be *Z. h. preblei* formed a relatively homogenous genetic group. However, the northernmost samples in the study, including several from southeast Wyoming, were more closely allied with *Z. princeps*; these samples could not be reliably assigned to species. The general consensus among regional mammalogists is that *Z. hudsonius* X *Z. princeps* hybridization in extreme northern Colorado and southeast Wyoming is the most parsimonious explanation for such results (Hafner 1997, Riggs et al. 1997, Pague and Grunau 2000, Schorr 2001). Hybridization between related species in areas of co-occurrence is well known for other vertebrates (see examples in Pague and Grunau 2000, Hafner 1997). Krutzsch (1954) stated that *Z. hudsonius* X *Z. princeps* hybridization did not seem to occur in other areas of sympatry, such as British Columbia, but his conclusion was informed by morphological comparisons only without any genetic information.

Genetics: Subspecies *Zapus hudsonius preblei* - Hafner et al. (1981) and Riggs et al. (1997; see also Hafner 1997) used genetic analyses to support subspecific status of *Z. h. preblei* as distinct from other *Z. hudsonius* subspecies, based on specimens form the South Platte and Arkansas river basins. However, as outlined above, genetic tests were unable to conclusively assign subspecies, or even species, identity to specimens from southeast Wyoming. New genetic studies, with the intent of resolving both the species- and subspecies-level distinctions of *Zapus* in this region, are underway (Ramey et al. 2002).

ECOLOGY

Ecology: Genus *Zapus* - All members of *Zapus* and *Napeozapus* show strong affinities for heavily-vegetated habitats in proximity to open and flowing water (Whitaker 1972, Whitaker 1999a, Whitaker 1999b, Cranford 1999, Gannon 1999). *Napeozapus* prefer forested and woodland habitats and are rarely found elsewhere; in contrast, *Zapus* commonly occupies grass- and forb-dominated wetlands as well as wooded sites. Fungi may be more important in the diet of *Napeozapus* than *Zapus*, with the latter genera depending more on seeds and vegetation. Members of both genera hibernate for approximately half the year (Whitaker 1999b).

Ecology: Species *Zapus hudsonius* - The general life history of *Z. hudsonius* has been described by several authors (e.g., Long 1965, Armstrong 1972, Whitaker 1972, Clark and Stromberg 1987, Fitzgerald et al. 1994, Whitaker 1999a), as has similar information for *Z. princeps* (e.g., Long 1965, Armstrong 1972, Clark and Stromberg 1987, Fitzgerald et al. 1994, Cranford 1999). The major distinction between the 2 species in this region appears to be elevation of occurrence: the distribution of *Z. princeps* is primarily montane, whereas that of *Z. hudsonius* is centered on prairie. Both species are strongly associated with riparian habitats. However, *Z. princeps* is known to range relatively frequently into uplands in montane and subalpine areas, whereas *Z. hudsonius* rarely strays from riparian zones in prairie environments (but see discussion of *Z. hudsonius* upland forays in Shenk and Sivert 1999, Ryon 1999, Schorr 2001). It is difficult to know whether this stems from an intrinsic biological difference between the taxa or is simply due to the fact that high elevation uplands are more mesic than prairie uplands.

Aside from elevation of occurrence, *Z. princeps* and *Z. hudsonius* are ecologically very similar in this region, although it must be recognized that there is a relative paucity of comparative field studies. There is no indication that these species diverge in life history traits to any substantial degree; with the currently limited knowledge base, it appears that within-species variation in most ecological traits may be as great as between-species variation.

Ecology: Subspecies *Zapus hudsonius preblei* - The basic ecology of *Z. h. preblei* has been outlined by several authors (see USDI 2002). All purported subspecies of *Z. hudsonius* in Wyoming and surrounding states are strongly associated with riparian habitats. It is assumed that *Z. h. campestris*, *Z. h. pallidus* and *Z. h. intermedius* range more into uplands than either *Z. h. preblei* and *Z. h. luteus*, but that this may be a function of climate (uplands are more mesic and heavily-vegetated in the Black Hills and central Great Plains relative to the Rocky Mountain front) rather than intrinsic differences in the subspecies' biology. Variations in food habits, hibernacula, reproductive characteristics, and other traits may all similarly vary with geography. As is the case with full species of *Zapus*, there is a general lack of field studies that compare subspecies. Current information suggests no great degree of ecological divergence between subspecies.

BIOGEOGRAPHY

Biogeography: Genus *Zapus* - Genera immediately ancestral to *Zapus* and *Napeozapus* are known from North American sites dating to the early Pliocene. *Zapus* in its current form has been relatively widespread in North America since the early Pleistocene, when the continent was occupied by at least *Z. hudsonius* and 2 other, now-extinct species. *Napeozapus* is thought to have achieved its current form in the mid-Pleistocene. Diversification of early *Zapus* into the 3 extant species likely occurred during repeated geographic isolation of eastern and western groups during Pleistocene glaciations. The eastern isolate generated *Z. hudsonius*, whereas the western isolate generated *Z. trinotatus* and *Z. princeps* (Krutzsch 1954). The current interglacial has allowed *Z. hudsonius* and *Z. princeps* to come into close contact, including broad zones of sympatry in the northern U.S. and southern Canada and narrower zones of sympatry along the Rocky Mountain front in New Mexico, Colorado, and Wyoming (Figure 2). Such "re-contact"

between the 2 species is assumed to have occurred during earlier interglacial periods as well, alternating in cycle with isolation during glacial periods.

Biogeography: Species *Zapus hudsonius* - During the late Pleistocene (ca. >10,000 years ago) the eastern slope of Southern Rocky Mountains and adjacent lowlands supported more cool and mesic grassland suitable for *Z. hudsonius*, presumably leading to larger and more widespread populations of the species here. At this time *Z. princeps* was probably isolated to the west of the Rocky Mountains in the Great Basin and adjacent regions. The warming and drying of the western United States during the early Holocene shifted mesic grassland, and thus the main center of occurrence of *Z. hudsonius*, to the north and east; *Z. h. campestris* now occupies the periphery of this shifted range (Figure 2).

However, pockets of suitable habitat remained along the Southern Rocky Mountain front, allowing disjunct populations to persist here. Through the combined forces of founder effect, genetic drift, and adaptation, these disjunct populations are thought to have diverged to the subspecies level and now exist as *Z. h. luteus* and *Z. h. preblei* (Hafner et al. 1981, Jones 1981, Morrison 1992, Hafner 1997). The Holocene climatic amelioration presumably also allowed *Z. princeps* to move east onto the Rocky Mountains to its present position (Figure 2).

It is generally accepted that *Z. princeps* occurs at higher elevations than *Z. hudsonius* in Colorado and Wyoming. The former species is thought to primarily occupy subalpine and montane zones, with peripheral extensions into foothills and possibly even prairie environments along riparian corridors. In contrast, *Z. hudsonius* is thought to primarily occupy prairie riparian environments, with peripheral extensions into the foothills and montane zones along riparian corridors. This pattern obviously suggests zones of *Z. princeps* X *Z. hudsonius* co-occupation along mountain-front riparian systems.

Zones of co-occupation are likely to be rather narrow along the Front Range of Colorado, where the abrupt mountain front and high terminal elevations can be expected to sharply divide prairie and montane biota. Some areas of likely sympatry between *Z. hudsonius* and *Z. princeps* along the Front Range are currently being studied (e.g., Trout Creek, Douglas County, Colorado; Schorr 1999).

Importantly, the biogeographic situation changes rather markedly in the extreme northern South Platte River basin (ca. Cache La Poudre River and points north) and North Platte River

basin. A large area of sympatry between *Z. hudsonius* and *Z. princeps* in northern Colorado and southeast Wyoming has been suspected, if not conclusively demonstrated, by mammalogists for quite some time (e.g., Long 1965, Armstrong 1972). The major mountain range here, the Laramie Mountains, has a rather gradual east slope (leading to much interdigitation of prairie, foothills, and montane biota), a low crest (<7500' in many places), and is bisected by a major river system (Laramie River) that connects large areas of mixed grass prairie on either side of the range. These factors suggest that the zone of co-occupation may be quite broad along the Laramie Mountains and that this range is not a western barrier to *Z. hudsonius*. Since 1998 the USDA Forest Service and other field workers have captured several suspected *Z. hudsonius* between 7500 - 8500 ft elevation in the Laramie Range (WYNDD, unpublished data).

Also, 4 capture locations to the west of the Laramie Range in Wyoming bear mentioning in this context:

1. A *Zapus* specimen captured in the Snowy Range (southwest Albany County, Wyoming) in the 1970's was originally identified as *Z. hudsonius*, but then was subsequently relabeled *Z. princeps* based on the relatively high elevation of the capture location. However, preliminary results using the methods of Conner and Shenk (2001) suggest that this specimen may in fact be *Z. hudsonius* (C. Jones, Denver Museum of Nature and Science, personal communication). It is assumed that the specific identity of this specimen is currently being investigated more thoroughly.

2. In summer 2000, WYNDD zoologists captured several *Zapus* on the floor of the Laramie Valley (central Albany County, Wyoming; ca. 7200'). These individuals were taken from a cottonwood-willow riparian corridor bordered by mixed grassland, several miles from the nearest montane forest; such habitat suggests *Z. hudsonius* rather than *Z. princeps.* It is assumed that the specific identity of these specimens is currently being investigated with methods of Conner and Shenk (2001), and that tissue from these specimens will be included in ongoing genetic analyses (Ramey et al. 2002).

3. In summer 2002 WYNDD zoologists captured several *Zapus* spp. along the Laramie River ca. 30 mi north of the town of Laramie, Wyoming (ca. 7100'). These individuals

were taken in a grass- and willow-dominated riparian corridor bordered by mixed grassland, several miles from the nearest montane forest; such habitat suggests *Z. hudsonius* rather than *Z. princeps.* Preliminary results using the methods of Conner and Shenk (2001) suggest that some of these specimens may be *Z. hudsonius*; oddly, others in this group (which were all captured within several meters of one another) appear to be *Z. princeps* (C. Meaney and C. Jones, Denver Museum of Nature and Science, personal communication). It is assumed that tissue from these specimens will be included in ongoing genetic analyses (Ramey et al. 2002).

4. In summer 2002 WYNDD zoologists captured several *Zapus* spp. at Hutton Lake National Wildlife Refuge, ca. 12 mi southwest of the town of Laramie, Wyoming. These individuals were taken in a grass- and reed-dominated wetland bordered by mixed grassland, several miles from the nearest montane forest; such habitat suggests *Z. hudsonius* rather than *Z. princeps.* Preliminary results using the methods of Conner and Shenk (2001) suggest that some of these specimens may be *Z. hudsonius* (C. Meaney and C. Jones, Denver Museum of Nature and Science, personal communication). It is assumed that tissue from these specimens will be included in ongoing genetic analyses (Ramey et al. 2002).

If further analyses continue to suggest that some of these specimens are *Z. hudsonius*, the suspected range of the species in southeast Wyoming may need to be extended west to include the drainage basins of the Upper Laramie River, Little Laramie River, Rock Creek, and possibly Medicine Bow River.

Biogeography: Subspecies *Zapus hudsonius preblei* - The uncertainty regarding the species-level taxonomy of *Zapus* in southeast Wyoming makes it difficult to accurately portray distributions of subspecies here. As currently understood, presumed *Z. h. preblei* have been documented in both the North Platte and South Platte river basins of Wyoming, with collection sites as far north as the town of Douglas, west to the town of Boxelder, and east to the vicinity of Slater (Figure 3). The crest of the Laramie Mountains is generally regarded as the western

boundary of *Z. h. preblei* in Wyoming. However, as discussed above, this may be untenable and further analyses may show the western boundary of *Z. h. preblei* farther to the west in Wyoming.

It is generally accepted that *Zapus* in southeast Wyoming are geographically isolated from populations to the north (*Z. h. campestris*) and east (*Z. h. pallidus*) because the intervening shortgrass prairie is too dry and sparsely-vegetated, even on the borders of streams, to provide suitable habitat (Figure 2). However, there have been very few surveys for *Zapus* in these intervening areas. Also, habitat suitability for *Zapus* has been increasing in these areas over the past century, largely due to the westward progression of gallery forests (Choate and Reed 1986, Knopf 1986, Knopf and Samson 1996), and both Choate et al. (1991) and Frey (1992) have demonstrated recent westward expansions in the ranges of *Z. h. intermedius* and *Z. h. pallidus*. These trends suggest increasing likelihood of connectivity between *Zapus* in southeast Wyoming and populations to the north and east. Connectivity between these populations could have 2 major management implications: (1) increased effective population size and genetic diversity, possibly reducing the risk of local extinction, and (2) erosion of any unique genetic and morphological characters currently maintained in the populations.

In summer 2000, *Zapus* surveys were performed on the USDA Forest Service Thunder Basin National Grassland on streams in the headwaters of the Cheyenne River. No *Zapus* were found (T. Byer, USDA Forest Service, personal communication). In summer 2002, *Zapus* surveys were performed at 6 sites in Goshen County, Wyoming, again with no *Zapus* captured. These efforts lend direct support to the geographic separation of *Zapus* in southeast Wyoming from *Z. h. campestris* and *Z. h. pallidus*. More such surveys are needed in these areas to corroborate these initial findings.

It is important to note that separation between *Z. hudsonius* subspecies is also an issue in southern Colorado where *Z. h. preblei* and *Z. h. luteus* approach each other. Indeed, this is another area where *Z. princeps* come into close contact, and possibly sympatry, with *Z. hudsonius*. The issues of range overlap, potential hybridization, and taxonomic clarity explored above for *Zapus* in southeast Wyoming may have parallels in southern Colorado.

Predictive range map for *Zapus* spp. in southeast Wyoming: In an effort to contribute more information to the debate over the distribution of *Zapus* in southeast Wyoming, WYNDD

zoologists produced a predictive range map for the taxon using points of known occurrence ("positive points") and points of suspected absence ("negative points").

The basic concept behind predictive range mapping is to first identify and model the environmental conditions at positive points, then identify other locations in the area of interest that also have those specific conditions. The modeling algorithm used here was the Classification and Regression Tree (CART) procedure within the S-Plus (Professional Release 1) statistical package. This procedure contrasts the values of environmental variables at positive and negative points to build a robust statistical model of environmental conditions at positive points. Then, by linking this output to the ArcView geographic information system (Environmental Systems Research Incorporated, Redlands, California), the model was spatially extrapolated across all 5 counties in southeast Wyoming (Figure 4). Details of the modeling and mapping procedures are presented in Appendix A, and results are presented in Figure 4.

It is important to note that this map portrays the predicted distribution of *Zapus from relatively low elevations in southeast Wyoming*. It cannot be said to portray the predicted distribution of *Z. hudsonius* or *Z. h. preblei*, because the current confusion over the taxonomic identity of *Zapus* species and subspecies in the region precludes such certainty in the input data. Nevertheless, these results support the notion that the range of low-elevation *Zapus* in southeast Wyoming spans the Laramie Mountains and in fact covers much of the Laramie Valley. Also, much of extreme eastern Wyoming appears unsuitable for the taxon. Similar results were obtained by Keinath (2001) in his predictive range mapping effort.

SUMMARY

Based on current knowledge of the morphology, genetics, ecology, and biogeography of *Zapus* in northcentral Colorado and southeast Wyoming:

1. *Zapus hudsonius preblei* appears to be a valid and identifiable taxon in the South Platte River basin (south of the Cache La Poudre River) and Arkansas River basin in Colorado. *Zapus* at low elevations here are consistent morphologically and genetically with *Z. hudsonius*, and additional genetic evidence indicates an identifiable within-species unit consistent with *Z. h. preblei*. The biogeographic history of the region indicates that *Zapus* here may have been derived from past *Z. hudsonius* populations and may have remained isolated from the main center of occurrence of *Z.*

hudsonius for several thousand years, setting the stage for subspeciation. There is likely some limited sympatry with low elevation *Zapus* to the south (*Z. h. luteus*) and high-elevation *Zapus* (*Z. princeps*) to the west. Any hybridization stemming from this sympatry is probably limited and apparently has not reduced the morphological or genetic uniqueness of *Z. h. preblei*, apparently the most abundant form in the area, to any great degree.

2. *Zapus hudsonius preblei*, as defined above for areas in Colorado, may occur at low elevations in the northern South Platte River basin (north of the Cache La Poudre River) and North Platte River basin in Wyoming, but there is substantial confusion between this form and *Z. princeps*. Some *Zapus* here are consistent morphologically with *Z. hudsonius,* others are more consistent with *Z. princeps*, and still other individuals show morphological characteristics of both species. Similarly, genetic tests appear to detect a mixture of *Z. hudsonius* and *Z. princeps* in individuals from this region. Biogeographic history indicates that *Zapus* here may have been derived from past *Z. hudsonius* populations and may have been isolated from the main center of occurrence of *Z. hudsonius* for several thousand years, setting the stage for subspeciation. However, current patterns in landform and vegetation clearly indicate a mixing of montane and prairie biota that would produce a relatively large area of sympatry between *Z. hudsonius* and *Z. princeps*. The clearest interpretation of this information is that southeast Wyoming supports some *Z. princeps,* some *Z. h. preblei,* and a relatively large group of hybrids between the 2 species.

The 1998 listing of *Z. h. preblei* has stimulated many *Zapus* surveys and specimen collections in southeast Wyoming. Collected specimens have been sent to various analytical labs, most commonly the Denver Museum of Nature and Science (Denver, Colorado), where they undergo a series of analyses and tests. The results of these tests are not always made widely available, nor are they organized in a discrete summary showing the results of all tests on all collected specimens. Such a summary for all specimens collected in southeast Wyoming (ideally, from throughout the entire suspected range of *Z. h. prebeli*) would substantially improve our understanding of *Zapus* taxonomy and distribution in the region.

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APPENDIX

APPENDIX A: PREDICTIVE RANGE MAP FOR *Zapus* spp. IN SOUTHEAST WYOMING

To inform the debate over the distribution of *Zapus* in southeast Wyoming, WYNDD zoologists produced a predictive range map for the taxon using points of known occurrence ("positive points") and points of suspected absence ("negative points"). The basic concept behind predictive range mapping is to first identify and model the environmental conditions at positive points, then identify other locations in the area of interest that also have those specific conditions. The modeling algorithm used here was the Classification and Regression Tree (CART) procedure within the S-Plus (Professional Release 1) statistical package. This procedure contrasts the values of environmental variables at positive and negative points to build a robust statistical model of environmental conditions at positive points. Then, by linking this output to the ArcView geographic information system (Environmental Systems Research Incorporated, Relands, California), the model was spatially extrapolated across all 5 counties in southeast Wyoming (Figure 4). A more thorough description of the procedure is given in Fertig and Thurston (2002) and Fertig et al. (2002).

For this model, the initial set of positive points included all 158 locations where individual *Zapus* have been observed (typically trapped) in Albany, Converse, Platte, Goshen, and Laramie Counties in Wyoming. The initial set of negative points included 51 locations where *Zapus* were trapped for, but not found, in the same 5 counties. Both positive and negative data are on file at the Wyoming Natural Diversity Database (University of Wyoming, Laramie, Wyoming). These data required several filtering steps prior to statistical modeling in order to produce an unbiased model of suitable environmental conditions:

Biogeographic filter: From the initial dataset we excluded:

- Positive points above 8500' elevation on the Snowy Range in southwest Albany County. Although the distribution of *Zapus* species has not yet been resolved for southeast Wyoming, these high-elevation areas are generally accepted as supporting only *Z. princeps* and no *Z. hudsonius*. Therefore, these points were removed to minimize the influence of *Z. princeps* on the final model and map.

- Positive points in Carbon and Natrona counties. These areas are outside the scope of the project and likely support many *Z. princeps*. These points were removed to minimize the influence of *Z. princeps* on the final model and map.

- Positive points labeled with "unmappable" precisions. These points could not be reliably mapped, and thus could not be reliably attributed with environmental variables.

- Two negative points in the Cheyenne River basin, northeast Converse County and southern Weston County (these were the only 2 points in these areas). These areas are outside the scope of this project, and are generally accepted as outside the range of *Z. hudsonius* and approaching the range of *Z. h. campestris*.

Spatial filter: Because the positive and negative points were collected opportunistically and did not result from an even application of sampling effort across the study area, the spatial pattern of the points is an artifact of sampling distribution rather than a true reflection of *Zapus* distribution. Unless this clustering is accounted for, the resulting model will be unjustly biased towards heavily-sampled environments. To minimize the influence of heavily-sampled sites, we eliminated one point from each pair of points (either positive or negative) that were within 2000m of each other. In cases where we had to choose between a positive point and a negative point, we eliminated the negative point. In cases where we had to choose between 2 positive or 2 negative points, we eliminated the point with the coarsest mapping precision. In cases where we had to choose between 2 positive or 2 negative points with the same mapping precisions, we eliminated the point with the oldest date-of-observation.

The post filtering dataset consisted of 53 positive and 21 negative points. After exploring these data spatially and statistically, we selected 5 environmental variables to enter into the CART analysis: elevation, mean annual precipitation, mean annual temperature, number of frost days per year, and primary landcover type as identified by the Wyoming Gap Analysis project (Merrill et al. 1996). Note that initial attempts at using more and finer-scale variables (e.g., mean April temp, max July temp, etc.) produced results qualitatively similar to the final results,

except that the results were not as immediately interpretable based on species life history. Thus the final variable set was chosen as producing the most parsimonious and biologically meaningful model. Note also that models including topographic slope and aspect as predictors produced results very similar to the final results, except that there was a much more fine-grained, "salt-and-pepper" structure to areas of predicted *Zapus* presence. It was decided that our positive and negative occurrence data were not mapped to a fine enough precision to allow valid use of slope and aspect, so these variables were eliminated.

The final CART model identified 3 combinations of environmental variables that predict presence of *Zapus* in southeast Wyoming. A total of 91% of the positive points were in areas that fit these descriptions, and 91% of the negative points were in areas that did not fit these descriptions.

> SUITABLE ENVIRONMENT 1. Number of frost days greater than 189.9, and land cover types of forest-dominated riparian, shrub-dominated riparian, mixed grass prairie, limber pine woodland and scrub, lodgepole pine, and human disturbed. 67.9% of the positive model points occurred in this environment.
>
> SUITABLE ENVIRONMENT 2. Number of frost days greater than 189.9, land cover types of ponderosa pine and xeric upland shrub, and elevation greater than 1998 m. 11.3% of the positive model points occurred in this environment.
>
> SUITABLE ENVIRONMENT 3. Number of frost days less than 189.9, elevations between 1419 m and 1822.5 m, and land cover types of forest-dominated riparian, shrub-dominated riparian, and human disturbed. 11.3% of the positive model points occurred in this environment.

After mapping this final model we eliminated all polygons of predicted presence that were less than 10,800 m^2 (3 contiguous 60m x 60m grid cells) in size. This spatial "smoothing" was intended to eliminate most of the very small and extremely isolated areas of predicted presence that are unlikely to support *Zapus* on their own.

Finally, because low-elevation *Zapus* in this area are riparian obligates, the smoothed output was intersected with a layer of riparian zones to more accurately restrict areas of predicted presence to riparian habitats. The riparian layer was created by buffering permanent streams, intermittent streams, ponds and other hydrologic features by certain distances to represent the general extent of riparian vegetation. Buffer distances for these features were as follows:

Hydrologic feature		Buffer width (m)
Stream - Strahler order	1	40
	2	40
	3	60
	4	90
	5	120
	6	150
	7	210
Reservoir		90
Lake or pond		90
Wide river		300
Marsh or wetland		0
Ephemeral wash		0

It is important to note that our final map portrays the predicted distribution of *Zapus from relatively low elevations in southeast Wyoming*. It cannot be said to portray the predicted distribution of *Z. hudsonius* or *Z. h. preblei*, because the current confusion over the taxonomic identity of *Zapus* species and subspecies in the region precludes such certainty in the input data. Nevertheless, these results support the notion that the range of low-elevation *Zapus* in southeast Wyoming spans the Laramie Mountains and in fact covers much of the Laramie Valley. Also, much of extreme eastern Wyoming appears unsuitable for the taxon.