Status of the Pygmy Rabbit (*Brachylagus idahoensis*) in Utah

prepared by

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Classification and Nomenclature

Scientific Name

Brachylagus idahoensis (Merriam, 1891) is the name currently accepted by most mammalogists (e.g., Jones et al. 1997, Hoffmann 1993) for the pygmy rabbit. *Brachylagus* is from the Greek *brachy* meaning "short" and the Greek *lagōs* meaning "hare." The specific epithet *idahoensis*, with its Greek suffix, means "of or inhabiting Idaho," the place from which the type specimen was collected. Under the rules of zoological nomenclature (International Code of Zoological Nomenclature, Article 51.3 [Ride et al. 1999]), parentheses must surround the name of Merriam, the author of the specific epithet, since the species *idahoensis* is no longer placed in the genus in which it was originally described (see Taxon History below).

Original Publication

The original description and naming of the pygmy rabbit (as *Lepus idahoensis*) was on pp 75–78 of

> Merriam, C. H. 1891. Results of a biological reconnoissance [*sic*] of south-central Idaho. *North American Fauna* 5: 1–113.

Type Specimen

Merriam's (1891) type specimen was collected on 16 September 1890 in Pahsimeroi Valley, which is near Goldburg, Custer County, Idaho. The holotype, an adult male, is specimen no. 24045/31461 (i.e., skin is no. 24045, skull is no. 31461; also referred to simply as specimen no. 24045) in the U. S. National Museum (USNM). In addition to the holotype, Merriam had four other specimens, USNM nos. 24046/31462 (skin/skull), 24047/31463, 23541/30959, and 23542/30960, all of which he referred to in the type description. Since Merriam used these other specimens in the type description, they are paratypes, although Merriam did not refer to them using this term.

Synonyms

Formerly the prevailing view among mammalogists (e.g., Hall 1981, Honacki et al. 1982) held that the pygmy rabbit was a cottontail (*Sylvilagus*) and applied to it the name *Sylvilagus idahoensis* (Merriam, 1891). Although nearly all authors now consider the species to be quite distinct from the cottontails, it is possible that a few mammalogists may still consider it to be a member of the genus *Sylvilagus* and continue to refer to it as *Sylvilagus idahoensis* as did some as late as the 1980s (see Taxon History below).

Common Name

The accepted English common name for *Brachylagus idahoensis* is the pygmy rabbit (Baker et al. 2003). Rabbits are leporids that are altricial (as opposed to hares, which are precocial leporids). "Pygmy" is in reference to the diminutive size of *Brachylagus idahoensis*, the smallest of North American leporids. Many authors (e.g., Grinnell et al. 1930, Hall 1946, Durrant 1952, Bradford no date [1975]) have used the spelling "pigmy"; the standardized spelling is now "pygmy" (Jones et al. 1997).

Merriam (1891), in the type description, proposed the common name Idaho pygmy rabbit, and this name was used by others (e.g., Nelson 1909, Stanford 1932). Bailey (1936) called this species both the pygmy rabbit and the sage rabbit, and he reported that its name in the Piute language is *tse-gu-oo*.

Taxonomic Arrangement

Placement of the pygmy rabbit in a generally accepted, conservative taxonomic hierarchy is represented below.

phylum Chordata
- subphylum Vertebrata
  - class Mammalia
    - subclass Theria
      - infraclass Eutheria
        - order Lagomorpha
          - family Leporidae
            - (subfamily Leporinae—recognized by some authors)
              - genus *Brachylagus* Miller, 1900
                - species *Brachylagus idahoensis* (Merriam, 1891)

The order Lagomorpha has been one of the most difficult of mammalian orders to place systematically. Lagomorphs were originally thought to be rodents, and even after it was recognized that they were sufficiently distinct to deserve separate ordinal status, Lagomorpha continued to be considered most closely related to Rodentia, the two orders being placed together in the cohort Glires. In recent decades the presumed close relationship of Lagomorpha to Rodentia has been repeatedly challenged, and there continues to be much debate concerning the nearest relatives of lagomorphs. In modern works Lagomorpha has been variously considered to be most closely allied to the orders Macroscelidea (elephant shrews), Primates (primates), Rodentia (rodents), and Artiodactyla (artiodactyls or even-toed ungulates), and even possible close relationship to marsupials has been suggested. That some of the taxa to which it has been argued that Lagomorpha shows closest affinity are only distantly related to each other (e.g., Primates and Artiodactyla) illustrates the degree of disagreement and the uncertainty of understanding of the relationships of this problematical group. The current trend among mammalian systematists is once again to regard Lagomorpha and Rodentia provisionally as sister taxa while acknowledging that their relationships are incompletely resolved.

No subspecies have been proposed in *Brachylagus idahoensis*.

Alternative Taxonomy

Changes and refinements of vertebrate and mammalian systematics continue to be made, and, with the application of modern molecular techniques, new taxonomic arrangements are proposed frequently. Mammalian hierarchies other than the one presented above are in use, one of these being that of McKenna and Bell (1997), which employs many non-Linnaean taxonomic levels. McKenna and Bell's (1997) hierarchy, which begins at the level of class and descends to genus, for the pygmy rabbit (to genus) is:

- class Mammalia
  - subclass Theriiformes
    - infraclass Holotheria
      - superlegion Trechnotheria
        - legion Cladotheria
          - sublegion Zatheria
            - infralegion Tribosphenida
              - supercohort Theria
                - cohort Placentalia (= Eutheria)
                  - magnorder Epitheria
                    - superorder Preptotheria
                      - grandorder Anagalida
                        - mirorder Duplicidentata
                          - order Lagomorpha
                            - family Leporidae
                              - genus *Brachylagus* Miller, 1900

There has been considerable disagreement concerning the phyletic relationship of *Brachylagus idahoensis* to other leporids. As Chapman and Flux (1990, p 3) noted,

> . . . the relationship between the cottontails (*Sylvilagus*) and the pygmy rabbit (*Brachylagus*) remains unclear. Some workers consider them to be the most distant of relatives, while others consider them members of the same genus, *Sylvilagus*.

Although most mammalogists now recognize *Brachylagus* as a genus distinct from *Sylvilagus* Gray, 1867 (cottontails), for many years *Brachylagus* was regarded as only a subgenus of *Sylvilagus* (as discussed below). Hibbard (1963), using a dental character, concluded that *Brachylagus* was not closely related to *Sylvilagus* and considered its only close relative to be the Sumatran rabbit, *Nesolagus netscheri*. The monotypic genus *Nesolagus* is considered the most primitive member of the family Leporidae, with no close relatives except, possibly, *Brachylagus idahoensis* (Dawson 1981). Likewise, *Brachylagus* appears to a primitive leporid and to have no close relatives except, perhaps, *Nesolagus* (see Chapman and Flux 1990, p 3, fig. 1.3). Probably *Brachylagus* and *Nesolagus* are not closely related to each other or to other living leporids but are alike only in their retention of primitive leporid characters.

Taxon History

When Merriam (1891) described and named *Lepus idahoensis*, he placed it in the hare genus *Lepus* based on the misconception that, like many members of the genus *Lepus*, there are two annual molts in the pygmy rabbit. Although most of the leporids of the New World were formerly placed in the very widespread genus *Lepus* Linnaeus, 1758, the current concept of this genus restricts it to hares and jack rabbits.

Miller (1900) created the new subgenus *Brachylagus* within the genus *Lepus* to contain the pygmy rabbit. Although the genus *Sylvilagus* had existed since 1867, Miller arranged *Brachylagus* as a subgenus of the genus *Lepus*, the genus in which Merriam had placed the pygmy rabbit; thus the name remained *Lepus idahoensis*.

Lyon (1904) elevated *Brachylagus* to generic status based on the distinctiveness of its dental and cranial characters, producing the new name combination *Brachylagus idahoensis*, a usage that was followed by Nelson (1909).

Grinnell et al. (1930, p 553) showed that there is only one annual molt in the pygmy rabbit but did not consider its distinctive cranial features sufficient to justify generic recognition and arranged it as a cottontail, *Sylvilagus* Gray, 1857, forming yet another new combination, *Sylvilagus idahoensis*. Most authors used the name *Sylvilagus idahoensis* from 1930 until 1980 and later, arranging *Brachylagus* again as a subgenus—but now a subgenus of *Sylvilagus*, not of *Lepus* as it had been established by Miller (1900).

Hibbard (1963) analyzed dental patterns of leporids and concluded that *idahoensis* should not be placed in the genus *Sylvilagus*. Gureev (1964) arranged *idahoensis* together with the species *bachmani* (*Sylvilagus bachmani* of other authors) in the genus *Microlagus* Trouessart, 1897, which had been treated as a subgenus of *Sylvilagus* by Lyon (1904) and synonymized with the subgenus *Sylvilagus* by Nelson (1909). Kenner (1965), analyzing cranial and dental characters of cottontails and the pygmy rabbit statistically, reached the same conclusion that Lyon (1904) and Hibbard (1963) had and resurrected *Brachylagus* as a full genus. Dawson (1967) also placed *idahoensis* in the genus *Brachylagus*. The work of Johnson and Wicks (1964) and Johnson (1968) using serum protein electrophoresis also demonstrated the dissimilarity of the pygmy rabbit from cottontails, corroborating the morphological studies of Hibbard (1963), and Kenner (1965), and Dawson (1967).

Green and Flinders (1980b) and most (e.g., Hoffmann 1993, Baker et al. 2003) but not all (e.g., Hall 1981, Honacki et al. 1982, Weiss and Verts 1984) subsequent authors have returned to Lyons' (1904) recognition of *Brachylagus* as a genus, calling the species *Brachylagus idahoensis*.

Although it has been frequently stated (e.g., Green and Flinders 1980b, Chapman and Ceballos 1990, Janson 2002) that *Brachylagus* is a monotypic genus, strictly speaking this is no longer true. Ramos (1999) described a fossil species, *Brachylagus coloradoensis*, from early and middle Pleistocene deposits in Colorado. This species, which is slightly larger than *Brachylagus idahoensis*, shows p3 (or P_3) enamel patterns that are intermediate between *Brachylagus idahoensis* and the extinct genus *Hypolagus* Dice, 1917, and Ramos suggested that *Hypolagus* may be ancestral to the genus *Brachylagus*.

Legal Status

International

The pygmy rabbit does not have international legal status; i.e., it is not listed by the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES).

Although not a legal designation, the International Union for Conservation of Nature and Natural Resources (IUCN or IUCN–The World Conservation Union) formerly listed the pygmy rabbit as "vulnerable" (Chapman et al. 1990, p 155), the IUCN category immediately below "endangered" and defined as "facing a high risk of extinction." The IUCN Red List (version 2.3, 1994) down-listed the pygmy rabbit to "lower risk—near threatened," defined as "close to qualifying for vulnerable," which is its current (2003) IUCN listing status.

Federal

Formerly the pygmy rabbit was a Category 2 Candidate for potential listing as endangered or threatened by the U. S. Fish and Wildlife Service under provisions of the Endangered Species Act, until Category 2 was eliminated 28 February 1996. Currently the disjunct population of the pygmy rabbit in Washington is considered a "distinct population segment" and is listed as endangered by the U. S. Fish and Wildlife Service (Warren 2003). However, in the rest of its range, including Utah, the species is not federally protected.

State

The pygmy rabbit is designated a "wildlife species of concern" by the Utah Division of Wildlife Resources (UDWR 2003).

Under statutes of the state of Utah (R657-3-24), collection (e.g., scientific) of the pygmy rabbit in Utah is prohibited, and importation and possession of this species are controlled.

Description

Non-technical

The pygmy rabbit is the smallest rabbit, readily distinguished from hares and jack rabbits (*Lepus*) on the basis of size alone. Its small size, its short ears, the buff (rather than white) underside of its inconspicuous tail, its gray color, its five pairs of mammae, and its scampering gait separate it from cottontails (*Sylvilagus*).

Technical

First incisors large; second upper incisors small, peglike, and located directly behind first incisors; three pairs of upper incisors present at birth, but outer pair soon lost; long post-incisor diastema present; canines absent; cheek teeth hypsodont, rootless, and evergrowing; jaw action is lateral or oblique; fore feet digitigrade, hind feet plantigrade; tail short; scrotum located anterior to penis;

uterus duplex; placenta discoidal and hemoendothelial; hind legs noticeably longer than fore legs, hind feet noticeably longer than fore feet; soles of feet covered with hair; lacking phallic bones (i.e., baculum and baubellum); ears longer than wide; 10 mammae; nasals widest posteriorly; frontal bone possessing a supraorbital process with both anterior and posterior "arms" or projections, the antorbital extension being more than half the length of the posterior extension; maxillae having numerous fenestrae; skull encircled by a clearly defined joint just anterior to occipital and otic bones; clavicle rudimentary; tibia an fibula fused distally; pubic symphysis present and distinct; dental formula incisors 2/1, canines 0/0, premolars 3/2, molars 3/3, total 28; 2nd upper maxillary tooth similar to 3rd; last lower molar double (not absent or simple); cutting edge of 1st upper incisor straight (not V-shaped); mental foramen of mandible located under 1st (not last) lower cheek tooth; first upper cheek tooth with only one reentrant angle on anterior face; reentrant angle of second upper cheek tooth not crenate; females usually larger than males; total length 250–290 mm; tail length 20–30 mm; hind foot length 65–72 mm; ear length ~50 mm; weight ~390–430 g in males, ~420–460 g in females. Diploid chromosome number (2n) is 44, with one pair of large metacentric chromosomes (van der Loo et al. 1981).

Field Characters

Smallest rabbit, distinguishable from all others, especially in Utah, by size alone, its weight rarely exceeding 1 lb. Tail short, inconspicuous, and buff below (rather than white as in Utah species of *Sylvilagus*); often appears not to have a tail. Pelage slate gray with a pinkish tinge. Ears proportionately short relative to other rabbits. Gait is scampering or scurrying rather than bonding or leaping. Produces a one- to seven-note alarm call unlike other rabbits. Regularly utilizes burrows in soil or snow unlike other rabbits within its range. Seldom encountered in habitat other than mature sagebrush.

Significance of Taxon

Natural Significance

The pygmy rabbit shows a Pleistocene relictual distribution, evidently much reduced from prehistoric times when it ranged farther south and east. In Utah it shows a further aspect of relictualism, being absent from the lakebed of prehistoric Lake Bonneville.

Although it is frequently stated (e.g., Merriam 1891, Nelson 1909, Green and Flinders 1980b, Dobler and Dixon 1990, Flinders 1999, Ramos 1999, Janson 2002) that the pygmy rabbit is the smallest rabbit in North America, this is an understatement. *Brachylagus idahoensis* actually is the smallest known species, living or extinct, of the family Leporidae (rabbits and hares) in the world.

Despite its having been long considered a species of cottontail (*Sylvilagus*), a growing body of evidence has demonstrated that *Brachylagus idahoensis* is the sole surviving representative an ancient and primitive lineage that diverged from other rabbits and hares very early in the evolution of leporids. It has been suggested that the pygmy rabbit's closest living relative is the Sumatran rabbit, *Nesolagus netscheri*, and, while, in a sense, this may be true, it is likely that the relationship between *Brachylagus* and *Nesolagus* is quite distant and that their similarities are simply shared primitive characteristics not seen in more recently evolved leporid lineages. Thus it appears that *Brachylagus idahoensis* is phylogenetically unique, with no close living relatives, and it is one of the two most primitive of living leporids (see Alternative Taxonomy above).

The pygmy rabbit is behaviorally distinctive. It is the only naturally occurring leporid in America north of central México that regularly utilizes burrows of its own construction. Unlike other leporids, it scampers or scurries rather than bounding or leaping. Also unlike other leporids, which are typically silent except for distress vocalizations (screams) when captured by predators, the pygmy rabbit emits alarm or warning calls—buzzing, one- to seven-note squeals—when disturbed (Green 1978, Green and Flinders 1981). The selective advantage of such calls may be related to the aggregated nature of pygmy rabbit populations and the poor visibility in their dense sagebrush habitat (Green and Flinders 1981). These alarm calls suggest more complex social structure within pygmy rabbit populations than exist in other leporids. As Flinders (1999) commented:

> The fact that pygmy rabbits readily give alarm calls signifies a degree of socialization not known in other North American leporids. This social system has yet to be fully described.

The pygmy rabbit is an ecological specialist, its niche being remarkably narrow. It inhabits almost exclusively areas dominated by big sagebrush and having deep soils, and it feeds primarily on sagebrush. Flinders (1999) noted concerning the key position of the pygmy rabbit in the sagebrush ecosystem:

> In the big sagebrush habitat type, the pygmy rabbit must be considered a keystone species for the following reasons: first, it does not flourish in habitats dominated by other vegetative species; second, it exhibits unique fossorial behavior, and its extensive burrow systems are utilized by invertebrates and other vertebrates in the habitat type; and third, it offers terrestrial and avian predators a dependable food supply.

Human Significance

Food

It is likely that native peoples hunted and ate pygmy rabbits, for skeletal remains of *Brachylagus idahoensis* are very common in archaeological sites (e.g., Hogup Cave, Box Elder County, Utah [Durrant 1970]; Danger Cave, Tooele County, Utah; Gatecliff Shelter, Nye County, Nevada [Grayson 1981]). Although such evidence usually does not prove that the rabbits were eaten by the human inhabitants of such sites, pygmy rabbits are often among the most abundant animal remains found in archaeological sites (e.g., Grayson 1981, Table 1, p 117), and it is likely that they were eaten and that their skins were used as well.

Medical and Veterinary Concerns

Tularemia has been documented in *Brachylagus idahoensis*, and sylvatic plague and other bacterial infections are known in other species of rabbits and hares in western North America. Hall (1946, p 618) commented, concerning *Brachylagus idahoensis*: "General observations indicate that these rabbits are killed by tularemia." Tularemia is a zoonotic disease caused by the bacterium *Francisella tularensis*. Tularemia produces acute febrile illness and rarely death in human beings. Utah is among the American states with the highest incidence of human infection with tularemia.

Bacon and Drake (1958) examined 558 rabbits and hares of four species in eastern and central Washington and tested these lagomorphs for the presence of bacteria of medical or veterinary importance, but only one of the animals included in the study was *Brachylagus idahoensis*. Serum from this one individual tested positive against *Pasturella tularensis* (= *Francisella tularensis*, tularemia) antigen. Two mountain cottontails (*Sylvilagus nuttallii*) from the same location showed strong titres against *Pasturella pestis* (= *Yersinia pestis*, plague) antigen. These authors also found *Staphylococcus aureus* infections in four black-tailed jack rabbits (*Lepus californicus*) and *Nocardia asteroides* infection of the lung in one mountain cottontail. Noting that *Nocardia* from soil can cause pathological infections in animals, the authors commented: "As a burrowing animal the cottontail rabbit might be exposed to a lung infection with this organism." Although cottontails (*Sylvilagus*) are not burrowing animals, the pygmy rabbit does burrow, and the comment might correctly apply to this species.

White (1978, p 141) did not find disease to be an important factor in pygmy rabbit mortality in his study of the species in eastern Idaho.

Other diseases of medical and veterinary concern, including the rickettsial diseases Rocky Mountain spotted fever, Lyme disease, and murine typhus, are known to infect a variety of wild mammals in western North America and may occur in *Brachylagus idahoensis*.

Geographic Distribution

Overall Distribution

Brachylagus idahoensis occurs in eastern Washington, much of southeastern Oregon, southern and eastern Idaho, extreme southwestern Montana, parts of northeastern California, most of northern Nevada, western Utah, and extreme southwestern Wyoming. Its distribution in Washington is considered to be widely disjunct from the rest of its current range. There also are many local discontinuities within the main range of this species, as noted by Bailey (1936, p 111).

The current distribution of the pygmy rabbit is relictual. Prehistorically the species was more abundant and more widespread in eastern Washington (Grayson 1987, Lyman 1991), and its disjunct population there "may have become isolated at about 7,000 B.P." (Grayson 1987, p 371). The pygmy rabbit also prehistorically occurred somewhat farther west and much farther south and east than it currently does—well beyond the Great Basin. Late Pleistocene (i.e., Wisconsin) evidence of *Brachylagus idahoensis* has been found as far south and west as southeastern California (Kokoweef Cave, San Bernardino County, California [Grayson 1987, p 371]) and extreme southern Nevada (Tule Springs, Clark County, Nevada [Mawby 1967; Grayson 1987, p 370; Harris 1990, Figure 3]) and as far south and east as central New Mexico (Isleta Cave, Bernalillo County, New Mexico [Harris 1977, 1985; Russell and Harris 1986, p 636]), and the species is speculated to have occurred in northern Arizona (see Harris 1990, Figure 3).

Climatic conditions provided by the Wisconsin glaciation (Pleistocene) had enabled the pygmy rabbit to inhabit areas that are now parts of the Mojave and Chihuahuan deserts, as Harris (1990, p 223) has explained:

> Both cool summers and more-effective cold-season precipitation probably played a part in the notable expansion of present-day Great Basin forms. During the full glacial, the . . . fauna of southeastern New Mexico was most similar to that in southeastern Idaho now . . . . These conditions allowed expansion of such forms as *Brachylagus idahoensis* (pygmy rabbit) . . . .

However, the warmer and drier conditions that followed the Wisconsin glaciation had the reverse effect on Great Basin species such as the pygmy rabbit. Grayson (1987, pp 365, 370 [also p 372]), reviewing mammalian evidence from archaeological and paleontological sites in the Great Basin, concluded:

> The sharp decrease in the abundance of [this taxon, i.e. the pygmy rabbit] correlates well with the retreat of Lake Bonneville from the Gilbert shoreline at about 10,000 B.P. . . . .
>
> . . . [D]ata suggest that the abundance of *S[ylvilagus] idahoensis* was greatly reduced at the same time as Pleistocene Lake Bonneville fell to a level characteristic of modern times.
>
> It is clear . . . that pygmy rabbits declined in number throughout the sagebrush steppe in the Great Basin at about 7,000 B.P.

In addition to the considerable evidence of post-Pleistocene contraction of the range of *Brachylagus idahoensis*, there may have been range expansion in certain places. It has been suggested (Riddle and Choate 1986, p 254) that there has been “a recent intrusion of sagebrush steppe species from the Great Basin/Columbia Plateau into southwestern Wyoming,” including *Brachylagus idahoensis*. The pygmy rabbit was not discovered in Wyoming until 1978 (J. N. Jensen in Green and Flinders 1980b), where it was first collected in 1981 (Campbell et al. 1982). Flinders (1999) stated that “[t]here has been some rather recent range expansion by the pygmy rabbit into northeastern [i.e., Rich County in north-central Utah] and southeastern [i.e., Garfield, Wayne, and Piute counties in south-central Utah] Utah and southwestern Wyoming . . . ,” alluding to the reports of Jensen (in Green and Flinders 1980b), Campbell et al. (1982), Stephenson (1966), and Pritchett et al. (1987).

Pritchett et al. (1987) speculated that corridors of suitable sagebrush habitat along rivers and streams have provided various dispersal routes by which the pygmy rabbit reached the Awapa Plateau of Utah from the Great Basin. Green and Flinders (1980b) extended this idea to include fencerows and road margins as dispersal routes:

> The dense stands of big sagebrush growing adjacent to permanent and intermittent streams, along fence lines, and in borrow ditches next to roadways may be avenues of dispersal for these rabbits.

Janson (2002, p 6), too, thought that “[c]orridors of sagebrush along the Sevier and Bear River valleys probably allowed colonization of these areas [i.e., the Awapa Plateau and Rich County and adjacent Wyoming] by the rabbits.” However, an alternative hypothesis has not been mentioned by others: It is possible that recent detection of the pygmy rabbit in such locations as the Paunsaugunt and Awapa plateaus (of Garfield, Piute, Wayne, and Sevier counties, Utah) and in Rich County, Utah, and adjacent southwestern Wyoming is not indicative of recent dispersal and range expansion of this species into these areas. Instead, the pygmy rabbit may simply have escaped detection in these areas, although it is possible that the pygmy rabbit has recently expanded its range into Wyoming. The pygmy rabbit's occurrence on the Awapa and Paunsaugunt plateaus of south-central Utah, however, probably represents no more than relictualism and the failure to detect it in this area until recently, rather than the recent colonization suggested by Pritchett et al. (1987), since the species is known to have ranged prehistorically even much farther to the south and east (i.e., to central New Mexico, see above).

Utah Distribution (within Historical Times)

The pygmy rabbit was first reported in Utah in 1932, having been detected in the state in 1931 (Stanford 1932).

In the various shaded range maps of pygmy rabbit distribution that have been produced, three general distribution patterns for this species in Utah can be seen:

- a large, solid area in western Utah; i.e., basically the Great Basin portion of Utah (Durrant 1952, Hall and Kelson 1959, Green and Flinders 1980b, Hall 1981, Dobler and Dixon 1990, Flinders 1999),
- a C- or G-shaped semicircle in western Utah, with an open center and the gap in the C facing east (Janson 2002), and
- a J- or backwards C-shaped semicircle in western Utah, with an open center and the backwards C facing west (Janson 1946, Bradfield no date [1975], Gabler 1997, Katzner 1994)

The distribution of the pygmy rabbit in Utah, and elsewhere, is marked by discontinuities. Durrant (1952) was the first to note the absence of this species from a large area within its Utah range:

> [T]he range of these small rabbits in Utah is thought to include nearly all of the state that is within the Great Basin. The localities from which animals have been reported, however, are all marginal to the area formerly occupied by Pleistocene Lake Bonneville. This ancient lake is known to have greatly affected the distribution of many kinds of mammals, and the lack of specimens of *S[ylvilagus] idahoensis* from the basin of the lake, where suitable habitats are known to exist, would indicate that the lake has also been operative in the distribution of these rabbits, by excluding them from certain areas and by permitting them to reach other areas.

This is an appealing hypothesis, and it may explain some or much of the distribution of *Brachylagus idahoensis* in Utah. However, correspondence of current distribution of the pygmy rabbit with various shorelines (levels) of prehistoric Lake Bonneville is not very close (see Figure 1). At least as plausible as Durrant's Lake Bonneville hypothesis is the possibility that pygmy rabbit distribution in Utah and the extent of ancient Lake Bonneville are both correlated with another factor or factors, such as elevation and phytogeography.

Durrant (1952) also commented that the species "[p]robably occurs in intervening areas along the eastern margins of Pleistocene Lake Bonneville," supporting the backwards C-shaped Utah distribution presented by several recent authors (see references above) or perhaps another possibility suggested below. Janson (2002, p 6) echoed and expanded on Durrant's comment, stating: "Before settlement, the strip of land between the Wasatch Mountains and Great Salt and Utah Lakes probably supported pygmy rabbits but this area is so heavily developed now that no suitable habitat remains." (A minor lapsus in Durrant's text should be noted. The statement "*Range*.—Known only from Boxelder, Cache, and Iron counties" [p 88] overlooks important records in Juab and Utah counties presented in Durrant's map [Figure 24, p 89] and his lists of localities [p 89] for this species.)

Shaded range maps of course are intended as generalizations, and the qualification "within proper habitat" is implicit in all such maps. Nonetheless, shaded maps usually are intended to show connections between local populations or the potential for dispersal and gene flow between populations. The solid shaded distribution throughout western Utah is misleading because much of this shaded area is not inhabited by *Brachylagus idahoensis*. Although the two hollow, forward and backward C-shaped shaded Utah distributions may be somewhat more accurate in their indication of the uninhabited central part of the former lakebed, it is unknown whether the connectivity (in Utah) suggested by either of these (to the west or to the east, respectively) actually exists.

Another possibility for a shaded range map for the pygmy rabbit in Utah has not been seen but could be envisioned. It would combine both of the hollow distributions—the forward C and the backwards C—to produce a hollow ring or ellipse (i.e., a doughnut- or O-shaped distribution) in Utah. Such a map would of course suggest connectivity of distribution in Utah both east and west of the bed of Lake Bonneville. However, since it is unknown whether such connectivity exists, such a map would scarcely be an improvement over the solid distribution map for Utah. Janson's (2002, Figure 4) range map for the pygmy rabbit in western Utah in fact comes close to being a closed, O-shaped distribution pattern.

It should be remembered that Utah contains only part of the distribution of the pygmy rabbit and that this species ranges to the northeast (Wyoming), north (Idaho), and west (Nevada) of Utah. In examining the distribution of pygmy rabbit occurrences in Utah (Figure 1), the appearance of disjunction of populations in the northern parts of the state from those in southern Utah probably is not real, as would be apparent if occurrences in Nevada were also considered. Similarly, if occurrences in southeastern Idaho were taken into account, the seeming disjunction of populations in Rich County from those in Box Elder County would again be seen to be an artifact of looking only at the distribution within the boundaries of Utah. (Discussions, above, of the various shapes of the Utah distribution of the pygmy rabbit should also be understood as pertaining only to Utah, these shapes being at least partly the product of truncation of the distribution at the state boundaries and of being taken out of the context of the species' range-wide distribution.)

Both the shaded range maps of generalized pygmy rabbit distribution in Utah (such as those discussed above) and dot maps of its occurrences in this state (e.g., Figure 1) can produce mistaken impressions. Shaded range maps are hypotheses—interpretative generalizations of particulate data—and typically overestimate distributions of species. On the other hand, dot maps of known local occurrences are empirical and have many obvious advantages over shaded range maps, but they require much more information, are more laborious to produce, and typically underestimate distributions. Accurate determination of the actual occurrence of the pygmy rabbit in Utah is a theoretical ideal that can be progressively approximated though field surveys, with awareness that the species' distribution will continue to change as populations are extirpated and colonization of new areas occurs.

Known occurrences of *Brachylagus idahoensis* in Utah within historical times are presented in Table 1 and Figure 1. (In Utah, unlike some other states, all reported prehistoric occurrences of the pygmy rabbit in Utah are near modern ones and add little, if anything, to understanding of the current or past distribution of this species.)

Table 1. Locational Records for the Pygmy Rabbit, *Brachylagus idahoensis*, in Utah[a]

ID	Date	County	Land Ownership	UTM_X	UTM_Y
3418	29-Jun-1986	Washington	private	231455	4114834
9867	18-Mar-1961	Box Elder	private	260194	4621344
9868	18-Mar-1961	Box Elder	private	258942	4615556
9869	18-Mar-1961	Box Elder	private	258980	4618675
20236	14-Apr-1940	Box Elder	private	387101	4618289
19959	14-Apr-1940	Box Elder	private	388084	4619552
9872	1-May-1961	Box Elder	private	322910	4647638
9873	1-May-1961	Box Elder	private	316286	4651497
3415	before 1975	Garfield	BLM	388292	4220660
3410	1946	Box Elder	BLM	258384	4588195
19974	7-Jul-1983	Piute	BLM	398468	4237253
3412	1946	Iron	private	256763	4174892
3409	1946	Box Elder	Golden Spike Nat. Hist. Site	371073	4608368
19965	before 1975	Sevier	state	426620	4271513

19960	before 1975	Box Elder	BLM	343160	4548921
3417	30-Oct-1949	Washington	private	259874	4161554
9862	1958	Box Elder	private	289396	4648340
19963	1958	Box Elder	private	289593	4646444
19978	1946	Cache	private	411945	4644569
3043	18-May-1957	Sevier	Fishlake National Forest	436963	4266772
19968	before 1975	Piute	BLM	413932	4227809
19969	before 1975	Piute	BLM	412615	4228987
3040	before 1975	Beaver	BLM	261684	4251170
19966	1-Jun-1961	Garfield	private	379151	4190006
3041	3-Oct-1950	Box Elder	Sawtooth National Forest	279009	4638960
19983	1946	Iron	private	329954	4194131
3042	before 1975	Box Elder	private	301449	4651654
19971	before 1975	Sevier	private	390408	4270523
20235	1946	Iron	private	310181	4171735
13035	1946	Iron	private	307214	4156497
13036	1946	Iron	private	313439	4172539
13037	1946	Iron	private	311733	4172637
13038	1946	Iron	private	309005	4172775
879	1946	Iron	private	301905	4170858
880	1946	Iron	private	307795	4161323
881	1946	Iron	private	317812	4171800
19970	1946	Iron	private	306195	4167511
9858	winter 1994	Rich	BLM	483894	4602285
19961	winter 1994	Rich	BLM	477952	4595153
1900	before 1975	Garfield	Dixie National Forest	411907	4199904
9870	before 1975	Garfield	Dixie National Forest	411676	4187399
9871	before 1975	Garfield	Dixie National Forest	414126	4206265
19964	before 1975	Garfield	BLM	375361	4201025
1905	13-Jul-2002	Wayne	private	433968	4251137
1903	13-Jul-2002	Wayne	private	431478	4243515
9874	13-Jul-2002	Piute	private	423937	4247630
9875	13-Jul-2002	Piute	private	420475	4254337
9876	13-Jul-2002	Piute	private	422962	4243227
9877	13-Jul-2002	Wayne	private	432534	4247486
9878	13-Jul-2002	Wayne	private	439761	4253263
9879	13-Jul-2002	Piute	private	418407	4247827
9880	13-Jul-2002	Wayne	private	426219	4252013
9881	13-Jul-2002	Wayne	private	432643	4257090
9882	13-Jul-2002	Wayne	private	441339	4247239
9883	13-Jul-2002	Wayne	private	433366	4252977
9884	13-Jul-2002	Wayne	private	444012	4250643
1415	13-Jul-2002	Piute	private	425564	4238018
1416	13-Jul-2002	Wayne	private	427453	4236730
3411	1946	Box Elder	private	348219	4647548
9860	11-Aug-1951	Tooele	private	249616	4434729

9859	11-Aug-1951	Tooele	private	245313	4435835
9863	before 1975	Millard	state	260810	4294061
9864	before 1975	Millard	state	260975	4284880
3413	1946	Iron	BLM	283728	4197458
19962	1994	Rich	BLM	480244	4628489
19975	1946	Box Elder		389029	4635919
19976	1946	Juab		249535	4396868
19977	1946	Box Elder	private	334392	4647666
19979	1946	Iron		307204	4177636
19980	1946	Iron	BLM	322543	4200197
19981	before 2002	Box Elder	private	272876	4643891
19982	before 2002	Iron	BLM	323068	4182348
19984	before 2002	Juab	BLM	249115	4384657
19985	before 1946	Utah		426353	4456848
19986	mid-1980s	Box Elder		350403	4635720
20417	11-Jul-2003	Rich		479113	4573407
20418	11-Jul-2003	Rich		479067	4573283
20419	11-Jul-2003	Rich		479223	4573255
20420	11-Jul-2003	Rich		479527	4573225
20421	11-Jul-2003	Rich		479188	4573143
20422	11-Jul-2003	Rich		479408	4573022
20423	11-Jul-2003	Rich		479397	4572974
20424	11-Jul-2003	Rich		479462	4572972
20425	11-Jul-2003	Rich		479514	4572978
20426	11-Jul-2003	Rich		479460	4572943
20427	11-Jul-2003	Rich		478992	4572673
20428	11-Jul-2003	Rich		479006	4572567
20429	11-Jul-2003	Rich		479038	4572585
20430	11-Jul-2003	Rich		479059	4572617
20431	11-Jul-2003	Rich		479566	4572616
20432	11-Jul-2003	Rich		479550	4572597
20433	11-Jul-2003	Rich		479549	4572536
20434	11-Jul-2003	Rich		479582	4572413
20435	11-Jul-2003	Rich		479364	4572347
20436	11-Jul-2003	Rich		479150	4572290
20437	9-Jul-2003	Rich	private	486537	4631622
20438	18-Jun-2003	Rich		486625	4633170
20439	1-Apr-2003	Rich	BLM	486158	4623864
20440	1-Apr-2003	Rich	BLM	488870	4635034

[a]Identification (ID) numbers for occurrences are from the Utah Natural Heritage Program database. Universal Transverse Mercator (UTM) coordinates are for centra of the occurrences in zone 12, using North American Datum 1927 (NAD 27).

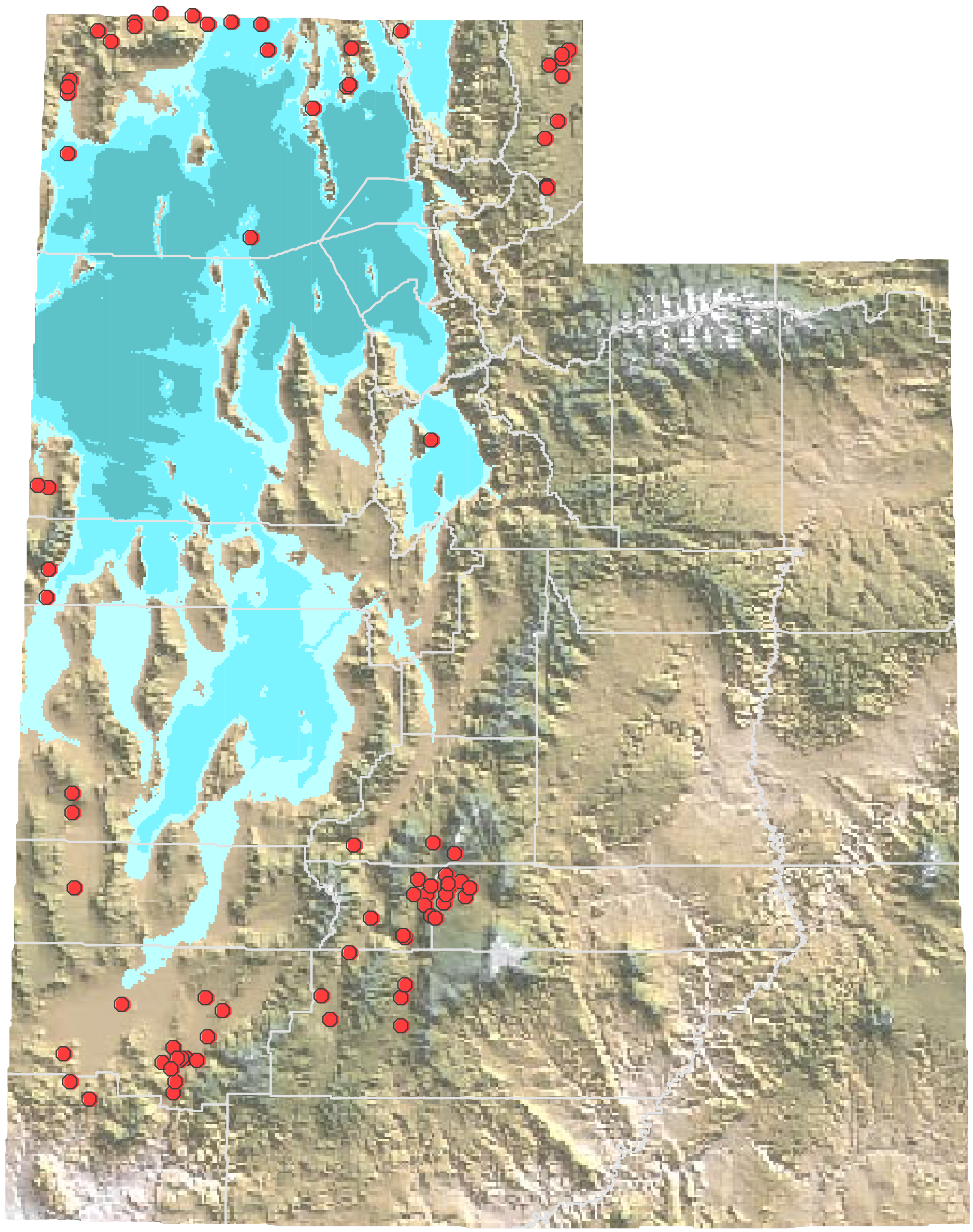

Figure 1. Known occurrences of the pygmy rabbit, *Brachylagus idahoensis*, in Utah (red dots) within historical times. Blue shading represents three levels of prehistoric Lake Bonneville showing Gilbert (innermost), Provo (middle), and Bonneville (outermost) shorelines.

Life History and General Biology

Reproduction

Induced ovulation, in which copulation stimulates ripening of ovarian follicles and ovulation, occurs generally in leporids. Presumably induced ovulation occurs in the pygmy rabbit, although it has not been demonstrated in this species.

Understanding of various aspects of the breeding biology of the pygmy rabbit has been difficult to achieve. Different research methods have produced differing kinds of data. These different lines of evidence have led to differing interpretations and to discordant conclusions (or hypotheses) about the length of gestation, the number of litters per year produced by a female, and the location of the natal site. The various studies and the differing opinions and conclusions reached by authors are reviewed below, followed by a summary of the conclusions based on the best evidence.

Bailey (1936) reported concerning the pygmy rabbit in Oregon:

> . . . [T]he number of young at birth are shown by sets of embryos to be usually 5 to 8. There is some evidence that two litters are raised in a season, but little is known of the actual breeding habits.

Janson (1940, p 30) reported a male pygmy rabbit collected on 30 December in southern Utah (near Cedar City) that was in breeding condition, but other males and all females taken at this time were reproductively quiescent. In northern Utah (Box Elder County), a male collected on 22 January was in breeding condition while a female obtained on that date was not. Females collected on 4 March were in reproductive condition, and two "contained embryos only a few days old." In southeastern Idaho a male collected on 19 February was in breeding condition as were females taken on 6 March and 17 March, none of which were yet pregnant. From these findings Janson (1940) concluded that male pygmy rabbits become "physiologically ready" for breeding before the females, a reproductive pattern that is seen in many animals. Janson (1940) thought that pairs of adults associate only during breeding and that "[t]his association probably continues only for a few days while copulation occurs, and the male are then possibly driven away." He observed: "After the birth of the young the males associate with the females again . . . ," possibly " . . . only for a few days while breeding for the second litter." Janson (1940) found that "at least two litters are raised in a season." Breeding for the first litter at a particular locality appeared to be synchronous, occurring within a period of a few days, but breeding for the second litter seemed to be temporally more variable. He noted: "Mating for the second litter occurs commonly within a few days after the birth of the first litter." Janson (1940) also thought that an unusually mild winter and early spring may have caused pygmy rabbits to breed earlier than usual. He found that in pygmy rabbits in southern Utah breeding occurred “about the middle of February.” In northern Utah “breeding for the first litter occurred about the first week in March, or about two weeks later than in Southern Utah, and the young are born during the last part of March and first of April.” In southeastern Idaho “breeding occurred during the last of March or first of April, about a month later than in the Blue Springs area [of northern Utah].” Though noting the lack of evidence for later litters, he mentioned the possibility of a third and even a fourth litter, but pointed out that pygmy rabbits “do not as a rule breed late into the summer” as evidenced by the fact that all young seen in late summer approximated adults in size. His counts of embryos of 11 gravid females ranged from four to eight (mean, derived from his data, 6.09) and commented: “There seems to be a tendency for the first litter to be small (4 to 6) and the second to be large (7 to eight).” Although unsuccessful in his attempts to find maternity nests, Janson (1940, p 35) hypothesized:

> The young are probably born in a nest, carefully hidden in some underground burrow. Several burrows from which lactating females were obtained were completely excavated, but no trace of young was found. It may be that the entrance to the nest chamber is plugged with earth, and thus apt to be missed by anyone excavating the main tunnel.

Janson (1946, p 69) reported: “The average number of foetuses for 14 pregnant females is 5.93 with extremes of four and eight.” (It is likely that these 14 included the four females that were from Utah that were among the 11 gravid females, from Utah and Idaho, considered earlier by Janson [1940]). Janson (1946, p 69) commented: “It is not known whether young are born in burrows or nests.”

In Idaho Wilde (1978) found males that were in reproductive condition from mid-December until early or mid-June, all males being so from mid- or late January until the beginning of June (pp 58–61). All females appeared to have copulated by early or mid-March and, in two of the three years of his study, to have ceased lactation by the end of June or beginning of July (p 61). He noted that change in reproductive condition was constant and uniform in males and concluded that in males reproductive activity is controlled by seasonal changes in photoperiod (p 120). In females, however, timing of reproduction varied across years, and Wilde suggested that availability of new vegetative growth determined timing of reproduction in females (p 121). Using distinguishable morphometric size categories, Wilde recognized three cohorts of juveniles each year (p 69) and concluded that females produced three litters each year (p 128). Based on trapping of females during breeding season, observations of young above ground, and the failure of others to find nest chambers in excavated burrows, Wilde (pp 114–115) hypothesized that young are not born in burrows but are scattered above ground under clumps of sagebrush.

Further developing a hypothesis that he had earlier proposed (Wilde 1978, pp 133–134), Wilde (1981) found that sex ratios of young captured changed as the spring season progressed, shifting from higher percentages of female offspring early in the season to lower percentages of females born late in the season. In a warmer year, with breeding commencing earlier, mostly female young were produced, and in a cooler year, with later onset of reproduction, most offspring were male. A warm winter and spring results in earlier snow melt, earlier greening of vegetation, and earlier reproduction in pygmy rabbits, but it may also portend drought, poorer food resources, and lower survivorship of rabbits later in the season. Wilde suggested that, since climate not only appears to determine female reproduction and time of first breeding in the spring but also may be an indicator of future conditions such as drought, pygmy rabbits may "know" the likelihood of drought and may be able to adjust sex ratios in favor of females in drought years, thus facilitating recovery of the population after the drought.

Fisher (1979, p 16) estimated the gestation period of pygmy rabbits in southeastern Idaho to be 39 days. His study showed breeding to be synchronous in this species. He found that males appeared to be reproductively active February through May. He calculated conception dates ranging from 27 February through 30 April (Table 2, p 27); however, in calculating these dates, he assumed gestation to be 39 days, which apparently is incorrect (actual gestation being ~24 days, as discussed below). Fisher found that many females produced two litters each spring. He found no evidence of third litters in Idaho, although he did consider third litters to be a possibility (albeit a low one). Noting that the breeding season appears to begin 3–4 weeks earlier in Utah (Janson 1946), Fisher suggested that the breeding season may be longer in Utah, resulting in third litters. Fisher (1979) found the mean litter size to be 6.0, the range being 4 to 8. He found no evidence of either partial or total resorption of litters and concluded that postimplantation mortality in the pygmy rabbit is low in contrast to other leporids that have been studied in North America. However, mean number of ova shed per female was 6.4, suggesting an average of 6.2% preimplantation loss. Despite the fact that he found no direct evidence of the production of third litters, Fisher calculated theoretical maxima of 17% and 29% of females, in the 2 years of his study, producing third litters. This resulted in the theoretical potential of 2.2 and 2.3 litters per female in the two years of his study. Fisher concluded that the theoretical average number of young per female per year was 13.0 and 13.7 for the two years that he considered, which is lower than the annual production of young reported in several species of *Sylvilagus* in America and suggests lower fecundity in the pygmy rabbit than in other North American rabbits.

Gahr (1993), who studied the pygmy rabbit in Washington, found that males were reproductively active from January through June and reproductively inactive July through November (pp 24, 40), but she had no data for December. She captured lactating females from March through September and five pregnant females—two in February and one each in March, July, and August (p 24). She also reported (p 24): "Juveniles were caught in May, June, and July, with one juvenile trapped in September." Although her observations of reproductive condition of males agrees well with studies in Utah (Janson 1946) and Idaho (Wilde 1978), times of pregnancy and lactation observed in females and captures of juveniles "indicate that the period of reproductive activity is longer in Washington" (p 41). Her observations also suggest the possibility of three litters per female per year in Washington. Commenting on the longer reproductive period, extending later into the year, Gahr (p 41) hypothesized: " . . . [I]t may be that milder weather in eastern Washington compared to the Great Basin does not require the juveniles to be as large to survive winter." She also reported that one female that died in a trap was gravid, carrying three embryos. As has been the experience of other investigators, she was unable to locate any maternity nests.

Flinders (1999) noted uncertainties concerning gestation and natal site in the pygmy rabbit and offered hypotheses:

> The gestation period has not been documented, but is probably 27 to 30 days. . . . Although pygmy rabbits are unique among North American leporids in their construction of burrows, no nesting chambers have been found in the few burrows excavated. This leads to speculation that the female pygmy rabbit may make a nest similar to those used by cottontail rabbits (*Sylvilagus*), a shallow hole at the ground surface that is lined with vegetation as well as hair plucked from her underside, give birth to altricial young in this nest, and crouch over the nest to nurse them.

Janson (2002, p 25) reviewed reproductive data for the pygmy rabbit and concluded that "breeding is limited to late winter and spring." Although Fisher (1979) had estimated gestation in the pygmy rabbit to be 39 days and Flinders (1999) suggested that it is probably 27 to 30 days (which would be similar to the smaller species of *Sylvilagus*), Janson (2002, pp 25–26) stated:

> The gestation period for the pygmy rabbit was not known until 2001–2002 when a captive breeding program initiated by the Washington Department of Fish and Wildlife revealed a gestation period of about 24 days (David Hays, personal communication). This would place first litter birth dates early to mid-March in Iron County [Utah], early April in the Blue Spring Hills [Box Elder County, Utah], mid to late April near Dubois [Idaho] and May and June in Montana.

Noting Stephenson's (1966) report of a gravid female with five small embryos near Panguitch, Garfield County, Utah, in June, Janson (2002, p 26) commented:

> This area is only slightly farther north than Cedar City [Iron County, Utah], but is at least 335 meters higher. The higher altitude and later development of green vegetation may be the reason for later breeding.

Discussing the long-debated mystery concerning where pygmy rabbits give birth to their young—particularly Wilde's (1978) hypothesis that young are born above ground and not in burrows (but not directly addressing Flinders' (1999) hypothesis of a special, vase-shaped natal "hole" like those of cottontails)—Janson (2002, p 27) reported:

> . . . [B]reeding observations of captive [pygmy] rabbits at the Oregon Zoo in 2001 and 2002, showed that the young are born naked in a nest of dry grass constructed by the female in a tunnel branching from the main burrow, or more commonly, in a separate burrow; and that the young leave the nest about 14 days after birth (David Hays, personal communication).

Although these observations apparently resolve the questions of natal site and gestation period in the pygmy rabbit, independent corroboration of these findings is desirable.

The information reviewed above concerning reproduction in the pygmy rabbit can be summarized:

- mating occurs in late winter and spring;
- breeding is synchronous (especially for first litters of the season)
- breeding begins earlier (1) at lower latitudes, (2) at lower elevations, and (3) in warmer years—in response to earlier availability of high-quality food resources in these circumstances;
- males become reproductively ready before females;
- reproductive activity in males appears to be triggered by increasing photoperiod, reproductive activity in females by spring availability of high-quality plant foods;
- breeding typically begins in early to mid-February in southern Utah and in early March in northern Utah, and first litters are born in early to mid-March in southern Utah and in early April in northern Utah, with reproductive activity in Utah ending by the end of June or early July;
- usually two or three litters per female are produced each year (probably only two in Utah);
- litter size is typically 4 to 8, average ~6, second litters usually being somewhat larger than first litters, perhaps because of increased food quality and availability;
- sex ratio of young born changes as season progresses, the proportion of females being higher in earlier litters;
- gestation is ~24 days;
- young are altricial and are born in a subterranean nest, usually in a separate nest burrow, which they leave after ~14 days;

Food Habits

Like other leporids, pygmy rabbits produce two kinds of fecal pellets, hard (or dry) pellets and soft (or moist or caecotrophic) pellets. Hard pellets are waste, like the feces of other animals, and are not eaten. The soft pellets, however, are produced by the caecum and are reingested, being taken directly from the anus and swallowed whole, without chewing. Reingestion of soft pellets allows maximum utilization of difficult-to-digest foods, facilitating absorption of plant nutrients and of certain B vitamins produced by bacteria in the caecum.

The foods of the pygmy rabbit have been studied, and its specialized diet, consisting mostly of sagebrush, is well known.

Bailey (1936, p 112) reported summer foods in Oregon

> At Crane, Oreg., in July 1916, when these little sage rabbits were abundant, many stomachs were examined and all were found filled, mainly with green leaves of sagebrush (*Artemisia tridentata*). . . . A few green leaves and stems of rye were found with the sage leaves near a grainfield. . . . At Malheur Lake in August 1920 they had been feeding on *Artemisia* and *Tetradymia* leaves, a little pigweed (*Chenopodium*), and other little green plants and grasses. In captivity, they ate rolled oats, three species of *Chenopodium*, *Atriplex nuttalli*, *Sarcobatus*, *Dondia*, dock, nettles, many grasses, including saltgrass, cabbage, cantaloup [*sic*], and apple parings, the last three the most eagerly.

Janson (1940, pp 23–25) reported foods of the pygmy rabbit in Utah and southeastern Idaho. He examined stomach contents of 32 pygmy rabbits collected in winter and spring (21 from Utah, 11 from Idaho). Sagebrush (*Artemisia tridentata* and *Artemisia tripartita*) was the main food, being found in all 32 stomachs, and only three of 22 winter-collected stomachs contained any other food, which was dry grass. Spring foods in addition to sagebrush were "grass (green)" (in all 10 spring-collected stomachs) and "broad-leaved herbs" (in four of 10 stomachs). Janson (1940, pp 24, 25) commented: "It is probable that sagebrush constitutes about 90 to 95 per cent of the winter food of the [pygmy] rabbits in the three areas studied. Leaves and twigs up to three-sixteenths of an inch in diameter are consumed. . . . In spring stomachs taken, grasses made up the bulk of the contents, while green forbs were a minor item." From field observations, Janson (1940) listed eight other plants "eaten to some extent during the winter": *Chrysothamnus nauseosus* (big rabbitbrush), *Chrysothamnus viscidiflorus* (little rabbitbrush), *Tetradymia canescens* (spineless horsebrush), *Agropyron inerme* (smooth wheat grass), *Elymus condensatus* (giant wild rye), *Agropyron spicatum* (spiked wheat grass), and "small amounts of" *Salsola pestifer* (Russian thistle), and *Amaranthus* sp. (pigweed) (plant names are those used by Janson 1940). He also reported that captive individuals "ate almost anything that was put into the pen," listing 19 plant foods.

Janson (1946, p 47) reported stomach contents of 15 pygmy rabbits from Utah (possibly the same as most of those that he reported earlier [Janson 1940]). All 15 stomachs contained sagebrush, 10 contained "grass & sedge," and one contained "unidentified weeds." From field observations he reported (p 53) that "[w]inter food consists principally of sagebrush" and small amounts of

Chrysothamnus nauseosus (rabbit brush), *Chrysothamnus viscidiflorus* (little rabbit brush), *Tetradymia canescens* (horse brush), *Salsola pestifer* (Russian thistle), *Amaranthus* sp., *Agropyron inerme* (smooth wheat grass), *Agropyron spicatum* (spiked wheat grass), *Elymus condensatus* (giant wheat grass) (plant names are those used by Janson 1946). Spring foods were "chiefly grasses, and some forbs." The plants that were eaten in late summer were *Atriplex pusilla* (small scale), *Atriplex canescens* (four winged salt bush), *Agropyron smithii* (winter wheat grass), *Artemisia tridentata* (sage brush), *Spharalcea* sp. (globe mallow), and *Gutierrezia sarothrae* (snake weed) (Janson 1946, p 54).

Bradfield (1975) studied the pygmy rabbit in southeastern Idaho and reported incidental observations on feeding (p 25):

> Pigmy rabbits were directly observed feeding on only two different species of plants, big sagebrush [*Artemisia tridentata*] and beard tongue (*Penstemon sp.*). Of these, feeding on beard tongue was observed only once, while feeding on sagebrush was observed on several occasions. The presence of pellet groups and clipped ends of plants indicated that the pigmy rabbit also fed on Sandberg blue grass [*Poa secunda*], squirrel-tail [*Sitanion hystrix*], and rabbit brush [*Chrysothamnus nauseosus*].
>
> Snow tunnels, large pellet masses . . . and condition of shrubs . . . indicated that sagebrush is fed upon almost exclusively in the winter.

Wilde (1978, pp 46–58) examined pygmy rabbit food habits in southeastern Idaho using fecal pellet analysis and found that more than 60% of all samples were composed of 90% or more sagebrush. In winter the diet was almost entirely sagebrush. In summer sagebrush made up a little more than 60% of the diet, with grasses and, to a lesser extent, forbs accounting for the remainder (Wilde 1978, Figure 10, p 51). Four grasses were important in the summer diet: *Agropyron* sp. and *Poa* sp. in early summer and *Elymus* sp. and *Stipa* sp. later in summer. Although Wilde (1978, Table 6, p 48) identified 30 species (or kinds) of plants in pygmy rabbit fecal pellets, most of these were represented in only trace amounts. In Wilde's (1978, p 49) study, "[f]orbs and non-sagebrush shrubs contributed little to the diet of pygmy rabbits."

Green (1978) (published as Green and Flinders 1980a) also studied pygmy rabbit diet in southeastern Idaho using fecal pellet analysis, and his results corroborated those of Wilde (1978). He found that sagebrush (*Artemisia* spp.) was the main food of the pygmy rabbit throughout the year, representing 51% of the diet in summer and 99% in winter. In summer, grasses (mainly wheatgrass, *Agropyron* sp.) represented 39% of the diet and forbs 10%, and there were strong preferences for wheatgrass (37 times as frequent in diet as in habitat) and Nevada bluegrass, *Poa nevadensis*, (14 times its relative abundance). Over the course of the year, the diet consisted of 67% shrubs (mainly sagebrush), 26% grasses, and 6% forbs.

The main food of pygmy rabbits, sagebrush, contains large amounts of monoterpenoids, which are volatile oils. Monoterpenoids have antibacterial properties and have been thought to reduce microbial digestion in ruminants and in some cases even to cause death. White et al. (1982) conducted captive feeding trials in which pygmy rabbits were offered two subspecies of big sagebrush (*Artemisia tridentata* sspp. *tridentata* and *vaseyana*). They found no significant feeding preference by pygmy rabbits for one subspecies over the other and no significant correlation between monoterpenoid content of sagebrush and dietary preference of pygmy rabbits. (Although the rabbits did show preferences for different source populations of sagebrush, these preferences were highly variable through time and apparently were inexplicable.)

White et al. (1982) examined stomach contents of 10 wild-collected pygmy rabbits from southeastern Idaho, and these stomach ingesta contained 97% big sagebrush. However, monoterpenoid content of the stomach ingesta was 77% less than in samples of big sagebrush from the locations where the rabbits were taken. The authors hypothesized that this major loss of monoterpenoids occurred during mastication. Testing this hypothesis using a captive pygmy rabbit in an air-tight chamber, they found that 12 times more monoterpenoids were released into the air of the chamber during rabbit feeding trials than in control tests of big sagebrush only, thus supporting their hypothesis.

Gahr (1993), studying the pygmy rabbit in Washington, reported field observations of feeding from March through September (mostly May and June); however, she cautioned that her “dietary data were incidentally obtained” and that her “list of food items is not a complete list, but consisted only of those items observed [and identified]” (p 43), and she had feeding observations for only half of the year (March through September). Of 53 observations of feeding in which the foods were identified, 45% of observations of consumed food were grasses, 19% were forbs, and 36% were shrubs (Gahr 1993, Table 1.4, p 27). She noted (p 25): “Sage was part of the diet in all months [i.e., March–September], except September when only one feeding observation was obtained.” She listed (Table 1.3, p 26) 13 plant species that were consumed—six species of grasses (*Agropyron spicatum*, *Agropyron desertorum*, *Stipa comata*, *Stipa thurberiana*, *Oryzopsis hymenoides*, and *Bromus tectorum*), five species of forbs (*Amsinckia* sp., *Comandra umbellata*, *Achillea millefolium*, *Orthocarpus* sp., and *Brassica* sp.), and two species of shrubs (*Artemisia tridentata* and *Chrysothamnus viscidiflorus*)—and did not find a difference in diet between grazed and ungrazed areas (p 25).

In a study of the winter ecology of the pygmy rabbit in southwestern Wyoming, Katzner (1994, p 109) reported:

> During 96.5 hours of observation, we never saw a pygmy rabbit eat any plant but [big] sagebrush (*Artemisia tridentata*) in winter 1993. In 1994, we saw them eat other plants (Shadscale, *Atriplex* spp. and rabbitbrush, *Chrysothamnus* spp.) on several occasions.

Katzner (1994, p 109) also reported that throughout the winter he observed pygmy rabbits eating snow.

Predators and Parasites

A number of avian and mammalian predators are known or are speculated to prey on pygmy rabbits.

Janson (2002, p 28 [also 1946, p 89]) stated: “Weasels seem to be the principal predators of pygmy rabbits, being able to follow them into burrows.” (Presumably Janson’s discussions of weasels refer mostly, if not entirely, to the long-tailed weasel.) Janson also reported predation on pygmy rabbits by great horned owls (Janson 1946, p 90) and by a Cooper’s hawk (Janson 2002, p 29). Janson (2002) commented: “Badgers dig up many pygmy rabbit holes, but as the rabbits are able to escape through other entrances, the badgers probably have limited success catching them.”

In southeastern Idaho Gaufin (unpublished 1939 data, reported by Janson 1946, Table 16, p 86; 2002, Table 4, p 29) found remains of pygmy rabbits in feces and castings (regurgitated pellets) of eight species of predators. These were the coyote and seven raptors—two owls (short-eared and burrowing) and five diurnal raptors (golden eagle, northern harrier, red-tailed hawk, Swainson’s hawk, and prairie falcon). Frequencies of pygmy rabbit remains in the scats and pellets of these eight species of predators ranged from 3.23 to 33.33% (mean = 14.97%); however, for the different species of predators, sample sizes varied from 3 to 365 scats or pellets, and the frequencies of pygmy rabbit remains in the smaller samples may be quantitatively less meaningful.

MacCracken and Hansen (1982) found pygmy rabbit remains in the scats of coyotes in southeastern Idaho during all seasons, especially in spring.

Other reported predators of the pygmy rabbit include the long-eared owl (Davis 1939, Borell and Ellis 1943), the northern harrier (Wilde 1978, p 143), and the bobcat (Gashwiler et al. 1960). Wilde (1978, pp 142) also reported predation on a trapped pygmy rabbit by a coyote.

Yet other species have been speculated to prey on pygmy rabbits, such as the American badger (Wilde 1978, p 142; Green and Flinders 1980b). To the list of speculated predators could be added a few snakes (especially the gopher snake and the western [or Pacific] rattlesnake), other hawks (such as the rough-legged hawk and especially the ferruginous hawk), other owls (e.g., the barn owl), perhaps the common raven, and foxes, especially red fox and the kit fox.

Pygmy rabbits are known hosts of various parasites, both internal and external (reviewed by Janson 1946, 2002, Green and Flinders 1980b). The most commonly reported ectoparasites of pygmy rabbits include mites, ticks, fleas, and bot flies (see Janson 1946, 2002; Wilde 1978; and Green and Flinders 1980b for details such as species). Reported endoparasites are nematodes (Janson 1946). Many researchers (e.g., Davis 1939; Janson 1946, 2002; Wilde 1978; and Wilde et al. 1976) have observed pygmy rabbits with such heavy flea infestations that the fleas caused the rabbits' fur to move in a waving motion. Such heavy parasite loads potentially could cause the death of the hosts.

Habitat

General observations of pygmy rabbit habitat by various authors (e.g., Merriam 1891, Bailey 1936, Grinnell et al. 1930, Borell and Ellis 1934, and Hall 1946) have noted the restriction of the pygmy rabbit to areas with dense shrub cover consisting mainly of tall sagebrush (*Artemisia* spp.).

Green and Flinders (1980a, p 141), in a study in southeastern Idaho, concluded that "cover appeared to be the critical habitat feature selected by the pygmy rabbit." They found that sites inhabited by pygmy rabbits had significantly greater percent woody vegetation cover and woody vegetation biomass than did sites that were not inhabited by this species. Mean height of shrub cover was also higher for inhabited sites (56 cm) than for uninhabited sites (25 cm). Although total mean grass and forb biomass was similar at inhabited and uninhabited sites, grass biomass averaged lower and forb biomass averaged higher on inhabited sites than on uninhabited sites. Three shrub species accounted for almost all of the woody vegetation, both as cover and as biomass, present on inhabited sites: big sagebrush (*Artemisia tridentata*), bitterbrush (*Purshia tridentata*), and threetip sagebrush (*Artemisia tripartita*). (Four other woody species were present in very low frequencies.)

Weiss and Verts (1984), working in Oregon, found evidence of pygmy rabbits at 51 of 211 sites considered potentially suitable for this species. They compared soil and vegetation components of 13 of the areas occupied by pygmy rabbits with 21 areas that were not inhabited by pygmy rabbits but were adjacent to inhabited sites. They found that mean shrub height (84.4 cm), mean shrub cover (28.8%), mean soil depth (51.0 cm), mean soil strength of surface (0.8 kg/cm^2), and subsurface (3.8 kg/cm^2) horizons were significantly greater at sites occupied by pygmy rabbits than at the adjacent unoccupied sites. However, percent basal area of perennial grasses, density of annual grasses, density of forbs, and cryptogam cover at inhabited sites were not significantly different from uninhabited sites. Also, except for percent clay of subsurface soils, components of soil texture were not significantly different between occupied and unoccupied sites. Weiss and Verts (1984) concluded that the affinity of pygmy rabbits for areas having greater shrub cover, shrub height, soil strength, and soil depth may be related to availability of forage, security from predation, and ease of burrow construction. Although three subspecies of sagebrush (*Artemisia tridentata*) were present at and near sites inhabited by pygmy rabbits, they did not find a correlation between presence of pygmy rabbits and a particular subspecies of sagebrush.

Gahr (1993, Tables 2.8 and 2.9 and Figure 2.8, pp 78–80), in eastern Washington, found very highly significant habitat differences between pygmy rabbit burrow sites and randomly selected sites within areas used by pygmy rabbits. Height of sagebrush averaged higher (82.0 cm), percent sagebrush cover averaged greater (32.7%), and percent bunchgrass cover averaged less (3.2%) where pygmy rabbit burrows were located. Microtopography also was significantly different, burrows sites being associated with mounds and with slopes along drainages rather than with plateaus, hillsides, or flats between mounds.

Katzner (1994; also Katzner and Parker 1997), who studied the pygmy rabbit in southwestern Wyoming in winter, found habitat characteristics that were very similar to those obtained by Green and Flinders (1980a) in their summer study in Idaho. Katzner (1994) reported:

> Vertical density and diversity of the habitat were directly related to pygmy rabbit use. Highest use areas had taller, more dense shrub biomass and more standing vegetation, with a thick canopy covering a large proportion of the area. These areas were characterized by basin big sagebrush and extensive vertical structure profiles.

Katzner (1994, p 53) also noted the importance of dead shrubs and dead parts of shrubs, which tend to be lower than the living parts. He observed that “the dead layer provides structure at lower heights” concluded that this dead layer “may contribute to predator protection and the maintenance of subnivean sites for burrowing.”

Gabler (1997; also Gabler et al. 2001), in a study of pygmy rabbit habitat in southeastern Idaho, performed habitat ordination and created a Geographic Information System (GIS) predictive model and a Habitat Suitability Model (using Principal Components Analysis of habitat variables) for this species. Most of her results corroborated those of other workers. She found greater density and cover of big sagebrush (*Artemisia tridentata*), greater cover and density of all living shrubs, and greater forb cover in “suitable pygmy rabbit areas.” However, unlike others, she did not find significant differences in shrub height between any of the five site types that she measured, including areas not utilized by pygmy rabbits. Also unlike previous studies, she found higher percentages of sand and lower percentages of clay at suitable areas than at non-use sites.

Spatial Biology and Movements

Janson (1940, pp 29–30) reported (apparently for a study area in Box Elder County, Utah):

> In January and February, the radius of activity of any rabbit was rarely over 30 yards, with the burrow as the center. Where several burrows were in the same vicinity and not separated by more than about 50 yards, trails connected them. The radius from any one hole was then considerably extended; however tracks were even then not found more than 30 yards from a hole.
>
> On March 3, all of the snow had melted, except a light mantle fallen the previous night. This showed a considerable increase in activity since the preceding visit to the area, and a greater radius of activity. This greater activity was believed to be a result of mating activities taking place at that time.

Janson (1946, p 75), discussing the pygmy rabbit (primarily in Utah), commented:

> Home range is very small. During the winter, track in the vicinity of holes indicates that the radius of activity was only about 30 yards from the burrows. In the spring, however, with the melting of the snow and the beginning of breeding, the radius of activity was lengthened somewhat.

In southeastern Idaho Bradfield (no date [1975]) observed tracks and tunnels of pygmy rabbits in snow. He noted that in winter pygmy rabbits utilize tunnels through snow and that the openings of the snow tunnels were clustered over small areas (0.017, 0.019, and 0.035 ha) (Bradfield no date [1975], p 15). He commented (p 20): "most of the movement in winter was confined to the area of the clusters of snow burrows and apparently was for the purpose of securing food." However, he also occasionally found tracks on the surface that led from the clusters of snow tunnels to sagebrush or to other burrows, these tracks covering distances of ~75, ~80, and ~100 m. Two marked individuals that "appeared to be immature males" were each recaptured twice (p 22): "The greatest distance either rabbit traveled between trapping periods was 54.9 meters; the shortest distance was 15.2 meters [which was the minimum distance between traps in his grid]."

Wilde et al. (1976, p 95) reported movements in Idaho in December and January of an adult female pygmy rabbit in Idaho that they fitted with a radiotelemetry collar. They detected the animal 10 times during the 2-month period and reported that "[t]his rabbit . . . has exhibited extreme fidelity to her burrow, and has only once been located more than 20 m from the burrow of original capture (in a neighboring burrow (Table 2)." Their Table 2, however, indicates that this animal twice was detected 75 m from the site of original marking. Even though some error—perhaps only the number of times (once versus twice) that she was detected >20 m from the original site—exists in either the text or the table, their point that this animal stayed remarkably close to the original burrow remains unchanged. Wilde et al. (1976) continued: " . . . [T]racking in the snow suggests that travel occurs between burrows within a colony, and this is confirmed by trapping of marked individuals. Table 3 contains movement data on three selected individuals and illustrates the amount of local movement which seems to be occurring." Their Table 3 shows distances of up to 500 m between original capture sites and locations of recapture.

Wilde (1978, p 97) followed 10 of 16 pygmy rabbits equipped with radiotelemetry collars for a total of 490 transmitter days but reported only: "Animals showed very restricted movements and did not appear to leave the area of capture while collars transmitted."

Green and Flinders (1979) reported homing by a juvenile female pygmy rabbit captured in Idaho. The pygmy rabbit escaped from a holding pen and was recaptured 211 days later only 200 m from the site of original capture but 2.5 km from the pen in which she had been held. They mentioned that the maximum movements that they had previously determined for two pygmy rabbits tracked in snow were two one-way distances of 140 and 450 m. Also, using McNab's (1963) method of predicting home range size in mammals from basal metabolism and body size, these authors calculated expected home range in pygmy rabbits to be ~0.8 ha.

Gahr (1993), in eastern Washington, determined home range sizes of pygmy rabbits and average and maximum distances moved. During the breeding season, average distances between telemetric relocations was 155.3 m for adult males, 33.0 m for adult females, and 106.4 for juveniles. Gahr interpreted the great movements of adult males in the breeding season to be related to finding mates and the long movements of juveniles to dispersal from natal sites. In the non-breeding season average distances between relocations was 75.9 m for adult males, 25.1 for adult females, and 31.0 for juveniles. Maximum distances between relocations were 1,200 m for adult males, 265 m for adult females, and 629 m for juveniles. Gahr used three methods to estimate home range sizes (see Gahr 1993 for details) that she referred to as "core areas," "areas used in normal movements," and "total areas used." Breeding season core areas averaged 0.7 ha for adult males, 0.3 ha for adult females, and 0.3 ha for juveniles. Breeding season areas used in normal movements averaged 20.2 ha for adult males, 2.7 ha for adult females, and 7.1 ha for juveniles. Breeding season total areas used averaged 24.9 ha for adult males, 0.8 ha for adult females, and 3.4 ha for juveniles. Noting that the average movement distances that she observed were greater than previous estimates, and particularly Wilde's (1978) statement that his radio-collared pygmy rabbits "showed very restricted movements and did not appear to leave the area of capture while collars transmitted," Gahr (1993, p 117) commented:

> Possibly, he concluded that the collars were no longer transmitting when actually the rabbits had moved long distances. On many occasions, I had to search over a large area before I relocated some of the males.

Gahr (1993, p 121) also found "significantly greater home range size during the breeding season and observed greater average and maximum distances between relocations during both seasons for males in the grazed area versus those in the ungrazed area." She attributed these greater movements and larger areas used by males in the grazed area to lower density of females, which, it can be speculated, may be related to poorer quality of grazed habitat.

Katzner (1994; also Katzner and Parker 1997) studied winter home range size of pygmy rabbits in southwestern Wyoming and found remarkable differences, more than 33-fold, in home ranges sizes between individuals (pp 14–16); however, he did not discuss whether such variation was related to sex or age. The smallest winter home range was 548 m^2, and the largest was 18,464 m^2. Differences in winter home range sizes between the 2 years of his study were also great, averaging 2,568 m^2 in 1993 and 10,204 m^2 in 1994, a 4-fold difference. He concluded that amount of vegetative cover is more important than amount of available forage in determining home range size in pygmy rabbits.

Katzner (1994, p 102) also reported individual movements of a male pygmy rabbit in Wyoming in winter. In a 12-day period it was located daily. Its "[d]aily movements averaged 29.5 $\pm$ 28.1 m ($\pm$ SD), with a maximum distance between telemetry locations of 104 m." On the 12^{th} day (8 February), however, this individual left the study area, and less than 6 hours later it was observed 600 m from its last detected location, half of the area that it presumably crossed having been marginal or unsuitable habitat. A day later it had moved 600 m in another direction. The following day it was located 2.4 km away. The next morning its remains were found 500 m from the last site. The minimum distance between its last location on the day that it left the study area and the site where it was last detected alive less than 2 days later was at least 3.5 km. Katzner (1994, p 105) thought that this individual's "movements were induced by the start of the breeding season and the scarcity of female [pygmy] rabbits in the immediate vicinity . . . ," where he had found only one female during that year. He reported also (p 105):

> During February of 1993, pygmy rabbits that had not previously been seen in our study area were observed near our collared females. Because we had accounted for all rabbits within at least 1 km of the study site, those animals must have travelled a considerable distance.

Summarizing what has been reviewed above, pygmy rabbits

- spend much time within ~30 m of a burrow (or burrow complex),
- venture up to 500 m from the burrow,

- show great variation in size of home range (at least 548–18,464 m^2 in winter in Wyoming, home range size predicted on the basis of metabolic rate and size, ~8,000 m^2, being near the middle of this observed range of winter variation), with total areas used (in Washington) in spring by males being much larger (mean 24.9 ha [= 249,000 m^2]) than those used by females (mean 0.8 ha [= 8,000 m^2]), and
- may disperse considerable distances, males during the breeding season sometimes moving ≥3.5 km and crossing unsuitable habitat in search of mates, and even juvenile females being capable of movements nearly as great.

Status

Abundance

Janson (1946, pp 83–84) estimated densities of pygmy rabbits in two areas in southeastern Iron County, Utah, which he considered to be “favorable” areas for pygmy rabbits, ranging from 0.75 per acre (from flush transects) to 1.75 and 3.5 per acre (from burrow counts). (Janson [2002, p 27–28] reported the same data in hectares—1.8 pygmy rabbits per hectare based on flush counts, 4.2 pygmy rabbits per hectare based on burrow counts; and 8.6 pygmy rabbits per hectare based on flush counts at the second area.)

Green (1978, p 62), working in southeastern Idaho, reported: “Some of our data indicate densities of 9 [pygmy] rabbits per 0.2 ha.” Green and Flinders (1981) repeated this as: “We found densities of 45 [pygmy] rabbits per ha.” Janson (2002, p 28) considered this to be “an unusually high density” and “on ideal habitat”.

Gahr (1993), in eastern Washington, estimated only 0.269 pygmy rabbits per hectare in an ungrazed area and 0.217 per hectare on a grazed tract (p 86). Although she was confident that she had captured most of the pygmy rabbits in the grazed area, she was less sure for the ungrazed area, which, she speculated, may have supported as many as 0.386 individuals per hectare. Aware that the densities that she found were much lower than those reported by Janson (1946) and Green (1978), she maintained that she did not think that the density of pygmy rabbits on her study areas were much greater than those that she calculated. It should be remembered, however, that she was working in an area where the pygmy rabbit has experienced an alarming decline in numbers and reduction of range in recent years.

Declines in local pygmy rabbit populations—some of them sudden and precipitous—have been observed by several workers. In his Utah study Janson (1946, p 84) noted: "Several areas where these rabbits [i.e., pygmy rabbits] were common in 1941 were found to have none occupying them in 1946." Bradfield (no date [1975], p 39) observed a decrease in the number of pygmy rabbits during his study of this species in southeastern Idaho and, having spent 2 days in Oregon where he found only old sign of pygmy rabbits, speculated that such a decline might have been widespread rather than local. Wilde (1978) abandoned one of three study sites in Wyoming because its population of pygmy rabbits had declined. Weiss and Verts (1984), in a 2-year study (October 1981 to September 1983) in Oregon, saw a marked decline in evidence of pygmy rabbits at their study sites in 1983, which, they said, "demonstrated that [pygmy rabbit] populations were susceptible to rapid declines and possible local extirpation."

Threats

Threats to the continued survival of the pygmy rabbit in Utah include loss, degradation, and fragmentation of habitat. Disease may be a lesser threat.

The deep soils required by the pygmy rabbit have value for farming and attract agricultural interests, potentially resulting in the reduction of habitat for this species. Even when sagebrush is not removed, overgrazing may degrade sagebrush habitat, making it unsuitable for the pygmy rabbit.

Janson (2002, pp 31–32) commented:

> Human activities are having a profound effect on pygmy rabbit populations in some areas. The elimination of sagebrush by developments such as housing, farming and pasture has reduced the rabbit's habitat. On grazing land, much of it public, sagebrush has been eliminated on a large scale, and the land planted to crested wheat grass. This has benefited the growers but has had a disastrous effect on native animals, including the pygmy rabbit, which are dependent on sagebrush for food and shelter[.] In Utah, much of the best habitat is privately owned and thus more prone to development.

Additionally, fire and drought are natural threats that have reduced the habitat of the pygmy rabbit in Utah. Cheatgrass (*Bromus tectorum*), an invasive exotic, is favored by fire and, following fires, replaces sagebrush and other natural plant communities in the Great Basin. Gabler (1997, pp 95–96) reported:

> Coupled with the apparently low pygmy rabbit population on the [study area] during this study, approximately 12.5% of predicted pygmy rabbit habitat, as determined from the GIS model, was destroyed by fires during the summers of 1994, 1995, and 1996. Sagebrush is very slow to recover after range fires. . . . It is suggested that the initial establishment of cheatgrass (*Bromus tectorum*) and its reestablishment after fires has caused . . . increase in fire frequencies.

> Subsequently, as cheatgrass cover and fire frequency increase, non-sprouting woody species like big sagebrush are unable to become re-established . . . . Range fires may currently be a much more serious threat to pygmy rabbit populations than they ever have been in the past. By preventing the re-establishment of big sagebrush, range fires related to cheatgrass invasions may cause permanent extirpation of pygmy rabbits from some areas.

Green and Flinders (1980a) found that "[s]agebrush is critical to the pygmy rabbit for both food and cover" and that "cover and height of woody vegetation appeared to be the critical features of the habitat selected for." They cautioned: "Due to specialized habitat features selected for by pygmy rabbits, prudent consideration should precede sagebrush eradication."

Chapman et al. (1990, p 163) stated:

> The main threat to the pygmy rabbit is habitat loss. The removal of big sagebrush to increase forage production or create cropland has greatly reduced and fragmented the available habitat.

Weiss and Verts (1984) emphasized the threat of habitat fragmentation to pygmy rabbits:

> Because of the specific nature of requisite soil and vegetative conditions, and because populations seem subject to perturbation and even local extirpation, successful dispersal of individuals from less affected populations into favorable habitats becomes crucial if pygmy rabbits are to persist as a component of the fauna of Oregon. Although their dispersal abilities are not understood clearly, pygmy rabbits are suspected of being reluctant or unable to cross open areas such as roads or lands cleared of sagebrush . . . . Fragmentation of sagebrush communities poses [a] . . . threat to populations of pygmy rabbits by reducing the size of these communities and increasing the interstitial distances . . . .

The effects of parasites and diseases on pygmy rabbit populations in Utah are not known. In other states it has been suggested that tularemia is lethal to pygmy rabbits and that they may be susceptible to plague. Although tularemia is apparently native to North America, plague is not, having been introduced from Asia in the nineteenth century.

Management and Conservation

Chapman et al. (1990, pp 163–164) proposed four priority actions to ensure the survival of the pygmy rabbit. These, somewhat abbreviated, are:

1. **Habitat Conservation and Management.** . . . Where populations have become small and fragmented, nature reserves should be established and, where possible, connected by corridors of sagebrush cover. . . . [A] fire protection plan should be developed for each critical site. . . . The conservation of this species

will . . . require compromises with livestock interests; these might include protecting the densest deep soil sagebrush areas and a surrounding buffer zone (of several hectares), which should be sufficient to maintain viable populations. Management plans should aim to ensure that such protected sites are not too widely scattered, thereby permitting some genetic interchange between subpopulations.

2. **Habitat Conservation.** Where sagebrush habitat has been removed, efforts should be made to restore it. In some regions . . . this may occur through natural succession; in other regions planting may be needed. In either case, twenty or more years may be required for this program. Restoration should be carried out adjacent to sites occupied by the species to increase the size of the conservation area and to reduce the fragmentation of populations.

3. **Research.** . . . The highest research priority now is to determine the dispersal capability of the pygmy rabbit and how different levels of habitat fragmentation relate to the genetic isolation of subpopulations. This should enable managers to plan for the correct areas and configurations of habitat patches needed to support genetically and demographically viable populations.

4. **Status Surveys.** The status of the pygmy rabbit varies widely across its range. . . . [I]n general its distribution is reduced from historic[al] levels. Survey efforts are needed, especially in areas where habitat has been fragmented, to determine the pygmy rabbit's status more accurately.

With regard to item 3 of Chapman et al. (1990) (quoted above) concerning research—particularly research relating to pygmy rabbit dispersal—some comments on the needs for research on dispersal and on techniques used for such research are appropriate.

Dispersal capability of the pygmy rabbit is much better known, especially from the works of Gahr (1993) and Katzner (1994) (see Spatial Biology and Movements above), than it was at the time when Chapman et al. (1990) were writing. The need now is to apply what has been learned and to connect understanding of dispersal in the pygmy rabbit with an understanding of population genetics in this species.

Radiotelemetry has become the most popular method for the study of movements, such as home range and dispersal, in mammals. However, the value and the appropriateness of the use of this method in studies of the pygmy rabbit are questionable. The use of radiotelemetry collars may unnaturally affect behavior of pygmy rabbits, leading to artificially distorted results—including unnatural and increased mortality. High rates of trap mortality in the pygmy rabbit have also been reported.

Wilde et al. (1976) reported pygmy rabbit mortality due to trapping technique and to predation by weasels after pygmy rabbits had entered traps and mortality of pygmy rabbits fitted with radio collars. They also reported (p 101) that pygmy rabbits trapped at night were found frozen in the morning and that pygmy rabbits in traps in the afternoon during summer succumbed to heat.

Of 16 pygmy rabbits that Wilde (1978, p 96) radio-collared (using 25-g collars), five were found dead and one was killed by a raptor. Possibly all six of the deaths were related to the collar. Certainly some were, for Wilde reported: "Two of the deaths resulted from the rabbit trying to remove the collar with its front feet, thereby entangling itself." (Wilde did note that he later used tighter fitting collars that eliminated this particular problem.) However, scraping of free whip antennas against vegetation may make it more difficult for collared pygmy rabbits to move quietly through their habitat and such scraping may attract the attention of predators; whip antennas also may cause the rabbits to spend more time in and to choose travel routes through more open areas where they are more susceptible to predation and where foraging is less efficient and food resources are of poorer quality.

Gahr (1993) also radio-collared pygmy rabbits, using collars that "weighed 11 g, about 10% of the rabbit's body weight" (pp 17, 59, and 97), but there is an error (perhaps typographical) in this statement, for 10% of an adult pygmy rabbit's weight would be ~40 g and 11 g would be ~2.75% of a pygmy rabbit's weight. Since, in addition to the transmitter and two batteries, "[t]he collar itself was brass," it seems very unlikely that the total weight was only 11 g and much more likely that overall weight was ~40 g. The brass collars that Gahr used served as antennas (i.e., whip antennas were not used in her study). She used only 16 of a total of 31 radio-collared individuals in her behavior analyses (p 101), these 16 having been relocated ≥20 times each. She reported (pp 31, 33, and 34) at least nine, and possibly 10, cases of predation on collared pygmy rabbits (fewer according to her account on p 101), which would have been 29% (possibly 32%) of those that she collared if the predation deaths determined from pp 31, 33, and 34 are accurate. Since "three rabbits were collared towards the end of the field season, and there was not enough time to relocate them at least 20 times" (p 101), it may be that predation on collared rabbits was even higher than supposed here. Gahr noted (p 101):

> Three of the [pygmy] rabbits sustained abrasions on the neck due to rubbing of the metal collar. The wounds on these animals healed eventually. Also, many animals were seen scratching their collars.

She stated that no mortalities of pygmy rabbits in her study were due directly to the radio collars. However (p 114), "[w]hether or not the predation incidents were indirectly related to inhibited movement or other alterations in behavior caused by the collar was unclear." She commented further (p 115):

> I recommend using a material other than metal for the collar itself because the brass collars used in this study seemed to irritate the skin of rabbits. One disadvantage to this would be the loss of the tuned loop antenna. A whip antenna . . . could be used instead. To minimize interference with the rabbits'

> burrowing activities, the whip antenna should be incorporated into the collar. Disturbance of the animal when radio-tracking was minimal but could be minimized further using the triangulation method to locate individuals . . . . However, some accuracy may be lost using this method, and behavioral data cannot be obtained.

Even though he used radio collars that weighed only 15 g, Katzner (1994, p 111) reported that all of the pygmy rabbits that he equipped with radiotelemetry collars died during the course of his study. He thought that this 100% mortality was related to the use of the collars, perhaps increasing the vulnerability of collared pygmy rabbits to predation. He noted, citing others, that such mortality resulting from the use of radiotelemetry collars is not unusual in rabbit studies (see Katzner 1994 for references). Of course, as electronic technology continues to develop, radiotelemetry equipment is likely to improve.

Considerable mortality of pygmy rabbits captured in live traps has also been reported. Wilde (1978, p 96) reported that in his study 32 pygmy rabbits died while in traps, 15 of these from exposure or stress and 17 as a result of predation (mainly by long-tailed weasels). Katzner (1994, p 6), however, reduced live-trap mortality by wrapping traps in polyethylene sacks to provide protection from predators and thermal stress and attached nest boxes to some traps so that they could be left open through the night.

It would be desirable to know the effects of diseases such as plague and tularemia on pygmy rabbits in Utah, even though there are no known methods for the effective control of these diseases in populations of wild mammals.

Literature Cited

Bacon, M., and C. H. Drake. 1958. Bacterial infections in wild rabbits of eastern and central Washington. *Northwest Science* 32: 124–131.

Baker, R. J., L. C. Bradley, R. D. Bradley, J. W. Dragoo, M. D. Engstrom, R. S. Hoffmann, C. A. Jones, F. Reid, D. W. Rice, and C. Jones. 3002. Revised checklist of North American mammals north of Mexico, 2003. *Occasional Papers, Museum of Texas Tech University* 229: 1–23.

Bailey, V. 1936. The mammals and life zones of Oregon. *North American Fauna* 55: 1–416.

Borell, A. E., and R. Ellis. 1934. Mammals of the Ruby Mountain region of northeastern Nevada. *Journal of Mammalogy* 15: 12–44.

Bradfield, T. D. no date [1975]. On the behavior and ecology of the pygmy rabbit[,] *Sylvilagus idahoensis*. M. S. thesis, Idaho State University, Pocatello, Idaho. vii + 43 pp.

Chapman, J. A., and G. Ceballos. 1990. Chapter 5: The cottontails. Pp 95–110 in J. A. Chapman and J. E. C. Flux (editors), Rabbits, hares and pikas[:] status survey and conservation action plan. International Union for Conservation of Nature and Natural Resources, Gland, Switzerland. iv + 168 pp.

Chapman, J. A., J. E. C. Flux, A. T. Smith, D. J. Bell, G. G. Ceballos, K. R. Dixon, F. C. Dobler, N. A. Formozov, R. K. Ghose, W. L. R. Oliver, T. Robinson, E. Schneider, S. N. Stuart, K. Sugimurua, and Z. Changlin. 1990. Chapter 14: Conservation action needed for rabbits, hares and pikas. Pp 154–167 in J. A. Chapman and J. E. C. Flux (editors), Rabbits, hares and pikas[:] status survey and conservation action plan. International Union for Conservation of Nature and Natural Resources, Gland, Switzerland. iv + 168 pp.

Davis, W. B. 1939. The Recent mammals of Idaho. Caxton Printers, Ltd., Caldwell, Idaho. 400 p.

Dawson, M. R. 1967. Lagomorph history and the stratigraphic record. Pp. 287–316 in C. Teichert and E. L. Yochelson (editors), Essays in paleontology and stratigraphy. University of Kansas, Department of Geology, Special Publication 2: 1–626.

Dobler, F. C., and K. R. Dixon 1990. Chapter 6: The pygmy rabbit. Pp 111–115 in J. A. Chapman and J. E. C. Flux (editors), Rabbits, hares and pikas[:] status survey and conservation action plan. International Union for Conservation of Nature and Natural Resources, Gland, Switzerland. iv + 168 pp.

Durrant, S. D. 1952. Mammals of Utah[:] taxonomy and distribution. *University of Kansas Publications, Museum of Natural History* 6: 1–549.

Durrant, S. D. 1970. Faunal remains as indicators of Neothermal climates at Hogup Cave. Pp 241–245 (Appendix II) in C. M. Aikens (editor), Hogup Cave. University of Utah Anthropological Papers No. 93, University of Utah Press, Salt lake City, Utah. xiii + 286 pp.

Fisher, J. S. 1979. Reproduction in the pygmy rabbit in southeastern Idaho. M. S. thesis, Idaho State University, Pocatello, Idaho. vii + 33 pp.

Flinders, J. T. 1999. Pygmy rabbit[,] *Brachylagus idahoensis*. Pp 681–683 in D. E. Wilson and S. Ruff (editors), The Smithsonian book of North American mammals. xxv + 750 pp.

Gabler, K. I. 1997. Distribution and habitat requirements of the pygmy rabbit (*Brachylagus idahoensis*) on the Idaho National Engineering and Environmental Laboratory. M. S. thesis, Idaho State University, Pocatello, Idaho. ix + 117 pp.

Gabler, K.I., L. T. Heady, and J. W. Laundré. 2001. A habitat suitability model for pygmy rabbits (*Brachylagus idahoensis*) in southeastern Idaho. *Western North American Naturalist* 61: 480–489.

Gahr, M. L. 1993. Natural history, burrow habitat and use, and home range of the pygmy rabbit (*Brachylagus idahoensis*) of Sagebrush Flat, Washington. M. S. thesis, University of Washington, Seattle, Washington. vi + 126 pp.

Gashwiler, J. S., W. L. Robinette, and O. W. Morris. 1960. Foods of bobcats in Utah and eastern Nevada. *Journal of Wildlife Management* 24: 226–229.

Grayson, D. K. 1981. A mid-Holocene record for the heather vole, *Phenacomys* cf. *intermedius*, in the central Great Basin and its biological significance. *Journal of Mammalogy* 62: 115–121.

Grayson, D. K. 1987. The biogeographic history of small mammals in the Great Basin: observations on the last 20,000 years. *Journal of Mammalogy* 68: 359–375.

Green, J. S. 1978. Pygmy rabbit and coyote investigations in southeastern Idaho. A manuscript of six journal articles for Ph. D., Brigham Young University, Provo, Utah. vii + 88 pp.

Green, J. S., and J. T. Flinders. 1979. Homing by a pygmy rabbit. *Great Basin Naturalist* 39: 88.

Green, J. S., and J. T. Flinders. 1980a. Habitat and dietary relationships of the pygmy rabbit. *Journal of Range Management* 33: 136–142.

Green, J. S., and J. T. Flinders. 1980b. Brachylagus idahoensis. *Mammalian Species* 125: 1–4.

Green, J. S., and J. T. Flinders. 1981. Alarm call of the pygmy rabbit (*Brachylagus idahoensis*). *Great Basin Naturalist* 41: 158–160.

Grinnell, J., J. Dixon, and J. M. Linsdale. 1930. Vertebrate natural history of a section of northern California through the Lassen Peak region. *University of California Publications in Zoology* 35: i–v + 1–594.

Gureev, A. A. 1964. Fauna SSSR, Mlekopitayushchie, tom. 3, vyp. 10, Zaitseobraznye (Lagomorpha) [Fauna of the USSR, mammals, vol. 3, pt. 10, Lagomorpha]. Nauka, Moscow–Leningrad, 276 pp. (In Russian.)

Hall, E. R. 1946. Mammals of Nevada. University of California Press, Berkeley, California. xi + 710 pp.

Hall, E. R. 1981. The mammals of North America, 2nd edition. John Wiley and Sons, New York. Volume 1, i–xv + 1–600 + 1–90.

Harris, A. H. 1977. Wisconsin age environments in the northern Chihuahuan Desert: evidence from the higher vertebrates. Pp. 23–52 in R. H. Wauer and D. H. Riskind (editors), Transactions of the symposium on the biological resources of the Chihuahuan Desert region, United States and Mexico. *National Park Service Transactions and Proceedings Series* 3: 1–368.

Harris, A. H. 1985. Late Pleistocene vertebrate paleoecology of the West. University of Texas Press, Austin, Texas. 293 pp.

Harris, A. H. 1990. Fossil evidence bearing on Southwestern mammalian biogeography. *Journal of Mammalogy* 71: 219–229.

Hibbard, C. W. 1963. The origin of the P_3 pattern of *Sylvilagus*, *Caprolagus*, *Oryctolagus*, and *Lepus*. *Journal of Mammalogy* 44: 1–15.

Hoffman, R. S. 1993. Order Lagomorpha. Pp 807–827 in D. E. Wilson and D. M. Reeder (editors), Mammal species of the world[:] a taxonomic and geographic reference, 2nd edition. Smithsonian Institution Press, Washington, D. C. xviii + 1,206 pp.

Honacki, J. H., K. E. Kinman, and J. W. Koeppl (editors). Mammal species of the world[:] a taxonomic and geographic reference. Allen Press and The Association of Systematic Collections, Lawrence, Kansas. ix + 694 pp.

Janson, R. 1940. Distribution and life history studies of the Idaho pygmy rabbit, *Sylvilagus idahoensis* (Merriam), in Utah and southeastern Idaho. B. S. thesis, Utah State Agricultural College, Logan, Utah. [iv +] 44 pp.

Janson, R. G. 1946. A survey of the native rabbits of Utah with reference to the classification, distribution, life histories and ecology. M. S. thesis, Utah State Agricultural College, Logan, Utah. [iv +] 103 pp.

Janson, R. G. 2002. The pygmy rabbit from Utah to Montana. Montana Cooperative Wildlife Research Unit, University of Montana, Missoula, Montana. iii + 41 pp.

Jennings, J. D. 1957. Danger Cave. University of Utah Anthropological Papers 27: 1–328.

Johnson, M. L. 1968. Application of blood protein electrophoretic studies to problems in mammalian taxonomy. *Systematic Zoology* 17: 23–30.

Johnson, M. L., and M. J. Wicks. 1964. Serum-protein electrophoresis in mammals: significance in higher taxonomic categories. Pp 681–694 in C. A. Leone (editor), Taxonomic biochemistry and serology. Ronald Press, New York. 728 pp.

Katzner, T. E. 1994. Winter ecology of the pygmy rabbit (*Brachylagus idahoensis*) in Wyoming. M. S. thesis, University of Wyoming, Laramie, Wyoming. xii + 125 pp.

Katzner, T. E., and K. L. Parker. 1997. Vegetative characteristics and size of home range used by pygmy rabbits (*Brachylagus idahoensis*) during winter. *Journal of Mammalogy* 78: 1063–1072.

Kenner, G. H. 1965. Comparative osteology of rabbits of the genera *Brachylagus* Miller and *Sylvilagus* Gray. M. S. thesis, University of Utah, Salt Lake City, Utah. 125 pp.

Lyman, R. L. 1991. Late Quaternary biogeography of the pygmy rabbit (*Brachylagus idahoensis*) in eastern Washington. *Journal of Mammalogy* 72: 100–117.

Lyon, M. W., Jr. 1904. Classification of the hares and their allies. *Smithsonian Miscellaneous Collections* 45: 321–447.

MacCracken, J. G., and R. M. Hansen. 1982. Seasonal foods of coyotes in southeastern Idaho: a multivariate analysis. *Great Basin Naturalist* 42: 45–49.

Mawbry, J. E. 1967. Fossil vertebrates of the Tule Springs site, Nevada. Pp. 105–128 in H. M. Wormington and D. Ellis (editors), Pleistocene studies in southern Nevada. *Anthropological Papers, Nevada State Museum* 13: 1–411.

McKenna, M. C., and S. K. Bell. 1997. Classification of mammals above the species level. Columbia University Press, New York, New York. xii + 631 pp.

McNab, B. K. 1963. Bioenergetics and the determination of home range size. *American Naturalist* 97: 133–140.

Merriam, C. H. 1891. Results of a biological reconnoissance [*sic*] of south-central Idaho. *North American Fauna* 5: 1–113.

Miller, G. S., Jr. 1900. A new subgenus for Lepus idahoensis. *Proceedings of the Biological Society of Washington* 13: 157.

Nelson, E. W. 1909. The rabbits of North America. *North American Fauna* 29: 1–314.

Pritchett, C. L., J. A. Nilsen, M. P. Coffeen, and H. D. Smith. 1987. Pygmy rabbits in the Colorado River drainage. *Great Basin Naturalist* 47: 23–233.

Russell, B. D., and A. H. Harris. 1986. A new leporine (Lagomorpha: Leporidae) from Wisconsin deposits of the Chihuahuan Desert. *Journal of Mammalogy* 67: 632–639.

Ramos, C. 1999. An Irvingtonian species of *Brachylagus* (Mammalia: Lagomorpha) from Porcupine Cave, Park County, Colorado. *Great Basin Naturalist* 59: 151–159.

Riddle, B. R., and J. R. Choate. 1986. Systematics and biogeography of *Onychomys leucogaster* in western North America. *Journal of Mammalogy* 67: 233–255.

Stanford, J. S. 1932. Idaho pygmy rabbit: Brachylagus idahoensis (Merriam). *Journal of Mammalogy* 13: 79–80.

Stephenson, S. N. 1966. Mammals of the Paunsagunt Plateau region, Utah. *Great Basin Naturalist* 26: 43–44.

Utah Division of Wildlife Resources. 2003. Utah sensitive species list. Utah Division of Wildlife Resources, Salt Lake City, Utah. ~146 pp including appendices.

van der Loo, W., A. James, and J. Schröder. 1981. Chromosome evolution in leporids. Pp. 28–35 in K. Myers and C. D. MacInnes (editors), Proceedings of the world lagomorph conference held in Guelph, Ontario August 1979. International union for conservation of Nature and Natural Resources, Gland, Switzerland. xix + 983 pp.

Warren, C. 2003. Endangered and threatened wildlife and plants; final rule to list the Columbia Basin distinct population segment of the pygmy rabbit (*Brachylagus idahoensis*) as endangered. *Federal Register* 68: 10388–10409.

White, D. B. 1978. A population analysis of the pygmy rabbit (*Sylvilagus idahoensis*) on the INEL site. Ph. D. dissertation, Idaho State University, Pocatello, Idaho. xiv + 172 pp.

White, S. M., J. T. Flinders, and B. L. Welch. 1982. Preference of pygmy rabbits (*Brachylagus idahoensis*) for various populations of big sagebrush (*Artemisia tridentata*). *Journal of Range Management* 35: 724–726.

White, S, M., B. L. Welch, and J. T. Flinders. 1982. Monoterpenoid content of pygmy rabbit stomach ingesta. *Journal of Range Management* 35: 107–109.

Wilde, D., J. S. Fisher, and B. Keller. 1976. A demographic analysis of the pygmy rabbit, *Sylvilagus idahoensis*. Pp. 88–105 in O. D. Markham (editor), 1975 Progress Report, Idaho National Engineering Laboratory Site Radioecology–Ecology Programs, v + 205 pp.

Wilde, D. B. 1978. A population analysis of the pygmy rabbit (*Sylvilagus idahoensis*) on the INEL site. Ph. D. dissertation, Idaho State University, Pocatello, Idaho. xiv + 172 pp.

Wilde, D. B. 1981. Pygmy rabbit reproduction: possible modification by drought conditions. Pp. 559–571 in K. Myers and C. D. MacInnes (editors), Proceedings of the World Lagomorph Conference Held in Guelph, Ontario August 1979, xix + 983 pp.