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Lepus othus. By Troy L. Best and Travis Hill Henry

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Lepus othus Merriam, 1900

Alaskan Hare

Lepus othus Merriam, 1900:28. Type locality "St. Michaels [Norton Sound—Elliot, 1905:360], Alaska."

Lepus poadromus Merriam, 1900:29. Type locality "Stepovak Bay, Alaska Peninsula."

CONTEXT AND CONTENT. Order Lagomorpha, Family Leporidae, Subfamily Leporinae, Genus Lepus, Subgenus Lepus (Hall, 1981; Lyon, 1904). There are ca. 19 species in the genus Lepus (Honacki et al., 1982). Anderson (1974) considered L. othus monotypic because it exhibits a latitudinal size cline, but Hall (1981) recognized two subspecies:

L. o. othus Merriam, 1900:28, see above. L. o. poadromus Merriam, 1900:29, see above.

DIAGNOSIS. Lepus othus can be distinguished from L. arcticus and L. timidus on the basis of skull morphology. In addition, these species are separated geographically (Anderson, 1974; Hall, 1981). L. o. othus resembles L. arcticus andersoni, but averages larger, has brownish rather than grayish summer pelage, the upper incisors are more strongly recurved, the rostrum is deeper, and the upper molars are heavier. Compared with L. arcticus monstrabilis, the skull of L. o. othus is similar in size, but the incisors are strongly recurved, the rostrum is heavier, and the upper toothrow is longer. The skull of L. o. poadromus is about the same size as that of L. a. andersoni, but the nasals of L. o. poadromus average smaller and the upper toothrow is longer (Howell, 1936).

Lepus timidus differs from L. othus in lacking the cinnamonbuff tone of the upperparts, the subterminal portions of the hairs are fuscous, and the tips of the hairs are pale buff. Skulls of the two taxa are similar in size, but in L. othus the rostrum and nasals are longer, narrower (Howell, 1936), and less flattened, the frontals are broader interorbitally, the supraoccipital shield is narrower (longer than broad), the jugal is narrower (less expanded vertically) and longer posteriorly (protruding farther behind the squamosal root of the zygoma), the muscular impression on the outer face is narrower anteriorly, the basioccipital is narrower, and the incisive vacuity is smaller (Merriam, 1900).

Lepus othus is partially sympatric with L. americanus in Alaska. Compared with L. americanus, L. othus has longer ears (usually >73 mm), a first upper incisor inscribing an arc of a circle the radius of which is >9.6 mm, a tail that always is white, pelage in winter that is white to the base of the hairs, and basilar length of skull >67 mm. In contrast, L. americanus has ears <73 mm in length, a first upper incisor inscribing an arc of a circle the radius of which is <9.6 mm, a tail that is not always white, pelage in winter that is white only on the tips of the hairs, and basilar length of skull <67 mm (Bee and Hall, 1956).

GENERAL CHARACTERS. Lepus othus (Fig. 1) is one of the largest species of hares (Dufresne, 1946; Howell, 1936). The skull (Fig. 2) is massive and the upper incisors are strongly recurved (Howell, 1936).

In winter pelage, *L. othus* is white, except for the extreme tips of the ears, which are black (Merriam, 1900). In summer pelage (23 August), the nose, sides of the face, and top of the head of *L. o. othus* are cinnamon-buff, but the top of the head appears darker because the subterminal fuscous bands on the hairs show through. The anterior one-half of the outer surface of the ears is similar to the head and the posterior one-half is white; the tips are fuscous. The general tone of upperparts is cinnamon drab; individual hairs are pallid neutral-gray at the base and fuscous subterminally, and the tips are pale pinkish-buff or cartridge-buff. There are numerous

blackish guard hairs intermixed. The front legs are white with a wash of cinnamon-buff on the anterior surface. The hind legs are white, washed with brown. The tail is white. A specimen obtained on 3 August is similar, but the underfur is pale pinkish-cinnamon, the rump is neutral gray, the front legs are more strongly washed with cinnamon-buff, the ears are extensively marked with blackish-brown, and the tail is washed with neutral gray (Howell, 1936).

In summer pelage (8 July), the general tone of the upperparts is verona brown in $L.\ o.\ poadromus$, with some admixture of white on the guard hairs (probably remains of winter pelage). The nose and sides of face are sayal brown; the top of the head is darker, like the back. A band of tilleul buff nearly encircles the eye. The ears are colored like the back, but shaded with fuscous and edged with white. The front legs are wood brown, with small patches of buffy white; the hind legs are similar to the front legs, but the hind feet mainly are white. The tail is smoke gray, shaded above with fuscous and with some white hairs intermixed. The flanks are shaded with brown, and the rump is shaded with fuscous. The chin and throat are pale smoke-gray. The underside of the neck is smoke gray, shaded with fuscous. The belly is yellowish-white in the center and pale smoke-gray on the sides (color nomenclature follows Ridgway, 1912-Howell, 1936).

Average and range of measurements (in mm) of L. o. othus and L. o. poadromus, respectively, are: total length, 624 (565-690), 570 (no range); length of tail, 83 (65-104), 65; length of hind foot, 179 (170-189), 164; greatest length of skull, 105.3 (101.9-108.7), 99.7 (97.0-101.5); basilar length, 80.5 (77.5-83.3), 76.2 (73.0-78.8); diagonal length of nasals, 43.2 (40.3-47.6), 39.5 (37.3-42.5); greatest width of nasals, 22.4 (21.3-23.8), 20.7 (19.0-22.6); depth of rostrum, 25.8 (24.7-27.0), 23.7 (22.7-24.9); cranial breadth, 36.0 (34.7-37.0), 35.1 (33.4-37.4); zygomatic breadth, 51.5 (49.3-53.8), 49.9 (48.1-51.7); length of maxillary toothrow, 20.0 (19.2-21.1), 19.6 (18.8-20.8-Howell, 1936). Average measurements (in mm) of subspecies combined are: total length, 676; length of body, 607; length of tail, 69; length of hind foot, 185; length of ear, 91 (Anderson and Lent, 1977); basilar length, 79.5; postorbital constriction, 16.5; length of nasals, 42.2; diameter of external auditory meatus, 4.8; breadth of braincase, 30.7; length of palatal bridge, 7.7; parietal breadth, 30.4; length of bullae, 12.7 (Dixon et al., 1983). Average mass (in g) is 4,806 (Anderson and Lent, 1977); range of mass usually is 3,900-4,813 (Cowan and Bell, 1986), but masses of 5,500 (Schiller and Rausch, 1956) and 7,200 have been reported (Howell, 1936).



Fig. 1. Lepus othus on the Seaward Peninsula, Alaska. Photograph courtesy of D. Klein.

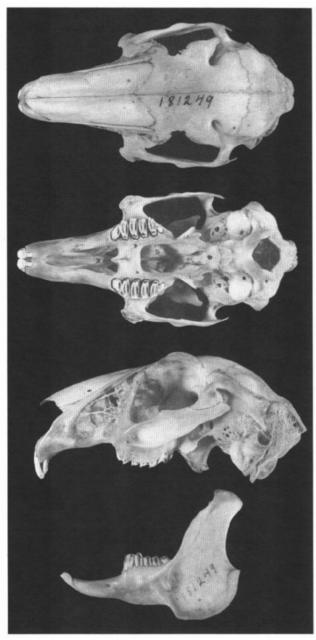


Fig. 2. Dorsal, ventral, and lateral views of cranium, and lateral view of mandible of *Lepus othus* from 75 miles below Bethel, Alaska (gender unknown, United States Museum of Natural History 181249). Greatest length of cranium is 104.0 mm. Photographs by T. H. Henry.

There is no sexual dimorphism in size. There is a latitudinal size cline in means of length of hind foot and 15 cranial measurements. This cline follows Bergmann's ecogeographic rule in which body size and latitude have a positive correlation (Anderson, 1974). Compared with L. o. othus, L. o. poadromus has a rostrum, nasals, braincase, palatal bridge, and incisive vacuity that are narrower, the frontal breadth remaining essentially the same. The nasals in particular are narrower and more arched transversely, the pterygoids are broader, the hamular processes are more pronounced and hooked, and the angular process of the mandible has an everted edge that is broader posteriorly (Merriam, 1900).

DISTRIBUTION. The Alaskan hare occurs in the Arctic tundra region of western and northwestern Alaska from sea level to >600 m (Nelson, 1909). The range extends from the Selawik-Kotzebue area in the north to the Cold Bay area on the south, and includes all of the Seward Peninsula, most of the Alaska Peninsula,

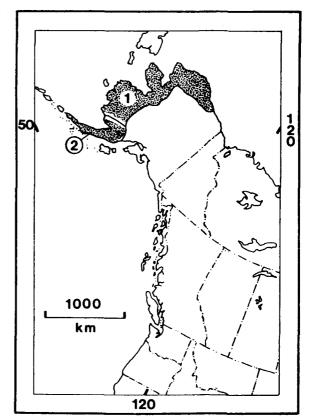


Fig. 3. Distribution of Lepus othus in northwestern North America (Hall, 1981): 1, L. o. othus; 2, L. o. poadromus.

and most of the western coast of Alaska (Anderson, 1978). The North Slope of Alaska often is indicated as part of the range of this species (Fig. 3—Bee and Hall, 1956; Hall, 1981; Howell, 1936), although no verifiable records exist (Anderson, 1978).

FOSSIL RECORD. The genus Lepus had its origin in the late Pliocene or early Pleistocene in the Holarctic. The genus spread southward in the later Pleistocene and now extends (excluding introductions) into South Africa (Dawson, 1967). Remains of L. othus have been found in two late Rancholabrean sites in Alaska; Canyon Creek roadcut (Weber et al., 1981) and Porcupine River Cave 1 (Dixon, 1984). These sites are outside the current range of L. othus, and the remains from Canyon Creek may be of L. arcticus (Weber et al., 1981).

FORM AND FUNCTION. The stout claws of *L. othus* facilitate digging through hard-crusted snow to reach vegetation (Dufresne, 1946). The dental formula is i 2/1, c 0/0, p 3/2, m 3/3, total 28, as in all *Lepus* (Nowak and Paradiso, 1983).

Change to white winter pelage begins in mid-September. Molting begins with the ears, which become entirely white by late September (except for the black tips), in strong contrast to the buffy color of the head and body. Gradually the white on the underparts spreads onto the sides and legs, then the hair on the back, sides, and shoulders becomes white; by the latter part of October the Alaskan hare is entirely white except for the face and ears. The face is slower in changing, with one small spot in the middle of the forehead remaining brown until late November. L. othus remains white until early May. The first appearance of brown is on the face and ears. These quickly change to brown followed by the front legs and shoulders (Walkinshaw, 1947). An Alaskan hare observed near Pavlof Mountain on 25 May was still in white winter pelage, with three small patches of brown hair appearing-two on the neck and one on the posterior region of the back. Two white hares were observed on 1 June, and on 7 June one was grayish. On 9 June, one from Sand Point was acquiring the summer coat. The winter fur was mostly shed from the head and back, but the ears and feet were mostly white and small patches of white fur were seen on the back and sides. On 23 October at Chignik, one was in brownish pelage with hairs white at the base, then cinnamon-buff, then fuscous, and then tipped with pale buff. The pelage of this animal appeared to be fresh, suggesting that some individuals do not become entirely white in winter (Howell, 1936).

ONTOGENY AND REPRODUCTION. There is one litter per year. Conception occurs 13–29 April (Anderson and Lent, 1977) and in May (Dufresne, 1946). There is a preimplantation loss of 34.6% of the ova, and postimplantation loss of 7.7% of the embryos (Anderson, 1974). For three females, there were 9, 8, and 9 corpora lutea, 3, 6, and 8 implantation sites, and 3, 6, and 6 embryos, respectively (Anderson and Lent, 1977). Prenatal mortality may be related to a combination of age of the female, food shortage, and severe weather conditions (Anderson, 1974).

Gestation period is ca. 46 days, similar to that previously reported for Lepus (Anderson and Lent, 1977; Cowan and Bell, 1986). Parturition occurs 29 May-4 June (as estimated from ages of embryos—Anderson and Lent, 1977). The parturition period seems to coincide with the loss of snow cover in late May. Because the young are precocial, their survival is enhanced if they are born after the snow has melted, when food is abundant, ambient temperatures are high, and when their brown pelage blends in with the color of the ground surface (Anderson, 1974).

Litters average 6.3 young (Anderson and Lent, 1977) with a range of five to seven (Dufresne, 1946). Weight at birth is ca. 105 g (Flux, 1981). On 10 June near Johnson River, a nest contained seven young (Fig. 4) with ca. 5 cm of umbilical cord attached. They struggled when picked up, but soon cuddled against the others when replaced in the nest. Subsequently, the young were moved a few meters away by the mother. Coloration of the seven young found in the nest on 10 June was as follows: upperparts and band across throat generally brownish-slate at base of hair, tipped with buff; nose, buff to base; eye ring, pale buff; tops of front feet, pale buff; hind feet, mixed white and buff above, buff below; belly, inner sides of front and hind legs, pure white; tips of ears black; tail, apparently white, might be dark at base above. On some of the young, a white center stripe ca. 10 mm long was present on the forehead. The pupil was dark and the iris was dark blue. Average measurements (in mm) were: total length, 176; length of tail, 20; length of hind foot, 45; length of ear, 24; mass, 104.8 g (Walkinshaw, 1947).

Females show signs of nursing 5-9 weeks after parturition. One juvenile, ca. 2 months old, had milk in its stomach. The prolonged nursing period likely enhances the survivorship of the young and helps maintain the rapid rate of growth (Anderson, 1974). In a few weeks after birth, the young begin drifting away from the mother (Dufresne, 1946).

The mass of an Alaskan hare captured on 13 June was 140 g, and on 18 June mass was 194 g. On 18 June when the hare was ca. 9 days old, the hind foot was 51 mm in length, on 12 August the length was 120 mm, and in late September the length was 170 mm. By late September, full growth had been attained. On 19 March, its mass was 3,525 g (Walkinshaw, 1947). The estimated average rate of growth for juvenile Alaskan hares is 37.2 g/day over a 102-day growth period, from a birth weight of 100 g to a minimum adult weight of 3,900 g. The hind foot attains 95% of the average adult size in 112 days, an average rate of growth of 2.56 mm/day. Rapid growth allows at least the minimum adult body mass to be reached during the short summer, thereby increasing the chances of survival through the following winter. The initial rate of growth of L. othus is greater than that in L. americanus, L. californicus and L. townsendi (Anderson and Lent, 1977).

The average life span and maximum longevity are not known (Anderson, 1974). Age can be estimated by examination of the epiphyseal closure of the femur, and by the degree of development of the anterior supraorbital process of the skull (Anderson and Lent, 1977). In addition, the presence of individuals having a mass of 6,490 g, 35% greater than the average mass of 4,800 g, suggests the presence of old individuals (Anderson, 1974).

Compared with most other species of *Lepus*, litter size is larger in the *L. othus-L. arcticus-L. timidus* group (average, ca. 5-6; range, 1-7). In addition, there are fewer litters per year (average, ca. 1-2; range, 1-4). The larger litters and fewer numbers of litters may be related to lower average annual temperature (average, ca. -5°C; range, -20-10°C-Flux, 1981).



Fig. 4. Seven young Lepus othus in a nest near Johnson River, Alaska (from Walkinshaw, 1947).

ECOLOGY. Lepus othus inhabits the tundra biome in the coastal regions of Alaska (Hansen and Flinders, 1969). Its distribution is almost wholly outside the limit of spruce tree growth (Dufresne, 1946). It lives in dense alder (Alnus) thickets (Howell, 1936; Murie, 1959), and in summer, when the vegetation is leafed out, it is nearly impossible to see (Murie, 1959). Near the Kashunuk River, L. othus was found in all habitats from the sedge flats and wet meadows to the upper slopes of the Askinuk Mountains, where the vegetation predominantly was Carex, Elymus arenarius, Potentilla egedii, Poa eminens, Empetrum nigrum, Salix, Ledum decumbens, Betula nana, Alnus crispa, Dryopteris, and lichens (Anderson, 1974). The two subspecies are associated with district habitat types, but this may simply reflect the kinds of habitats available to each. The habitat of L. o. othus primarily is tundra or alluvial plain, whereas that of L. o. poadromus primarily is coastal lowland areas (Bittner and Rongstad, 1982).

The Alaskan hare has been reported from many localities throughout the Seward Peninsula, but population density varies. In one year, the only sign of its presence was two molar teeth found in cave deposits on Trail Creek, near Cloud Lake (Quay, 1951). It was reported as numerous along the coast of Alaska as far north as Cape Lisburne, but on the north coast from Point Barrow eastward it apparently is absent, although occurring sparingly at a few points away from the coast (Howell, 1936). Pilots flying over the region of the Alaska Peninsula observed many Alaskan hares (Schiller and Raush, 1956), but hares previously were rare in that area (Osgood, 1904). L. othus was fairly numerous on the tundra near Kotzebue, in northwestern Alaska, and its tracks were common on the south shore of Kotzebue Sound (Bailey and Hendee, 1926). It was rare around St. Michael (Osgood and Bishop, 1900). Alaskan hares are particularly difficult to see in summer when their pelage is brown (Howell, 1936).

Young may be born in nest sites above ground with no brush (Cowan and Bell, 1986), or in the thick shelter of willow or alder brush (Dufresne, 1946). A nest was located on a naturally hollowedout spot on an east-facing slope of a ravine on 10 June near Johnson River (Fig. 4). The nest was a mere depression in the moss and cotton-grass (Eriophorum angustifolium), and had no lining. The nest was well-packed where the mother had been lying. The backs of the young were well beneath the top of the surrounding tundra, but continously were exposed to the cold, wind, and rain. There was no brush for several hundred meters, and then only a few bushes. The predominant plant was moss, through which grew large cottongrass. Near the nest were Alaska tea (Ledum decumbens), alpine bearberry (Arctostaphylos alpina), dwarf birch (Betula), salmonberry (Rubus), blueberry (Vaccinium ulginosum), crowberry (Empetrum nigrum), and numerous lichens (Walkinshaw, 1947).

The food habits of *L. othus* do not differ substantially between sexes. During April and May, the diet consists mainly of shrubs, with *Salix alaxensis* and *E. nigrum* the most commonly eaten plant species. The *Salix* material predominately is woody tissue and the *Empetrum* primarily is leaves. In early spring, Alaskan hares were seen feeding at the edge of melting snow patches, where crowberries

from the previous summer were abundant; the stomachs of two adults contained large quantities of crowberries and leaves (Anderson, 1974).

An Alaskan hare held in captivity was fond of canned milk and also ate leaves from alder and dwarf birch as well as sporangia from mosses placed in its nest box. When hungry, it used the front feet alternately to beat on the side of the nest box. It ate clover, grass, carrot tops, dandelion leaves, some corn, wheat, oats, lettuce, parsley, water cress, twigs from forsythia, sumac, and apricot. Twigs of apricot seemed to be preferred (Walkinshaw, 1947).

Potential predators include the golden eagle (Aquila chrysaetos), rough-legged hawk (Buteo lagopus), snowy owl (Nyctea scandiaca - Anderson, 1974), gyrfalcon (Falco rusticolus - Dufresne, 1946), Arctic fox (Alopex lagopus), red fox (Vulpes vulpes Anderson, 1974), weasel (Mustela), wolverine (Gulo gulo), gray wolf (Canis lupus), and polar bear (Thalarctos maritimusfresne, 1946). Examination of 98 raptor castings and 43 fox fecal pellets revealed that one golden eagle casting, one unidentified raptor casting, and one fox pellet contained remains of L. othus. Because the red fox is present throughout the year and probably capable of taking adult and juvenile hares, it may represent the most important predator. The Arctic fox also is present all year, but may not be able to kill a healthy adult hare; its predation is believed to be primarily on young hares. The golden eagle is present from spring to autumn and can take any hare. The snowy owl is present from late autumn to early spring and also is capable of taking any hare. Juveniles may be preyed upon by rough-legged hawks during the summer (Anderson, 1974).

No ectoparasites have been found on *L. othus*. The small intestine of an adult female contained 12 trichostrongylid nematodes (Anderson, 1974).

BEHAVIOR. Alaskan hares are solitary, except during the April-May mating season when groups of 20 or more may be seen (Dufresne, 1946). In May, they may still be in winter pelage and remain near snow fields at higher elevations (Schiller and Rausch, 1956). They may be observed loping over the tundra in the distance, their pale underparts flashing, and their large hind feet conspicuous (Walkinshaw, 1947). L. othus comes out of the denser alder thickets in the evenings to feed (Howell, 1936; Murie, 1959).

Tail flagging is present in *L. othus* (Cowan and Bell, 1986). When attacked by a snowy owl, the Alaskan hare may strike at the owl with its forefeet when the bird swoops low, and between attacks it races toward the nearest patch of willows for shelter (Dufresne, 1946). In captivity, one showed no fear of cats, but obviously was afraid of dogs. During snow and rain it would not attempt to seek shelter. It seldom drank water and never bathed, but became soaked with each rain. Fecal pellets were voided in a pile in one corner of its pen (Walkinshaw, 1947).

GENETICS. As in all Lepus, L. othus has a diploid number of 48 chromosomes (Rausch and Ritter, 1974; Robinson et al., 1983; Uribe-Alcocer et al., 1989; van der Loo et al., 1981). There appear to be 16 pair of submetacentric and 30 pair of subtelocentric autosomes; these numbers may vary, because lengths of arms are inconstant. The X chromosome is metacentric and the Y is acrocentric (Rausch and Ritter, 1974).

REMARKS. Lepus arcticus, L. othus, and L. timidus may be conspecific (Chapman et al., 1983; Dixon et al., 1983; Flux, 1983; Honacki et al., 1982), or L. othus may be conspecific only with L. timidus (Bee and Hall, 1956; Corbet and Hill, 1980; Hall, 1951; Hall and Kelson, 1959; Rausch, 1953, 1963). However, Rausch (reported by Anderson, 1974) has suggested that L. othus is a valid species and is not conspecific with L. timidus of Siberia or L. arcticus of Canada. Jones et al. (1986) considered L. othus to be a distinct species, and L. timidus was not listed as occurring in North America.

Multivariate analysis of phenetic relationships among samples of L. arcticus, L. othus, and L. timidus indicated that the sample from Chukot Peninsula, Russia, did not link with any other Eurasian samples, but was closely allied with samples from Alaska, Banks Island, and Prince Patric Island (Baker et al., 1983). Baker et al. (1983) concluded that the discontinuity between the sample from Chukot Peninsula and that from northeastern Siberia indicated that only L. arcticus and L. timidus should be recognized as distinct species, and that L. othus was conspecific with L. arcticus. Unfortunately, no other species were included in their analyses to obtain

an estimate of the degree of variation needed to detect species-level differences.

In his comparisons of *L. arcticus*, *L. othus*, and *L. timidus*, Anderson (1974) included *L. townsendi* to obtain a measure of the degree of differentiation expected between species. The generalized distance between each pair of the three species of Arctic-dwelling hares was greater than the minimum generalized distance between *L. townsendi* and each of the three species of Arctic-dwelling hares. His analysis suggested that *L. timidus* was closer to *L. arcticus* than to *L. othus*, which is opposite of that expected from geographic distributions (Anderson, 1974).

The Latin word *Lepus* means hare (Jaeger, 1955). Additional common names are tundra polar hare, peninsula Arctic hare (Merriam, 1900), St. Michaels' hare, swift hare (Elliot, 1905), Arctic hare (Rausch, 1953), Alaska Arctic hare (Osgood and Bishop, 1900), Alaska tundra hare, Alaska Peninsula hare (Howell, 1936), tundra hare, ukalisukruk (Bee and Hall, 1956), ugalishugruk (Rausch, 1951), ushkánuk (Osgood, 1904), zaisch, okhotsk, gichiga, marcova, and oo-skon (Murie, 1959).

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