

Lepus timidus. By Anders Angerbjörn and John E. C. Flux

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Lepus timidus Linnaeus, 1758

Mountain Hare

- Lepus timidus* Linnaeus, 1758:57. Type locality "Uppsala" Sweden.
Lepus algidus Pallas, 1778:2. Renaming of *alpinus* (=timidus).
Lepus borealis Pallas, 1778:2. Renaming of *alpinus* (=timidus).
Lepus variabilis Pallas, 1778:2. Renaming of *timidus*.
Lepus septentrionalis Link, 1795(2):73. Renaming of *variabilis* (=timidus).
Lepus hibernicus Bell, 1837:341. Type locality "Ireland".
Lepus sclavonius Blyth, 1842:102. Based on Polish or Russian trade skins.
Lepus canescens Nilsson, 1844:133. Renaming of *borealis sylvaticus* Nilsson, 1831 (see below).
Lepus lugubris Kastschenko, 1899:57. Type locality "Ongudai am Altai", Russia.
Lepus varronis Miller, 1901:97. Type locality "Grisons, Heinzenberg, Canton of Granbünden, Switzerland".
Lepus gichiganus Allen, 1903:155. Type locality "Gichiga, west coast of Okhotsk Sea".

CONTEXT AND CONTENT. Order Lagomorpha, Family Leporidae, Subfamily Leporinae. The genus *Lepus* contains about 30 species (Wilson and Reeder, 1993). Corbet and Hill (1986) regard *L. arcticus* as conspecific with *L. timidus*, but we adopt here the intermediate position of Baker et al. (1983) linking *L. othus* and *L. arcticus* and separating *L. timidus*. However, the relationship between these arctic species of *Lepus* is unclear, and so also is the border between them, but we consider *L. tschuktschorum*, Nordquist, 1883, conspecific with *L. othus/arcticus*. The populations in Ireland, Scotland, the Alps, Hokkaido, the Kurile Islands, and Sakhalin, are geographically separated and morphologically distinct, and thus can be treated as subspecies. We follow Ognev (1940), recognizing 16 subspecies although this division must be considered preliminary. Ognev (1940) based his division in subspecies in Asia mainly on pelage characteristics including colors. Corbet (1978) included most of the subspecies in *L. t. timidus*.

- L. t. abei* Kuroda, 1938:42. Type locality "Toshimoi, in Yetorofu, Kurile Islands".
L. t. ainu Barrett-Hamilton, 1900:90. Type locality "the Island of Yezo" [Hokkaido, Japan]
L. t. begitschevi Koljushev, 1936:304. Type locality "Western coast of the Pyasina Gulf" Taimyr, Russia.
L. t. gichiganus Allen, 1903:155, see above (*kamtschaticus* Dybowski is a synonym).
L. t. hibernicus Bell, 1837:341, see above (*lutescens* Barrett-Hamilton is a synonym). This taxon is considered a species by Barrett-Hamilton (1912) because it has remained distinct in the presence of *L. t. scoticus* on Mull since 1860.
L. t. kolymensis Ognev, 1922:106. Type locality "Pokhodskoe Village, 80 km below Nizhne-Kolymk along the Kolymk river", northeastern Siberia.
L. t. kozhevnikovi Ognev, 1929:79. Type locality "bei dem Dorfe Tschernaja, Kr. Bogorodski, Mosk. Gouvernement".
L. t. lugubris Kastschenko, 1899:57, see above (*altaicus* Eversmann is a synonym).
L. t. mordeni Goodwin, 1933:1. Type locality "Monoma river, eighty miles east of Troitskovo, Maritime Province, eastern Siberia".
L. t. orii Kuroda, 1928:223 (*saghalienis* Abe and *rubustus* Urita are synonyms). Type locality "Nayoro, Tomariora, Sakhalin" Russia.
L. t. scoticus Hilzheimer, 1906:511. Type locality "northern Scotland".
L. t. sibiricorum Johansen, 1923:58. Type locality "Western Si-

beria, valley of Chulym", southwestern Siberia and northern Kazachskaja.

- L. t. sylvaticus* Nilsson, 1831: planch 22 (*canescens* Nilsson is a synonym). Type locality "Mörkö, Södermanland", Sweden.
L. t. timidus Linnaeus, 1758:57, see above (*algidus* Pallas, *alpinus* Erxleben, *borealis* Pallas, *collinus* Nilsson, *septentrionalis* Link, *sclavonicus* Blyth, *variabilis* Pallas, *typicus* Barrett-Hamilton, are synonyms).
L. t. transbaikalicus Ognev, 1929:81. Type locality "Sosnowka, Bargusinische Taiga (am Baikal-See)", Siberia.
L. t. varronis Miller, 1901, see above (*breviauritus* Hilzheimer is a synonym).

DIAGNOSIS. *L. timidus* is smaller than *L. europaeus*, with shorter forelimbs and ears, but longer hind feet; the tail is shorter, white below, and the back is paler; summer fur is softer, grayer, and in winter most individuals turn white (Ognev, 1940). Compared with *L. europaeus*, *L. timidus* has a shorter facial cranium, more concave frontal region, longer bony palate; a stronger mandible, deeper in the molar region, more vertical condylar process, and the posterior inner margin of the symphyseal region not as sharp; anterior branch of supraorbital process is less distinct; foramen mesopterygium often is broader than incisive foramen; zygomatic arch is not less deep towards the front, and anterior process is less developed (Fig. 1). The upper incisors are squarer in cross-section and less curved, thus the roots rise between the premaxilla and maxilla, farther posterior than in *L. europaeus*. The third lower premolar is erect in *L. timidus*, but curved backward in *L. europaeus*. The tibia and phalanges of the hind foot are longer in *L. timidus* than in *L. europaeus*, and the radius of the forearm is shorter (Angermann, 1967). The scapula is broader (especially so in *L. t. hibernicus*) than in *L. europaeus* (Barrett-Hamilton, 1912).

GENERAL CHARACTERS. The mountain hare is large, but not as large as *L. europaeus* where sympatric. The relatively large head has prominent eyes with a yellowish iris in the adult but dark brown in the young. The basal length of the skull is greater in northern populations, supporting Bergmann's Rule as indicated by the following measurements (in mm): Ireland, 73; Scotland, 70; Scandinavia, 73.2; northern Scandinavia and Russia, 77.8; northern Siberia, 87.5 (Barrett-Hamilton, 1900). European subspecies show a similar trend: the smallest subspecies, *L. t. varronis*, has a mass of 2,397 g (1,404-3,228); length of head and body, 509 mm (460-560); tail length, 53-65 mm; hind foot length, 159 mm (145-172); ear length, 98-106 mm, $n = 94$. The largest subspecies is *L. t. timidus*, which at Murmansk had a mass of 3,438 g (2,900-4,700); length of head and body, 546 mm (430-610); length of tail 63 mm (40-70); hind foot length, 164 mm (150-180); ear length, 88 mm (76-100, $n = 29$ —Angermann, 1967). The overall length of the skull (in mm) of *L. t. varronis* is 86.4 (76.6-93.1, $n = 26$ —Couturier, 1964), and of *L. t. kozhevnikovi* from Moscow region, 99.6 (95-104, $n = 41$ —Gaiduc and Syarzhani, 1967). *L. t. ainu* is a large hare, with a hind foot length of 160 mm, skull length of 97.2, 98 mm, and body mass of 3,000, 3,200 g (Imaizumi, 1970). Ear length in *L. t. canescens* (86.2 mm) is shorter relative to skull length (97.7 mm) than in *L. t. timidus* (86.7 and 94.8). *L. t. hibernicus* is larger than *L. t. scoticus*, with a skull length of 93.3 mm (88.5-98.1), and a zygomatic width of 45.2 mm (43.1-47.7, $n = 28$ —T. H. Manning, pers. comm., 1978). The average adult mass in *L. t. hibernicus* is 3,190 g (2,725-3,630, $n = 27$ —Barrett-Hamilton, 1912). *L. t. kozhevnikovi* has a skull length of 99.4 mm (94-106), a zygomatic width of 48.7 mm (45-51, $n = 100$), and a body mass of 3,062 g (1,680-4,590, $n = 20-34$ —Angermann, 1967). *L. t. scoticus* has an adult mass of 2,750 g ($n = 1,097$), skull length of 89.2 mm (83.3-95.1), and a zygomatic width of



FIG. 1. Dorsal, ventral, and lateral views of the skull, and lateral view of the mandible of *Lepus t. timidus* from County Jämtland, northern Sweden. Museum of Natural History, Stockholm, A855046; collected 15 December 1989. Greatest length of skull is 88.0 mm. Photographs by Bengt-O. Olsson.

44.2 mm (42.4–45.8, $n = 26$ —T. H. Manning, pers. comm., 1978). The ears of *L. t. timidus* are relatively long (see *L. t. canescens*). Skull length of *L. t. timidus* in Norway was 95.6 mm (92.3–103.2), and zygomatic width was 47.5 mm (45.3–49.8, $n = 15$ —T. H. Manning, pers. comm., 1978), and adult mass 3,395 g (2,500–4,300, $n = 68$ —Walhovd, 1965). In Russia the same measures were: 97 (95.2–101.7), 49 (48–50.8, $n = 13$ —Ognev, 1940); 96.4, 48.1, $n = 20$ —Gaiduc and Syarzhnin, 1967); 97.8 (92–103), 48.9 (46–52), and mass 3,438 g, 2,900–4,700, $n = 29$ —Angermann, 1967). *L. t. varronis* has a skull length of 91.1 mm (85.5–94.6), and zygomatic width of 44.6 mm (43.1–45.6, $n = 9$ —T. H. Manning, pers. comm., 1978), but 93.6 (89–101), 46.1 (43–49, $n = 20$ –21—Angermann, 1967). The average mass of 20 adult males was 2,337 g (1,825–3,002), and of 11 adult females was 2,397 g (2,110–2,700—Couturier, 1964).

The ears are short and narrow with a black tip 30 mm long on the exterior surface and ca. 5 mm long on the interior surface. The hind feet are long, with hairy soles and widely spreading toes. The head and body are dusky brown in summer, and often richer brown on head, with gray-blue underfur showing through especially on the flanks. The limbs, lower throat, and upper breast are lighter than the back. The chin, upper throat, and insides of limbs are dirty white; the abdomen and tail are white. The line of demarcation is not abrupt, and varies with season (Barrett-Hamilton, 1912). The coat tends toward reddish brown at low latitudes (*L. t. ainu*, *L. t. hibernicus* and *L. t. kozhevnikovi* in the region of Moscow) but is grayish brown at high altitudes and toward the arctic, probably matching the color of the habitat (Ognev, 1940).

Most workers have reported two molts per year (Miller, 1912), but a detailed study showed three molts in *L. t. scoticus*: spring, white to brown, February–May; autumn, brown to brown, June–September; winter, brown to white, October–February (Hewson, 1958).

There are two morphs of winter coat, white = W (dominant) and blue = w (Bergengren, 1969). In white morphs *L. t. timidus* and *t. varronis*, the coat is finer, woollier, and the external appearance is almost pure white except for a small brown spot on the nose and above the eye, and black ear tips. In blue forms, *L. t. scoticus* and *L. t. canescens*, the fur is 15 mm long, supporting fibers of winter underfur 25 mm at mid-back, black underfur hair 25 mm long with white or pale buff subterminal bands, white or white-tipped guard hairs, and white or black and white vibrissae. The front of the ears is gray-brown, with a whitish back, the nose and forehead are rust brown with a brown spot over each eye, and little rust-brown below it. The outside of the forelimbs and the top of the paws are rust brown; the hind feet are white, but rust brown between the toes; back, sides and flanks are pale blue-gray with few black hairs, and the base of the fur is ash-blue with a light brown layer above (Bergengren, 1969). In European Russia the underfur of *L. t. timidus* is snow white, and in *L. t. kozhevnikovi* is straw white with the blue form occasionally present in the southwest (Ognev, 1940); only 10% are pure white in Belorus (Gaiduc, 1975). *L. t. ainu* is white except for sepia ear tips (Imaizumi, 1970). The winter fur of *L. t. hibernicus* is partially white and patchy, usually restricted to the rump, flanks, and legs, with the upper back and head remaining brown. A sprinkling of reddish hair is always present.

The summer coat in *L. t. scoticus* fur mid-dorsally is ca. 15 mm long, gray proximally and brown toward the tip. The underfur hair is ca. 25 mm long, dark gray with 2–4 mm brown subterminal band, and a black tip. The guard hairs are ca. 40 mm long and black, although some white ones may persist from the winter coat (Hewson, 1958). The head is rich brown, and the nape is gray-brown and woolly. There are variations in color of the upper parts from warm brown overlying dark gray-black to pale brown, due to difference in color and length of the subterminal band of underfur hair. In *L. t. canescens* the summer coat is yellowish gray-brown, blending evenly with an off-white abdomen. The dark upper parts of *L. t. timidus* contrast sharply with the white underside (Bergengren, 1969). The upper parts of *L. t. ainu* are grayish brown; under parts and legs are white (Imaizumi, 1970). The head of *L. t. kozhevnikovi* is rich rust-brown, and the body is the same with grayish-black mottling; the underfur has gray roots, and dull rust tips (Ognev, 1940). The summer coat of *L. t. hibernicus* is russet, not smoky brown or “blue”, and the coat of *L. t. varronis* is dull smoky gray mixed with brown, faint red and pale yellow, with the extremities lighter and more reddish; the chest is yellowish gray (Couturier, 1955, 1964). The coat of juveniles is softer and duller than that of adults, and has fewer guard hairs. Growth of late-season young may be stunted, and they may not acquire a full winter coat. Albino, melanic, and buff variations in coat color have been reported (Fraguglione, 1959; Ognev, 1940; Ritchie, 1926).

The molt to the white winter coat (Fig. 2) begins on the dorsum and is relatively rapid; the spring molt, in contrast, begins ventrally. The color change is slower in cold springs (Watson, 1963). Females turn brown ca. 2 weeks before males (Bergengren, 1969; Flux, 1970a). Hares at higher altitudes and latitudes remain white longer, in correlation with the average ambient temperature (Couturier, 1955; Lind, 1961; Salomonsen, 1939), and hence with the duration of snow cover; the timing of molt, however, is most strongly influenced by photoperiod (Küderling et al., 1984; Novikov and Blagodatskya, 1948). The spring color change is initiated by daylength and its rate is influenced by temperature (Flux, 1970a; Gaiduc,

1975, 1983; Watson, 1963). A similar process occurs in autumn, but the extent of late winter whitening is more closely correlated with snow cover (Jackes and Watson, 1975). Each part of the body has its own temperature threshold for pigment formation (Gaiduc, 1975). Dominant males may molt earlier (Verkaik and Hewson, 1986, but see Flux, 1987).

DISTRIBUTION. The geographic distribution of the mountain hare is circumpolar in tundra and taiga habitats from Britain to Japan (Fig. 3). *L. timidus* occurs over the whole of Norway and in Sweden south to 56°N, including Öland, Gotland, and there have been recent introductions to many small islands. It inhabits all Finland including Åland (Nordberg, 1951); Russia, from Kola Peninsula southward to 53°N with isolated pockets to 49°N; Mongolia, China, and eastward to Sakhalin, Kamchatka, and Hokkaido (Gruzdev and Osmolovskaya, 1969; Luo, 1988; Mallon, 1985; Ognev, 1940); Estonia, including Hiiumaa and Saaremaa (Aul et al., 1957); and Latvia and Lithuania (Grevé, 1969). In Poland it is found only in the Augustów and Rominty forests (54°N, 23°—Cabon-Raczynska, 1963). Isolated alpine populations occur above 1,300 m in the mountains of southern Germany, with introductions also in eastern Prussia (Hantel, 1963); France (detailed distribution given in Couturier, 1964); Italy; Slovenian Alps (Isakovic, 1970), and all Switzerland except Jura (Bauman, 1949). It has never been present on Iceland (E. Einarsson, pers. comm., 1978). *L. a. groenlandicus* and *L. t. timidus* were introduced into Spitzbergen in 1930 and 1931 (Myrberget, 1972), but there are "none there now" (R. Grammelvedt, pers. comm., 1980). *L. t. timidus* × *L. t. canescens* was introduced into the Faroe Islands in 1854 (Bergengren, 1969).

Reports of mountain hares from the Pyrenees are not substantiated. It is indigenous to Scotland, Ireland, and the Isle of Man. It has been introduced (mainly 19th century) to the Shetland Islands (Mainland, 1907; Vaila, 1900—Berry and Johnston, 1980), Orkney, Outer Hebrides, Skye, Raasay, Scalpay, Mull, Arran, Bute, Jura, Eigg, and Islay (now extinct—Arnold, 1978; Corbet and Southern, 1977; Hewson, 1955).

The subspecies *L. t. timidus* range includes all Norway, Sweden south to 59°N, all Finland, Russia south to 57 to 58°N and east of Ural mountains. Polish hares may belong to this subspecies but exact determination is not possible (Cabon-Raczynska, 1963). *L. t. sylvaticus* is the hare of southern Sweden, extending in hybrid zones with *L. t. timidus* to west Latvia, south coast of Norway, and Faroes (introduced). *L. t. kozhevnikovi*, the Central Russian hare, ranges from 57 to 58°N, where it apparently intergrades with *L. t. timidus*, south to 53°N. The western boundary is unclear; most authors refer to eastern Baltic hares as *L. t. timidus* although Ognev (1940) suggests *L. t. kozhevnikovi* reaches Leningrad. The distribution of the other Asian subspecies is unclear, but see Ognev (1940). To the east, *L. t. sibiricum*, is found on the plains of western Siberia, and in Altai mountains, *L. t. lugubris*. Farther to the east, in Transbaikalia, is *L. t. transbaikalicus*, and along the coast south to Manchuria, *L. t. mordeni*. In northern Siberia *L. t. begitschevi* is found in Taimyr, and east of that *L. t. kolymensis* at the river Kolyma. *L. t. gichaganus* occurs in Kamchatka, along the coast of the Sea of Okhotsk, and in central Yakutia, southward to the range of *L. t. mordeni*. *L. t. ainu* is restricted to Hokkaido, Japan, and *L. t. orii* to Sakhalin Island, but might also be present on the mainland along the coast (Ognev, 1940).

The original distribution of *L. t. scoticus* in the Scottish Highlands has been extended by introduction to southwestern Scotland in 1834–62 (Ritchie, 1929), the English Peak District, north Wales, and many islands (Hewson, 1956; Yalden, 1984). *L. t. hibernicus* occurs over the whole of Ireland on moorland and pasture down to sea level. *L. t. hibernicus* was introduced to southwestern Scotland, Mull, and the English Lake District about 1890 (Corbet and Southern, 1977; H. G. Hurrell, pers. comm., 1959). *L. t. varronis* consists of relict populations in the Alps above ca. 1,300 m, in Germany, France, Switzerland, Italy, Austria, and Yugoslavia.

FOSSIL RECORD. The Leporinae arose in the Pliocene, and *Lepus* in the early Middle Pleistocene (Kurtén, 1968). *L. timidus* appears in the F-Eemian (e.g., Lambrecht Cave, Hungary) and is common in 4-Würm, with numerous Magdalenian sites from the Pyrenees (Altuna, 1971) to southeastern Europe (Malez, 1972). *L. timidus* was present in the Kraków-Wielun Uplands (southern Poland) in beds from the last glaciation; Pleistocene hares from the Sudetic Caves might also be *L. timidus* (Kowalski, 1959). There

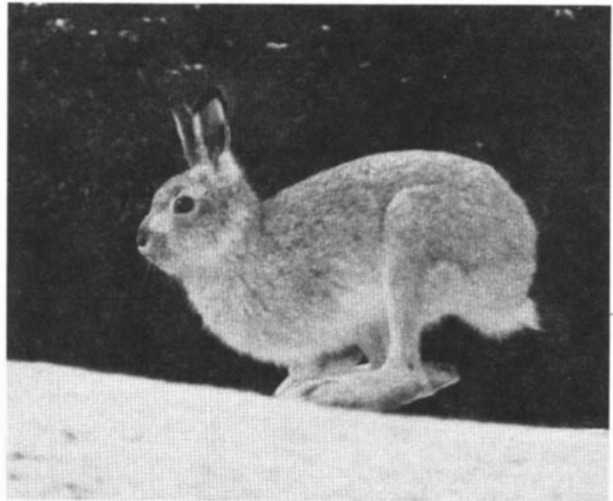


FIG. 2. The mountain hare, *Lepus timidus*, in winter pelage. Hällö, Bohuslän, Sweden, 1977. Photograph by A. Angerbjörn.

were remains from Bohemia (Mostecky, 1964, 1969) and from Germany (Heller, 1960; Luttschwager, 1956), and in general were common in the Pleistocene (Koby, 1960). In central Europe, *L. timidus* appears at the end of the Riss glaciation in the Bocksteinhöhle in Würtemberg of Acheulian age, with *L. t. varronis* recognizable from the Mousterian and becoming abundant in the upper Palaeolithic, especially the Magdalenian (Couturier, 1964). *L. timidus* was eaten by humans 28,000 years ago in Belgium (Gautier, 1973) and remains are common in Pleistocene middens (Adam, 1982). The general pattern of distribution (Barrett-Hamilton, 1912) suggests an origin in Asia or even North America, spreading eastward to Greenland, and westward to Britain; there are many remains in southern England, Italy, Spain, and in glacial deposits in the Crimea (Dahl, 1928).

FORM AND FUNCTION. As in most species of Leporidae, males of *L. timidus* tend to be smaller than females; adult males of *L. t. scoticus* average 2,510 g ($n = 507$), and females 2,890 g ($n = 590$). There also is seasonal variation in mass, with males 2,650 g ($n = 206$) in winter (September–February), 2,610 g ($n = 301$) in summer (March–August); but females 2,850 g ($n = 218$) in winter, 3,000 g ($n = 372$) in summer (combined data, Flux, 1970b; Hewson, 1968). In Norway, 37 adult females *L. t. timidus* averaged 3,504 g, 30 males 3,257 g; hares from northern Norway, 3,345 g ($n = 47$), were heavier than those from the south, 3,063 g ($n = 37$ —Walhovd, 1965). In an unaged sample of 51 *L. t. hibernicus*, males averaged 2,810 g, and females 2,860 g (Fairley, 1974), but 14 adult males averaged 3,070 g and 13 adult females 3,289 g (Barrett-Hamilton, 1912). For *L. t. kozhevnikovi*, 217 males averaged 3,336 g and 158 females 3,758 g (Ognev, 1940).

Young hares can be aged by size up to 3 months of age. They reach adult size in ca. 4 months, but can be distinguished up to 8–10 months by the notch between the apophysis and diaphysis of the tibia and humerus (Flux, 1970b).

Dried eye lenses with a mass less than ca. 250 mg distinguish young up to 1 year old from older individuals (Flux, 1970b; Walhovd, 1965). Growth of the supraorbital process with age also has been used (Borg et al., 1952; Walhovd, 1965), but annual increments in the mandible provide the most accurate technique (Ohtaishi et al., 1976).

Fat deposits in both sexes are very low from June to October, increasing to a peak in January–March, and declining when breeding starts. Fat and body mass are positively correlated for all age and sex groups (Flux, 1970b; van der Merwe and Racey, 1991). Artificial winter feeding in Finland allows hares in poor habitats to put on more fat in winter (Soveri and Aarnio, 1983). In Sweden, body condition affects the number of young weaned (Angerbjörn, 1986a).

The dental formula is: i 2/1, c 0/0, p 3/2, m 3/3, total 28. Mammæ are 2 pectoral + 6 abdominal, total 8 (Barrett-Hamilton, 1912).



FIG. 3. Distribution of *Lepus timidus* (Chapman and Flux, 1990).

ONTOGENY AND REPRODUCTION. In captivity the gestation period of *L. t. timidus* is 50.3 days (47–55, $n = 192$) with no difference between first (50.8) and second (50.0) litters (Höglund, 1957a). The breeding season in Ireland based on 51 *L. t. hibernicus* appears longer than in Scotland (Barrett-Hamilton, 1912; Fairley, 1974); Webb (1955) reported two gestation periods of 49 days. For *L. t. varronis* the gestation period is 50.8 days ($n = 4$ —Couturier, 1964). Postpartum estrus, with copulation a few hours after parturition, is the rule (Höglund, 1957a). Superfetation is not as common as in *L. europaeus* (Borg et al., 1952), but does occur (Collett, 1912). Ectopic pregnancy has been recorded once (van der Merwe and Racey, 1982). *L. t. timidus* normally has one or two litters per year, but can have three in years having early springs (Myrberget, 1983). *L. t. canescens* regularly has three litters, and starts breeding in the first half of March. Its gestation period does not differ between northern Sweden (50.0, 47–54, $n = 50$), and southern Sweden (50.1, 47–53, $n = 35$ —Angerbjörn, 1986a; Bergengren, 1969), and does not vary with nutritional levels (Pehrson and Lindlöf, 1984). The start of breeding on Swedish islands varies with temperature (Angerbjörn, 1986a). The photoperiodic control of reproduction acts through the pineal organ and its secretion of melatonin (Iason, 1987).

In *L. t. scoticus* testes are abdominal and in a regressed state (1–2 g) from July to December, but are scrotal and well developed (7–9 g) from February to May. Ovaries of 25 nonpregnant adults averaged 16.7 by 5.7 mm, and of 34 pregnant females 20.8 by 9.8 mm. Graafian follicles reach 3–5 mm in diameter before rupturing at estrus, and corpora lutea grow from 7.4 mm (5–10, $n = 23$) to 11.0 mm (8–14, $n = 27$) during gestation. In 164 adult and 61 juvenile females examined in monthly samples, pregnancies occurred during February–August; all adults were pregnant March–June. Juvenile females did not breed in the year of their birth. The average number of corpora lutea, 2.4 (1–5), increased with age, body weight, and seasonally from 1.8 (February) to 3.7 (June), followed by a decline to 2.7 (August). The mean monthly number of embryos per female was 2.1, and the average number of litters was 2.6, giving an annual production of 5–6 young per female despite 47% prenatal mortality (Flux, 1970b). Females in their first breeding year suffered heavier pre-natal losses of ova or embryos (13.6%), than did older females (6.3%), but this difference was not

statistically significant (Iason, 1990). In two areas in northeastern Scotland, from 1956 to 1967 average embryo counts varied from 1.4 to 2.7 in spring, and from 1.9 to 2.6 in summer. On less productive habitat litters were 12% smaller and breeding began 16 days later. Among 1,331 females, pregnancies occurred January–September, with over 50% pregnant March–July (Hewson, 1970). Only 63.5% ($n = 52$) of females were fertile for the first litter, but fertility rose to 95.8 ($n = 98$) and 87.1% ($n = 31$) for second and third litters respectively. The total number of young produced was correlated with hind foot length in old female hares, and hares with a large first litter had small third litters and vice versa (Iason, 1990). In captivity one-year-old females averaged 1 litter of 2.4 young ($n = 150$) compared with 1.5 litters of 4.0 ($n = 104$) for two-year-old hares (Höglund, 1957a).

First litters averaged 2.15 young (1–5, $n = 342$) and second litters 3.24 (1–8, $n = 311$). The mean number of litters, and of young per litter, were highest for hares 3–6 years old and declined at 8–10 years (Höglund, 1957a). In northern Russia (Yakutia) there is only one litter per year, which varied from 6.4 to 6.9 (1–11) young over five years (Naumov and Shatalova, 1974), but in the southwest (Belarus) three or four litters are usual. First litters averaged 2.0 young, second, 3.1; third, 3.0; and fourth, 2.7 (Gaiduc, 1973). Near Moscow, first litters averaged 5.0 corpora lutea and 3.5 embryos, and second litters 4.5 and 3.8 respectively (Naumov, 1947). For *L. t. varronis* there usually are two or three litters of 2–5 and the young are born April to July; one captive female produced 13 young in three litters in one year (Bauman, 1949). Breeding in *L. t. ainu* begins in January–February, and litter size is 1–5 (Imaizumi, 1970).

At birth the young are fully furred, their eyes are open, and they start suckling at once (Höglund, 1957a; Ognev, 1940). In *L. t. scoticus* the birth-mass (nine full-term embryos) averaged 87.3 g (71–106—Flux, 1970b); *L. t. hibernicus*, 167, 182 g ($n = 2$ —Fairley, 1974); *L. t. timidus*, 61–83 g ($n = 5$ —Walhovd, 1965), 109–150 g, depending on quality of food fed to the mother, and 80–130 g depending on litter size (Pehrson and Lindlöf, 1984), and on mother age and mass (Angerbjörn and Pehrson, 1986); *L. t. kozhevnikovii* 84–140 g (Ognev, 1940). The growth rate is 14 g per day (7–21, $n = 9$) in *L. t. scoticus* (Flux, 1970b; Hewson, 1968), 23 g (14–30, $n = 4$) in *L. t. timidus* in Norway (Walhovd,

1965), and 30 g per day ($n = 11$) in captivity (Pehrson, 1984). Young in captivity depend on milk for 10–20 days (Borg et al., 1952) but those of the final litter may continue to suckle for 6 weeks (Flux, 1970b). Young born early in the breeding season grow for a longer period, and reach a larger size (hind foot length and body mass) than do young born later, which show a more rapid growth rate but for a shorter period (Iason, 1989a; 1989b). In captivity growth of *L. t. timidus* during lactation was related to birth mass, and juvenile females grew faster than males (Angerbjörn and Pehrson, 1986). Over a longer period of growth (up to 320 days), juvenile males had a faster growth rate as indicated by hind foot length, than females; females continued to grow for a longer period, however, and ended up averaging larger (Iason, 1987).

ECOLOGY. The mountain hare is predominantly a species of mixed forest in Europe (Naumov, 1947) reaching highest densities in transition zones with open clearings (Lindlöf et al., 1974), and in swamps, river valleys, and patches of regrowth among fallen trees. In Finland, bogs with *Salix* and *Vaccinium* are favored, followed by stands of spruce (*Picea*) and birch (*Betula*). Fewer hares live in pines (*Pinus*) and mature forests (Koskimes, 1957), but less favorable habitats, such as birch forests on windy slopes, may be occupied when populations are high (Pulliainen, 1983). A second major habitat is tundra, where hares can survive to the limits of vegetation if there is cover such as cliffs or rocks. In North America, where *L. americanus* occupies forests, *L. arcticus* is restricted to tundra (Keith, 1983). In southern Russia, forests with aspen (*Populus*) and shrub thickets are the normal habitat (Ognev, 1940). Hares in Scotland reach high densities (ca. 50/km²) on well-managed *Calluna* moorland in the northeast at 300–900 m, and on arctic-alpine ground over rocks rich in nutrients (Hewson, 1984; Watson and Hewson, 1973). Hares in Ireland occupy moorland and agricultural land at all altitudes, and groups of 100 may be seen on airfields. *L. t. varronis* lives on alpine pastures, up to 4,000 m elevation in summer, and at 3,200 m in January, but most move to shelter in woodland escarpments (Billie, 1974). In Hokkaido, *L. t. ainu* is common in grassy fields, scrublands, and open forests from sea level up to the mountains (Imaizumi, 1970).

The food eaten by hares in forest habitats includes leaves and twigs of *Salix*, *Sorbus*, *Betula*, *Juniperus*, and *Populus*; in tundra, alpine plants, especially dwarf *Salix*, which is rich in nutrients; on Scottish moorlands and Swedish islands, *Calluna* (Angerbjörn, 1981; Angerbjörn and Pehrson, 1987; Pehrson, 1983a). Palatable grasses and clovers are eaten when available, and hares prefer plants growing on fertilized soil (Miller, 1968), or having a high nutrient content (Angerbjörn and Pehrson, 1987; Hewson, 1989; Lindlöf et al., 1978; Rousi et al., 1987). Snow cover may restrict the diet to twigs, bark, moss, and lichens. The diets of both sexes were similar (September–November), although reproductively active females ate more grasses and less *Calluna* than did males (Iason and Waterman, 1988), and young ate more *Agrostis* and less *Nardus* than did adults (Flux, 1970b). Studies on captive *L. t. timidus* demonstrated that dry matter digestibility is the basic factor in meeting energy requirements. Secondary plant compounds in the twigs of *Calluna* or *Betula* may reduce digestibility by causing hares to excrete sodium, but they maintained a sodium balance on a mixed diet (Pehrson, 1981, 1983a, 1983b). Plant phenolic compounds have been suggested to be involved in this reduced digestibility, but they were not reliable as a predictor of food consumption (Rousi et al., 1987).

The winter food of mountain hares in Scotland and Ireland is dominated by heather, 30 to 90% frequency from stomach analyses, whereas grasses (especially *Agrostis* and *Deschampsia*), *Eriophorum*, and dicotyledons like *Galium*, are more frequent in the summer diet (Flux, 1970b; Iason, 1987; Walker and Fairley, 1968). In Fennoscandia, the winter diet (from browsed plants) is dominated by *Betula* (15–62%), *Sorbus* (5–72%), and *Salix* (10–34%—Lindlöf et al., 1974; Lund, 1960; Pulliainen, 1972; Seiskari, 1963), whereas in Russia *Salix* (20–36%), *Populus* (6–20%), and *Vaccinium* (5–25%) are more important (Naumov, 1939). Little *Pinus* and *Picea* are eaten (0–3% in all areas) but more *Juniperus* (3–10% in all areas). In summer, captive hares in Finland avoided many of the winter foods, instead preferring *Corylus avellanus*, *Carex echinata*, *Elytrichia repens*, *Lathyrus pratensis*, *Vicia cracca*, *Trifolium pratense* and *Equisetum* spp. (Helminen et al., 1966; Seiskari, 1963); winter trials indicate the preference order of *Salix*, *Betula*, *Populus*, and *Sorbus* (Aarnio, 1983; Karlson, 1983). In Russia, seasonal food consumption is largely determined by avail-

ability rather than preference (Belkin, 1979). Other species eaten in low frequencies include *Molina*, *Nardus*, *Scirpus*, *Carex*, *Juncus*, *Alnus*, *Rubus*, *Ribes*, *Prunus*, *Rosa*, *Hippophae*, *Erica*, *Arctostaphylos*, *Empetrum*, *Myrica*, *Ledum*, *Potentilla*, *Filipendula*, *Chamerium*, *Saxifraga*, *Gentiana*, *Ranunculus*, *Achillea*, *Rumex*, *Fragaria*, *Taraxacum*, *Quercus*, *Acer*, *Fagus*, *Larix*, and *Rhododendron* (Couturier, 1964; and authors cited above).

Hares may damage cereals, brassica crops, fruit trees, and tree plantations, especially in winter (Allman, 1946; Dinesman, 1959; Wahlin, 1950), and ring-bark pines (Borisenko, 1983). They seldom drink but may eat snow. At least 500 g/day of *Betula* and *Salix* food is eaten (Sperber, 1974). The energy requirement for maintenance in winter is about 105 kcal kg⁻¹ day⁻¹, with a maximum intake of 150 kcal (Pehrson, 1984). Reingestion increases digestibility up to 25%, the soft pellets containing three times as much protein (Pehrson, 1983c), and takes place from 0900 to 1600 h; 208 hare pellets (33–450—Flux, 1970b), or 200–450 (Lampio, 1952) are produced daily.

Sex can be determined at birth by the circular genital aperture in males (Höglund and Viklund, 1953); the sex ratio is equal, with 49.3% male ($n = 140$) in captive Swedish hares (Bergengren, 1969). Among adults, females often predominate slightly: Norway, 46.2% male ($n = 474$ —Walhovd, 1965); near Moscow, 46.8% male ($n = 406$ —Naumov, 1947); Belarus, 52.8% male ($n = 286$ —Gaiduc, 1973); Japan, 50.9% male ($n = 487$ —Shibata and Yamamoto, 1980); northeastern Scotland, 46.4% male ($n = 1,492$ —Flux, 1970b), with 50.1% male ($n = 796$) in adult snared hares, declining significantly from 59% ($n = 239$) in April–May to 39% ($n = 166$) in July–August (Hewson, 1976). An increasing proportion of males at weaning was reported by Angerbjörn (1986b) for an island population with increasing densities.

The percentage of young *L. t. scoticus* in samples shot from August to January (42.9%, $n = 1,561$) in Scotland increased seasonally from 21.7% young ($n = 286$) in August to 55.3% young ($n = 921$) in December. The percentage of young in samples from four estates in December–January varied from 27.4% young ($n = 329$) to 72.8% ($n = 195$), but the overall pattern based on lens weights ($n = 1,000$) was 47.8% young, 32.2% 1 year old, and the remaining 29% 2 years or older indicating ca. 50% juvenile mortality per year (Flux, 1970b). The percentage of young snared from June to December varied with the stage of the population cycle: 36.5% young ($n = 167$) at the population peak in 1956–1958, 38.5% ($n = 322$) when numbers were low in 1959–1966, and 50% ($n = 100$) during a population increase phase in 1967–1969 (Hewson, 1976). In Norway, over the entire hunting season, 62.5% ($n = 512$) were young (Walhovd, 1965), and on a Swedish island the ratio of young to adults in autumn reached 84%; the ratio was negatively correlated with spring population density (Angerbjörn, 1986a). Among captive hares there was an average mortality of 30% for hares 1–8 years old (Höglund, 1957a), far lower than in the recaptures of marked hares liberated in Fennoscandia (Höglund, 1956, 1957b; Myrberget, 1965; Vuolanto, 1972). In Japan, the average age of a wild population of 560 hares was 0.83 years, compared with 1.11 years for captive animals (Shibata and Yamamoto, 1980). In Sweden the average winter survival for adult hares was 0.42 at low predation pressure, and 0.19 under high predation. Juvenile survivorship was 0.75 from weaning to autumn, 0.36 during a winter with low predation pressure, and 0.16 during a winter with high predation. Overall juvenile survivorship from birth to the following spring averaged 0.20 (Angerbjörn, 1992). A monthly survival rate for hares liberated in Sweden in winter, spring, and summer was 0.18 compared with 0.93 for wild hares in the same area (Lemnell and Lindlöf, 1982). A few *L. t. scoticus* reach an age of 9 years in the wild (Hewson, 1976), and 1 of 102 hares marked in 1957–1958 was shot 18 years later (R. Bain, pers. comm., 1977).

Densities are variable: 1 hare/km² over large parts of Sweden (Bergengren, 1969); 1–2/km² in European Russia (Novikov et al., 1970); 1–15/km² in Japan (Abe and Ota, 1987); 2–6/km² in central Finland (Lind, 1961); higher on Baltic islands, 25/km² on Krumnian (Nyholm, 1968) and ca. 60/km² on Signilskär (Häkkinen and Jokinen, 1974); 200–400/km² in parts of Yakutia (Labutin, 1988); up to 245/km² on the best areas in northeastern Scotland, but only 0.14/km² in western Scotland (Watson and Hewson, 1973); and 400/km² on Vedholmen, Sweden (Angerbjörn, 1986a).

In Europe numbers fluctuate less, and less regularly, than in Russia (Azarov, 1976) or in Canadian populations of *L. americanus*

(Bulmer, 1974). Peaks normally are 8–12 years apart, but 3–4 years in Fennoscandia (Hansson and Henttonen, 1989; Lindén, 1991); they are synchronous within a region, but not between countries. Populations of mountain hares may crash because of predation (Angerbjörn, 1989), parasites (Angerbjörn, 1983; Häkkinen and Jokinen, 1981), starvation (Angerbjörn, 1981; Keith, 1974), with or without a weather effect (Angerbjörn, 1983). Hares may increase and overeat their food supply, and the subsequent decline is emphasized and prolonged by predation (Keith, 1974, 1983). The cycle may be a side effect of predators shifting from voles (Angelstam et al., 1984; Hörnfeldt, 1978; Marcström et al., 1989), but snow may have an influence (Osmolovskaya, 1980). In areas of no cycles, predation may not be responsible in Scotland (Hewson, 1985), although it may be in Sweden (Lindström et al., 1986). For non-cyclic populations on islands, red fox (*Vulpes vulpes*) showed a type II or III functional response curve when preying on hares, and at lower hare densities predation might diminish fluctuations in hare numbers (Angerbjörn, 1989).

The most important mammalian predator on mountain hare is the red fox. Of 84 *L. t. scoticus* killed by predators, red fox took 63, wild cat (*Felis silvestris*) 14, dog 2, stoat (*Mustela erminea*) 2, golden eagle (*Aquila chrysaetos*) 1, buzzard (*Buteo buteo*) 1, hen harrier (*Circus cyaneus*) 1 (combined data, Flux, 1970b; Hewson, 1976). In Kuusamo, Finland, of 18 *L. t. timidus* killed, pine marten (*Martes martes*) took 6, wolf (*Canis lupus*) 4, golden eagle 4, goshawk (*Accipiter gentilis*) 2, eagle owl (*Bubo bobo*) 1, stoat 1 (Nyholm, 1968). Mountain hares represented 4–10% by volume of the diet of red foxes in Sweden in winter, as estimated from stomach analyses, and during summer from 1 to 14% by volume depending on vole abundance (Englund, 1965). In early summer, mountain hares constituted 39% by volume of the diet of juvenile foxes, but only 11% by volume during late summer (Englund, 1969). Hares, depending on their density, formed 38 to 94% by volume of the winter diet for red foxes on islands, based on fecal analysis (Angerbjörn, 1989). The diet for wolf (Rukovsky and Kupriyanov, 1972) and lynx (Azarov, 1976; Haglund, 1966; Pulliainen, 1981; Yurgensen, 1955) can be up to 70% of mountain hares, and from 1 to 33% for pine marten (Danilov and Ivanter, 1967; Lockie, 1961; Parovschikov, 1961). In northern Fennoscandia mountain hare remains were found in 5% of Arctic fox (*Alopex lagopus*) scats during the winter diet (Angerbjörn, unpubl.). *L. timidus* was found in 4% of the stomachs of wolverine (*Gulo gulo*—Myhre and Myrberget, 1975); up to 2% of mink (*Mustela vison*) fecal droppings (Tolonen, 1982); and up to 3% of stoat scats (Ben'kovsky, 1971; Lavrov, 1956; Nyholm, 1959).

The proportion of pellets from birds of prey and owls with remains of mountain hare has been used as an indication of diet. Mountain hare formed 21–26% of the diet of golden eagles in Finland (Sulkava et al., 1984); in Norway, 28–34%; in Scotland, 50%; in north Russia, 35%; in the Alps, 10%; and in Estonia, 19% (Sulkava, 1967; Sulkava et al., 1984). The proportion of mountain hare in the diet of eagle owls varied: for Norway, 2–7%; Finland, 4%; Sweden, 4%; and Germany, 7% (Mysterud and Dunker, 1983; Sulkava, 1966). Fewer hares were taken by goshawks (6% in Norway—Bergman, 1961), and hen harriers in Norway (1%), but in Scotland hares made up 11% of the diet of harriers (Picozzi, 1978). Mountain hares are taken in small amounts (less than 1%) by white-tailed eagle (*Haliaeetus albicilla*; 1.7% in Norway—Willgohs, 1961), peregrine falcon (*Falco peregrinus*), gyrfalcon (*F. rusticolus*), buzzard, snow owl (*Nyctea scandiaca*—Bergman, 1961), ural owl (*Strix uralensis*—Mysterud and Hagen, 1969), and long-eared owl (*Asio otus*—Hagen, 1965).

Parasites include the flea, *Spilopsyllus cuniculi*; lice, *Haemodipsus lyriocephalus*, *H. leporis*, and *Listrophorus gibbus* (Muroma, 1951; Sosina and Novozhilova, 1985); ticks, *Ixodes ricinus*, *I. hexagonus*, *I. persulcatus*, *Rhipicephalus sanguineus*, and *Haemaphysalis punctata* (Galimov and Galimova, 1988; Raitis and Ermala, 1972; Muroma, 1951); trematode *Fasciola hepatica* (Ognev, 1940); the pentastomid, *Linguatula taenioides* (Ognev, 1940); cestodes, *Dicrocoelium lanceolatum*, *D. dendriticum*, *Cittotaenia pectinata*, *Taenia serrata*, *T. pisiformis*, *Multiceps serialis*, *Paranoplocephala wimerosa*, *Andrya cuniculi*, and *A. rhopaloccephala* (Burgaz, 1970; Mead-Briggs and Page, 1967); nematodes, *Protostrongylus pulmonalis*, *P. commutatus*, *Trichostrongylus retortaeformis*, *T. instabilis*, *Graphidium strigosum*, *Passalurus ambiguus*, *Trichurus leporis*, and *Microfilaria* spp.; coccidia, *Eimeria leporis*, *E. robertsoni*, *E. townsendi*, *E. semisculpta*, and *E. hun-*

garica (Berg, 1981; Burgaz, 1973); and microorganisms and bacteria such as *Toxoplasma gondii*, *Pasteurella pseudotuberculosis*, *P. leipseptica*, *P. multocida*, *P. tularensis*, *Listeria monocytogenes*, *Brucella bronchiseptica*, and *Fusiformis necrophorus* (Borg et al., 1952; Couturier, 1964; Lampio, 1946; Naumov, 1941). Inkoo arbovirus has been recorded (Brummer-Korvenkontio, 1973), *Campylobacter jejuni* (Rosef et al., 1983), *Cynomys mortuorum* (Itamies and Koskela, 1980), and isolated cases of myxomatosis (Thompson, 1957). Heavily parasitized hares are more frequent in high-density populations, and have enlarged spleens, less coronary fat, and less body mass (Berg, 1981); these populations might be controlled by parasitism (Angerbjörn, 1983; Häkkinen and Jokinen, 1981), but there was no relationship between prevalence of *Trichostrongylus retortaeformis* and body mass, fatness or fecundity of hares in Scotland (Iason and Boag, 1988). Tularemia has been reported in mountain hares in Asia (Antsiferov and Brikman, 1969) and central Sweden (Christenson, 1984), and toxoplasmosis in Japan (Kitazawa, 1963).

BEHAVIOR. The mountain hare is primarily nocturnal, but shows increased daylight activity in summer when nights are short (Lemnell and Lindlöf, 1981). The hare rests by day in a "form" with ears back and eyes half closed, but sleeps for only a few minutes (Webb, 1955). They groom themselves carefully, especially in early morning and evening, and can be seen rolling in dust in dry weather. When disturbed, *L. t. scoticus* rise from their forms at ca. 20 m ($n = 376$) but this is variable and affected by temperature: 54 m ($n = 25$) at 13°C, 5 m ($n = 14$) at 21°C (Flux, 1970b). *L. t. timidus* in Finland rises at 16 m (0° to -10°C) to 43 m (-15° to -30°C), and from April to June more hares are active by day than in other months (Hewson, 1990a; Lind, 1961; Nyholm, 1968). The main feeding period begins ca. 2 h before sunset in June, 1 h before sunset in March, and less than 1 h, or after, sunset in September–February, and ends 2–3 h after sunrise in June, and about sunrise in winter (Hewson, 1962). At night they are active for 13 h in winter, 8–9 h in spring, and 8 h in summer (Bayfield and Hewson, 1975). Hares feed with their back to the wind, and can clear snow from vegetation with forepaws, but when the snow is hard, they move 5–10 km to lower ground to feed; long migrations have been recorded in Russia (Ognev, 1940). In open country, 50–300 hares may gather on good feeding areas. In continental Europe they confuse tracks and jump to the side before resting for the day (Billie, 1974; Ognev, 1940; Siivonen, 1972) but not in Scotland (Flux, 1981).

From January to July male hares often follow 2–20 m behind a female for hours. Males obviously use scent to track females; the activity of inguinal glands increases during reproduction (Sokolov et al., 1987). Females dominate males, and may strike with their forepaws with ears laid backward if the male approaches too closely. Copulation can involve five or more males and a female (Flux, 1970b), and males can be seen in long fights (Angerbjörn, in litt.) as in *L. europaeus* (Schneider, 1976). Copulatory behavior is described by Höglund (1957a), parturition by Ognev (1940), and play by Webb (1955). *L. timidus* appears to dominate *Oryctolagus cuniculus* (Flux, 1970b; Hewson, 1990b) but the relationship to *L. europaeus* is unclear; they show competitive exclusion (Hewson, 1976; Lind, 1963).

The size of the home range of *L. t. scoticus* males was 112.9 ha ($n = 16$) and for females 88.9 ($n = 17$ —Hewson and Hinge, 1990). In Japan, 11 hares that were tracked in snow averaged 1,373 m (610–1,857) in one night (Hayashi et al., 1979). The daytime range for adult males was 16.2 ha ($n = 18$), and 10.1 ($n = 17$) for adult females but only 3.7 for 14 breeding females (February–July); and 1.6 ha for small young ($n = 14$). Adult hares may travel 2.4 km to feed (Flux, 1970b). In Finland, home range sizes varies with food supply, 72 and 305 ha for two hares tracked January–March (Seiskari, 1957), but only 6.6 ha ($n = 9$) on a 92-ha island (Häkkinen and Jokinen, 1974). Ranges may overlap, and no territorial fighting, or dispersal of young, have been recorded (Hewson, 1990a). The distances moved by 99 hares recovered after game-stocking in Finland (Vuolanto, 1972), Norway (Myrberget, 1965), and Sweden (Höglund, 1956, 1957b) are: 54 hares 0–4 km; 20, 5–9 km; 15, 10–29 km; 9, 30–100 km; and 1, 200 km.

Hares make several depressions (forms) to sit in by day, trimming protruding vegetation but adding no lining. Forms can reduce wind speeds as much as 90% (Thirgood and Hewson, 1987). If undisturbed, the same form may be used for weeks, or may be

changed depending on the weather. On Scottish moors forms may last 25 years. Hares use deep vegetation for concealment in summer, and exposed positions or rocks in winter (Flux, 1970b; Håkkinen and Jokinen, 1974). In Finland, of 287 forms in forest, 189 were in spruce, 51 below fallen trees, 46 in juniper, and 1 in willow; of 72 in the open, 27 were among ice, 14 in rocks, 12 were unsheltered, 11 were beside fences, and 8 were in reeds (Nyholm, 1968). The forms are restricted to forest if *L. europaeus* is present (Lind, 1963).

In snow, hares burrow to reach or make forms and enter rock crevices or marmot burrows for shelter or escape (Bille, 1974; Thirgood and Hewson, 1987). They sometimes dig permanent burrows 1–2 m long in the ground, often used by young but seldom by adults. Hares in Ireland do not burrow (Barrett-Hamilton, 1912), nor do those in the Alps, but in Khatanaga, Russia, complex burrows up to 7 m long have been reported (Ognev, 1940).

GENETICS. The diploid number of chromosomes is 48 (Gustavsson, 1971). *Lepus* is highly conservative karyotypically, with G-banding patterns identical in most species (Robinson et al., 1983; Schröder et al., 1987). Hybrids with *L. europaeus* are rare in the wild, but easily produced in captivity; the hybrids are intermediate in form, and fertile (Fraguglione, 1966; Gustavsson, 1971; Schröder et al., 1987).

REMARKS. There has been no recent revision of *L. timidus*, although Rossolimo (1979) mapped the variation of skull size across the Palaearctic. Six currently recognized subspecies occur in Europe (*L. t. hibernicus*, *L. t. kozhevnikovi*, *L. t. scoticus*, *L. t. sylvaticus*, *L. t. timidus*, and *L. t. varronis*), seven in Asia (*L. t. begitschevi*, *L. t. gichiganus*, *L. t. kolymensis*, *L. t. lugubris*, *L. t. mordeni*, *L. t. sibericorum*, and *L. t. transbaicalicus*), and one each in the Kurile Islands (*L. t. abei*), Japan (*L. t. ainu*), and Sakhalin Island (*L. t. orii*) (Chapman and Flux, 1990).

Common names for "mountain hare" in English include: varying hare, arctic hare, and snow hare. Because the name "arctic hare" also refers to *L. arcticus*, we suggest it not be used for *L. timidus*.

LITERATURE CITED

- AARNIO, M. 1983. Selection and quality of winter food of the mountain hare in southern Finland. Finnish Game Research, 41:57–65.
- ABE, H., AND K. OTA. 1987. Fluctuation of a hare population in the Tomakomai Experiment Forest. Research Bulletin College Experiment Forestry, Hokkaido University, 44:667–674.
- ADAM, K. D. 1982. Der Mensch im Eiszeitalter. Stuttgarter Beiträge zur Naturkunde, C, 15:1–72.
- ALLEN, J. 1903. Report on the mammals collected in northeastern Siberia by the Jessup North Pacific expedition, with itinerary and field notes, by N. G. Buxton. Bulletin of the American Museum of Natural History, 19:101–184.
- ALLMAN, D. 1946. Observations on damage by hares at Clonegal Forest. Irish Forestry, 3:92.
- ALTUNA, J. 1971. Fauna de Maníferos de los Yacimientos prehistóricos de Guipuzcoa. Con Catálogo de los Muníferos Cuaternarios del Cantabrico y del Pirineo occidental. Aranzadi Ciencias Naturales, Munibe, San Sebastian, 24:1–465.
- ANGELSTAM, P., E. LINDSTRÖM, AND P. WIDÉN. 1984. Role of predation in short-term fluctuations of some birds and mammals in Fennoscandia. Oecologia, 62:199–208.
- ANGERBJÖRN, A. 1981. Winter food as a limiting factor of dense mountain hare populations on islands, a comparative study. Pp. 529–535, in Proceedings of World Lagomorph Conference (K. Myers and C. D. MacInnes, eds.). Guleph, Ontario, 983 pp.
- . 1983. Proximate causes of mountain hare population crashes: a review. Finnish Game Research, 41:29–38.
- . 1986a. Reproduction of mountain hares (*Lepus timidus*) in relation to density and physical condition. Journal of Zoology (London), 208:559–568.
- . 1986b. Population dynamics of mountain hares *Lepus timidus* L. on islands. Ph. D. dissert., Stockholm University, 143 pp.
- . 1989. Mountain hare populations on islands: effects of predation by red fox. Oecologia, 81:335–340.
- . 1992. Mortality pattern in mountain hares (*Lepus timidus*) on islands. Pp. 87–93, in Global trends in wildlife management, Vol. 1 (B. Bobek, K. Perzanowski, and W. L. Reglin, eds.). Swiat Press, Krakow, 660 pp.
- ANGERBJÖRN, A., AND Å. PEHRSON. 1986. Maternal investment in mountain hares under different feeding regimes. Pp. 46–68, in A. Angerbjörn, Population dynamics of mountain hares *Lepus timidus* L. on islands. Ph. D. dissert., 1986b, Stockholm University, 143 pp.
- . 1987. Factors influencing winter food choice by mountain hares (*Lepus timidus* L.) on Swedish coastal islands. Canadian Journal of Zoology, 65:2163–2167.
- ANGERMANN, R. 1967. Beiträge zur Kenntnis der Gattung *Lepus* (Lagomorpha, Leporidae) III. Zur Variabilität palaearktischer Schneehasen. Mitteilungen aus dem Zoologischen Museum in Berlin, 43:161–178.
- ANTSIFEROV, M. I., AND D. I. BRIKMAN. 1969. Study of infective sensitivity of *Lepus timidus* to tularemia. Zoologicheskii Zhurnal, 48:942–943.
- ARNOLD, H. R. 1978. Provisional atlas of the mammals of the British Isles. Abbots Ripton, Huntingdon, 58 pp.
- AUL, J., R. LING, AND K. PAAVER. 1957. Eesti nsv Imetajad. Eesti Riiklik Kirjastus, Tallinn, 351 pp.
- AZAROV, V. I. 1976. Distribution and migration of *Felis lynx* in the south of West Siberia and North Kasakgstan. Zoologicheskii Zhurnal, 55:624–628.
- BAKER, A. J., J. L. EGER, R. L. PETERSON, AND T. H. MANNING. 1983. Geographic variation and taxonomy of arctic hares. Acta Zoologica Fennica, 174:45–48.
- BARRETT-HAMILTON, G. E. H. 1900. Exhibition of skins of the variable hare. Proceedings of the Zoological Society of London, (1900):87–92.
- . 1912. A history of British mammals. Gurney and Jackson, London, 748 pp.
- BAUMANN, F. 1949. De freilebenden Säugetiere der Schweiz. H. Huber, Bern, 492 pp.
- BAYFIELD, N. G., AND R. HEWSON. 1975. Automatic monitoring of trail use by mountain hares. Journal of Wildlife Management, 39:214–217.
- BELKIN, V. V. 1979. The feeding of the mountain hare in Karelia. Biologii Nauk, Moscow, SSSR, 1979(5):59–62.
- BELL, T. 1837. A history of British quadrupeds including the Cetacea. London, 526 pp.
- BEN'KOVSKY, L. M. 1971. *Mustela erminea* on Sakhalin Island. Zoologicheskii Zhurnal, 50:1264–1266.
- BERG, C. 1981. Endoparasitism in wild Norwegian hares (*Lepus timidus*). Parasitologiska Institutionen Åbo Akademi Information, 16:88–89.
- BERGENGREN, A. 1969. On genetics, evolution and history of distribution of the heath-hare, a distinct population of the Arctic hare, *Lepus timidus* Lin. Viltrevy, 6:381–460.
- BERGMAN, G. 1961. The food of birds of prey and owls in Fennoscandia. British Birds, 54:307–320.
- BERRY, R. J., AND J. L. JOHNSTON. 1980. The natural history of Shetland. Collins, London, 380 pp.
- BILLE, R. P. 1974. Les animaux de montagne. Éditions Danoël, Paris, 219 pp.
- BLYTH, E. 1842. The report of the curator of the society. Journal of the Asiatic Society of Bengal, 11:95–115.
- BORG, K., N. HÖGLUND, AND G. NOTINI. 1952. Nytt om haren. Svenska Jägar Meddelanden, 17:1–90.
- BORISENKO, V. A. 1983. "Ringing" of the pine by the alpine hare. Biulletin Moskovskogo Obshchestva Ipsyatelay Prirody, Biologii, 88:32–44.
- BRUMMER-KORVENKONTIO, M. 1973. Arboviruses in Finland: V. Serological survey of antibodies against Inkoo virus (California group) in human, cow, reindeer, and wildlife sera. American Journal of Tropical Medicine and Hygiene, 22:654–661.
- BULMER, M. G. 1974. A statistical analysis of the 10-year cycle in Canada. Journal of Animal Ecology, 43:701–718.
- BURCAZ, I. 1970. The endoparasites of the varying hare (*Lepus timidus*) and the European hare (*Lepus europaeus*). Zoological Review (Stockholm), 32:61–66.
- . 1973. A cross infection experiment with coccidia concerning mountain hares *Lepus timidus* and tame rabbits. Norwegian Journal of Zoology, 21:327.
- CABON-RACZYNSKA, K. 1963. Occurrence of the blue hare, *Lepus timidus* Linnaeus, 1758 in Poland. Acta Theriologica, 6:303–305.

- CHAPMAN, J. A., AND J. E. C. FLUX (EDS.). 1990. Rabbits, hares and pikas: status survey and conservation action plan. IUCN, Gland, Switzerland, 168 pp.
- CHRISTENSON, B. 1984. An outbreak of tularemia in the northern part of central Sweden. *Scandinavian Journal of Infectious Disease*, 16:285-290.
- COLLETT, R. 1912. *Norges pattedyr*. H. Aschehoug & Co., Kristiania, 744 pp.
- CORBET, G. B. 1978. The mammals of the Palaearctic region: a taxonomic review. British Museum (Natural History), Cornell University Press, Ithaca, New York, 314 pp.
- CORBET, G. B., AND J. E. HILL. 1986. A world list of mammalian species. British Museum (Natural History), London, 254 pp.
- CORBET, G. B., AND H. N. SOUTHERN. 1977. The handbook of British mammals. Second Ed. Blackwell, London, 520 pp.
- COUTURIER, M. 1955. Das Haarkleid des Alpenschneehasen *Lepus timidus varronis* Miller, 1901. *Zeitschrift für Jagdwissenschaft*, 1:8-23.
- . 1964. Le gibier des montanges francaises. Arthaud, France, 461 pp.
- DAHL, S. K. 1928. Ueber das Vorkommen des Scheehasen (*Lepus timidus* L.) in der Krim. *Bulletin Societe Naturales Crimée Simférapol*, 10:37-39.
- DANILOV, P. I., AND E. B. IVANTER. 1967. The pine marten in Karelia. *Uchenye zapiski Petrozavodsk Universitet*, 15:179-197.
- DINESMAN, L. G. 1959. The effect of *Lepus timidus* on the regeneration of larch forests in central Yakutia. *Biulletin Moskovskogo Obshchestra Ispyatelai Prirody*, 64:17-25.
- ENGLUND, J. 1965. Studies on food ecology of the red fox (*Vulpes v.*) in Sweden. *Viltrevy*, 3:377-485.
- . 1969. The diet of foxes (*Vulpes vulpes*) in Sweden. *Viltrevy*, 6:1-39.
- ERXLEBEN, I. C. P. 1777. *Systema regni animalis per classes, ordines, genera, species, varietates cum synonymia et historia animalium*. Classes I, Mammalia. Weygandianis, Lipsiae, 636 pp.
- FAIRLEY, J. S. 1974. Notes on the winter breeding condition of hares in the west of Ireland. *Irish Naturalist Journal*, 18:17-19.
- FLUX, J. E. C. 1970a. Colour change of mountain hares (*Lepus timidus scoticus*) in north-east Scotland. *Journal of Zoology* (London), 162:345-358.
- . 1970b. Life history of the mountain hare (*Lepus timidus scoticus*) in north-east Scotland. *Journal of Zoology* (London), 161:75-123.
- . 1981. Field observations of behaviour in the genus *Lepus*. Pp. 377-394, in *Proceedings of the World Lagomorph Conference* (K. Meyers and C. D. MacInnes, eds.). Guelph, Ontario, 983 pp.
- . 1987. Moults, condition and body weight in mountain hares (*Lepus timidus*). *Journal of Zoology* (London), 212:365-367.
- FRAGUGLIONE, D. 1959. Les anomalies du pelage chez les lièvres commun et variable. *Diana*, 4:57-59.
- . 1966. L'hybridation du lièvre commun et du lièvre variable, *Lepus e. europaeus* × *Lepus timidus varronis* (Pallas, 1878). *Säugetierkundliche Mitteilungen*, 14:92-100.
- GAIDUC, V. E. 1973. Reproduction of *L. timidus* in Belorussia. *Vestnik Akademii Nauk SSSR*, 1973(4):107-108.
- . 1975. Influence of some abiotic factors upon moulting and pigmentation of hair cover in *Lepus timidus*. *Zoologicheskii Zhurnal*, 54:425-431.
- . 1983. Rhythms of molts in animals with seasonal dimorphism of hair cover color. *Zhurnal Obshchei Biologii*, 44:269-279.
- GAIDUC, V. E., AND I. M. SYARZHANIN. 1967. Systematic position of the snow hare in Belorussia. *Vestnik Akademii Nauk SSSR*, 1967(3):115-118.
- GALIMOV, V. R., AND E. Z. GALIMOVA. 1988. Hosts of the adult *Ixodes persulcatus* P. Soh. and their role in the circulation of tick-borne encephalitis. *Meditsinskaiia Parazitologiiia i Parazitornye Bolezni*, 57:39-41.
- GAUTIER, A. 1973. The fauna of the Palaeolithic site of Maisières-Canal: Fossil Mammalia. Institut Royal Sciences Naturelles de Belgique, *Memoires*, 172:1-20.
- GOODWIN, C. G. 1933. Mammals collected in the Maritime province of Siberia by the Morden-Graves North Asiatic expedition, with the description of a new hare from the Amur river. *American Museum Novitates*, 681:1-18.
- GREVÉ, K. 1969. *Säugetiere Kur-Liv-Estlands*. Mellin and Co., Riga, 183 pp.
- GRUZDEV, V. V., AND V. I. OSMOLOVSKAYA. 1969. The areal structure of blue hare in the European part of the USSR. *Biologicheskie Nauki*, 1969(2):27-30.
- GUSTAVSSON, I. 1971. Mitotic and meiotic chromosomes of the variable hare (*Lepus timidus* L.), the common hare (*Lepus europaeus* Pall.) and their hybrids. *Hereditas*, 67:27-34.
- HAGEN, Y. 1965. The food, population fluctuations and ecology of the long-eared owl (*Asio asio* (L.)) in Norway. *Papers of the Norwegian State Game Research Institute*, 23:1-43.
- HAGLUND, B. 1966. Winter habits of the lynx (*Lynx lynx* L.) and wolverine (*Gulo gulo* L.) as revealed by tracking in the snow. *Viltrevy*, 4:81-310.
- HÄKKINEN, I., AND M. JOKINEN. 1974. On the winter ecology of the snow hare (*Lepus timidus*) in the outer archipelago. *Suomen Riista*, 25:5-14.
- . 1981. Population dynamics of the mountain hare on an island in the outer archipelago of S.W. Finland. Pp. 469-477, in *Proceedings of World Lagomorph Conference* (K. Myers and C. D. MacInnes, eds.). Guelph, Ontario, 983 pp.
- HANSSON, L., AND H. HENTTONEN. 1989. Rodents, predation and wildlife cycles. *Finnish Game Research*, 46:26-33.
- HANTEL, E. 1963. Schneehasen in Ostpreussen. *Der Pirsch*, München, 15:1103.
- HAYASHI, C., T. KOMAZAWA, AND F. HAYASHI. 1979. A new statistical method to estimate the size of animal population—estimation of population size of hare. *Annals of the Institute of Statistical Mathematics*, 31:325-348.
- HELLER, F. 1960. Das Diluvialprofil in der Jungfernhöhle bei Tiefenellern, Landkreis Bamberg. *Erlangergeol. Abhandlungen*, 34:3-17.
- HELMINEN, M., K. VALANNE, A. PIKOLA, AND I. STÉN. 1966. Summer feeding habits of the mountain hare (*Lepus timidus*) and of the brown hare (*L. europaeus*). *Suomen Riista*, 18:133-144.
- HEWSON, R. 1955. The mountain hare in the Scottish Islands. *Scottish Naturalist*, 67:52-60.
- . 1956. The mountain hare in England and Wales. *The Naturalist*, London, 858:107-109.
- . 1958. Moults and winter whitening in the mountain hare *Lepus timidus scoticus* Hilzheimer. *Proceedings of the Zoological Society of London*, 131:99-108.
- . 1962. Food and feeding habits of the mountain hare *Lepus timidus scoticus* Hilzheimer. *Proceedings of the Zoological Society of London*, 139:415-426.
- . 1968. Weights and growth rates in the mountain hare *Lepus timidus scoticus*. *Journal of Zoology* (London), 154:249-262.
- . 1970. Variation in reproduction and shooting bags of mountain hares on two moors in north-east Scotland. *Journal of Applied Ecology*, 7:243-252.
- . 1976. A population study of mountain hares (*Lepus timidus*) in north-east Scotland from 1956-1969. *Journal of Animal Ecology*, 45:395-414.
- . 1984. Mountain hare, *Lepus timidus*, bags and moor management. *Journal of Zoology* (London), 204:563-565.
- . 1985. Long-term fluctuations in populations of mountain hares (*Lepus timidus*). *Journal of Zoology* (London), 206:269-273.
- . 1989. Grazing preferences of mountain hares on heather moorland and hill pastures. *Journal of Applied Ecology*, 26:1-11.
- . 1990a. Behaviour, population changes and dispersal of mountain hares (*Lepus timidus*) in Scotland. *Journal of Zoology* (London), 220:287-309.
- . 1990b. Interactions between mountain hares (*Lepus timidus*) and other mammals. *Journal of Zoology* (London), 221:302-305.
- HEWSON, R., AND M. D. C. HINCE. 1990. Characteristics of the home range of mountain hares *Lepus timidus*. *Journal of Applied Ecology*, 27:651-666.
- HILZHEIMER, M. 1906. Die europäischen Hasen. *Zoologischer Anzeiger*, Leipzig, 30:510-513.

- HÖGLUND, N. H. 1956. Swedish Sportsmen's Association's marking of game 1945-1954. *Viltrevy*, 1:162-224.
- . 1957a. Fortplantningen hos skogsharen (*Lepus t. timidus* Lin.). *Viltrevy*, 1:267-282.
- . 1957b. Svenska Jägarförbundets viltmärkningar 1955 och 1956. *Viltrevy*, 1:283-317.
- HÖGLUND, N. H., AND J. VIKLUND. 1953. On determining the sex of young hares. *SUOMEN RIISTA*, 8:175-176.
- HÖRNFELDT, B. 1978. Synchronous population fluctuations in voles, small game, owls, and tularemia in Northern Sweden. *Oecologia*, 32:141-152.
- IASON, G. R. 1987. Seasonal reproduction in the mountain hare: ecological and physiological constraints. Ph. D. dissert., University of Aberdeen, 167 pp.
- . 1989a. Growth and mortality in mountain hares: the effect of sex and date of birth. *Oecologia*, 81:540-546.
- . 1989b. Mortality of mountain hares in relation to body size and age. *Journal of Zoology (London)*, 219:676-680.
- . 1990. The effect of size, age and a cost of early breeding on reproduction in female mountain hares. *Holarctic Ecology*, 13:81-89.
- IASON, G. R., AND B. BOAG. 1988. Do intestinal helminths affect condition and fecundity of adult mountain hares? *Journal of Wildlife Diseases*, 24:599-605.
- IASON, G. R., AND P. G. WATERMAN. 1988. Avoidance of plant phenolics by juvenile and reproducing female mountain hares in summer. *Functional Ecology*, 2:433-440.
- IMAIZUMI, Y. 1970. The handbook of Japanese land mammals. Shin-Shicho-Sha Co., Tokyo, 360 pp.
- ISAKOVIC, I. 1970. Game management in Yugoslavia. *Journal of Wildlife Management*, 34:800-812.
- ITAMIES, J., AND P. KOSKELA. 1980. Cynomyia mortuorum myiasis in *Lepus timidus*. *Annales Entomologici Fennici*, 46:24.
- JACKES, A. D., AND A. WATSON. 1975. Winter whitening of Scottish mountain hares (*Lepus timidus scoticus*) in relation to daylength, temperature and snow-lie. *Journal of Zoology (London)*, 178:403-409.
- JOHANSEN, H. E. 1923. Po Chulymu. *Izvestiya Tomskogo gosudarstvennogo universiteta*, 72:1-68.
- KARLSEN, S. 1983. Winter food preferences of the mountain hare in Norway. *Finnish Game Research*, 41:67-74.
- KASTSCHENKO, N. F. 1899. Rezul'tati Altajskoj zoologii eskj ekspedicii 1898 goda. Pozvono nye Tomsk: tipolit M. N. Cononova i I. F. Skulimovskogo, 158 pp.
- KEITH, L. B. 1974. Some features of population dynamics of mammals. *Proceedings of International Congress for Game Biologists*, 11:17-58.
- . 1983. Role of food in hare population cycles. *Oikos*, 40:385-395.
- KITAZAWA, K. 1963. Histopathological studies on toxoplasmosis in various mammals. *Memoirs of Ehime University Section Vi (Agriculture)*, 9:265-324.
- KOBY, F. 1960. Sur l'extension maxima vers le sud-ouest de quelques représentants de la faune froide Würmienne. *Anthropos* 1, Supplement, 1960:101-107.
- KOLJUSHEV, I. I. 1936. Mlekopitayushchie krainego severa, zapadnoi i srednei Sibiri. *Trudy Biologicheskogo nauchno-issledovatel'skogo instituta, Tomsk*, 2:304-306.
- KOSKIMIES, J. 1957. Studies on the winter habitat preferences of the snow hare, *Lepus timidus* L. *Archivum Societatis Zoologicae Botanicae Fennicae 'Vanamo'*, 12:29-37.
- KOWALSKI, E. 1959. A catalogue of the Pleistocene mammals of Poland. *Akademia Nauk, Warszawa*, 267 pp.
- KÜDERLING, I., M. C. CEDRINI, F. FRASCHINI, AND M. SPAGNESI. 1984. Season-dependent effects of melatonin on testes and fur color in mountain hares (*Lepus timidus*). *Experientia (Basel)*, 40:501-502.
- KURODA, N. 1928. The mammal fauna of Sakhalin. *Journal of Mammalogy*, 9:222-229.
- . 1938. A list of the Japanese mammals. Published privately by the author, Tokyo, 122 pp.
- KURTÉN, B. 1968. Pleistocene mammals of Europe. *Weidenfeld and Nicholson, London*, 317 pp.
- LABUTIN, Y. V. 1988. Features of spatial distribution and behaviour of the arctic hare (*Lepus timidus*) in Yakutia as adaptations of the species to conditions of the north. *Soviet Journal of Ecology*, 19:102-105.
- LAMPIO, T. 1946. Game diseases in Finland, 1924-43. *Suomen Riista*, 1:93-142.
- . 1952. An experiment in the control of disease in the snow hare. *Papers on Game Research, Helsinki*, 8:139-142.
- LAVROV, N. P. 1956. Characteristics and causes of the prolonged depression in numbers of the ermine in forest-steppe and steppe zones of USSR. *Trudy Vses. Nauk Issledovatel'skii Institut Okhot. Promyshlennosti*, 16:89-107.
- LEMNELL, P. A., AND B. LINDLÖF. 1981. Diurnal and seasonal activity pattern in the mountain hare. Pp. 349-356, in *Proceedings of the World Lagomorph Conference* (K. Myers and C. D. MacInnes, eds.). Guelph, Ontario, 983 pp.
- . 1982. Experimental release of captive-reared mountain hares. *Viltrevy*, 12:115-128.
- LIND, E. A. 1961. On the occurrence, daily activity, and spring moult of the snow hare (*Lepus timidus*) at Kilpisjärvi in Entontekio. *Suomen Riista*, 14:106-111.
- . 1963. Observations on the mutual relationship between the snow hare (*Lepus timidus*) and the field hare (*L. europaeus*). *Suomen Riista*, 16:128-135.
- LINDÉN, H. 1991. Analysis of game questionnaires: the validity of the alternative prey hypothesis in Finland. *Suomen Riista*, 37:67-78.
- LINDLÖF, B., E. LINDSTRÖM, AND Å. PEHRSON. 1974. On activity, habitat selection and diet of the mountain hare (*Lepus timidus* L.) in winter. *Viltrevy*, 9:27-43.
- LINDLÖF, B., Å. PEHRSON, AND A. JOHANSSON. 1978. Summer food preference by penned mountain hares in relation to nutrient content. *Journal of Wildlife Management*, 42:928-932.
- LINDSTRÖM, E., H. ANDRÉN, P. ANGELSTAM, AND P. WIDÉN. 1986. Influence of predators on hare populations in Sweden: a critical review. *Mammal Review*, 16:151-156.
- LINK, H. F. 1795. Über die classification der Säugetiere. Pp. 42-112, in *Beiträge zur Naturgeschichte*. Bd. 1:2, Karl Christoph Stiller, Rostock und Leipzig, 126 pp.
- LINNAEUS, C. 1758. *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*. 10th revised edition. *Impensis Laurentii Salvi, Stockholm*, 824 pp.
- LOCKIE, J. D. 1961. The food of the pine marten *Martes martes* in west Ross-shire, Scotland. *Proceedings of the Zoological Society of London*, 136:187-195.
- LUND, H. M.-K. 1960. The winter food of *Lepus timidus* L. in Norway (A preliminary report). *Proceedings of the International Congress of Game Biologists*, 4:52-56.
- LUO, Z. 1988. The Chinese hare. *China Forestry Publishing House, Beijing*, 186 pp.
- LÜTTSCHWAGER, J. 1956. Vorgeschichtliche Säugetierwelt in Schleswig-Holstein. *Säugetierkundliche Mitteilungen*, 4:27-30.
- MALEZ, M. 1972. On the distribution of ice-age animals in the late Pleistocene of southeastern Europe. *Radovi Jugoslavenske Akademija Znanosti i Umjetnosti*, 364:133-180.
- MALLON, D. P. 1985. The mammals of the Mongolian People's Republic. *Mammal Review*, 15:71-102.
- MARCRSTRÖM, V., L. B. KEITH, E. ENGREN, AND J. R. CARY. 1989. Demographic responses of arctic hares (*Lepus timidus*) to experimental reductions of red foxes (*Vulpes vulpes*) and martens (*Martes martes*). *Canadian Journal of Zoology*, 67:658-668.
- MEAD-BRIGGS, A. R., AND R. J. C. PAGE. 1967. Ectoparasites from hares collected throughout the United Kingdom, January-March 1964. *Entomologists Monthly Magazine*, 103:26-34.
- MILLER, G. R. 1968. Evidence for selective feeding on fertilized plots by red grouse, hares, and rabbits. *Journal of Wildlife Management*, 32:843-853.
- MILLER, G. S. 1901. The alpine varying hare. *Proceeding of the Biological Society of Washington*, 14:97-98.
- . 1912. Catalogue of the mammals of western Europe. *British Museum (Natural History) London*, 1019 pp.
- MOSTECKY, V. 1964. Pleistozäne Säugetiere aus dem Steinbruch auf 'Chlum' Mittelböhmen, unweit von Beroun, spatenes Würumstadial. *Sbornik Národního Muzea Praze*, 20:153-188.
- . 1969. Late Pleistocene mammals from the "Chlupac Cave" on Kobyla hill near Koneprusy (Bohemian Karst). *Sbornik Národního Muzea Praze*, 25:1-55.
- MUROMA, E. 1951. A list of parasites and diseases of the most

- important game animals in Finland. Suomen Riista, 6:159-162.
- MYHRE, R., AND S. MYRBERGET. 1975. Diet of wolverine (*Gulo gulo*) in Norway. Journal of Mammalogy, 56:752-757.
- MYRBERGET, S. 1965. Returns of game species marked by the Norwegian Hunting and Fishing Association, 1947-62. Papers of Norwegian State Game Research, 21:1-24.
- . 1972. Introduction of hares to Spitzbergen in 1930 and 1931. Fauna, 25:126.
- . 1983. Early reproduction in 1983 of mountain hares on Tranoy study area in northern Norway. Suomen Riista, 30:35.
- MYSTERUD, I., AND H. DUNKER. 1983. Food and nesting ecology of the eagle owl, *Bubo bubo* (L.) in four neighbouring territories in southern Norway. Viltrevy, 12:71-113.
- MYSTERUD, I., AND T. HAGEN. 1969. The food of the Ural owl (*Strix uralensis* Pall.) in Norway. Nytt Magasin for Zoologi, 17:165-167.
- NAUMOV, S. P. 1939. Winter food habits of the white hare (*Lepus timidus* L.). Zoologicheskii Zhurnal, 18:1055-1063.
- . 1941. Methods for forecasting population changes in the white hare (*Lepus timidus* L.). Transactions of the Central Laboratory of Biology for the Game Industry, 5:46-60.
- . 1947. Ecology of the white hare *Lepus timidus* L. Moscow Society of Natural Research, Moscow, 206 pp.
- NAUMOV, S. P., AND S. P. SHATALOVA. 1974. Species indices of reproduction in mammals and peculiarities of their geographic variation (Leporidae taken as an example). Zoologicheskii Zhurnal, 53:1856-1864.
- NILSSON, S. 1831. Illuminerade figurer till Skandnaviens Fauna, planch 22. Band 1: Häfte 9, (text referring to this plate in Band 1: Häfte 8, 18 pp.). Academie Boktryckeriet, C. F. Berling, Lund, 274 pp.
- . 1844. Öfversigt af Kongliga Vetenskaps-Akademiens Förhandlingar, 1844:133.
- NORDBERG, S. 1951. Game and game management in the Åland archipelago. Suomen Riista, 5B:7-59.
- NOVIKOV, B. G., AND B. I. BLAGODATSKIA. 1948. Mechanism of development of protective seasonal colorations. Doklady Akademii Nauk, SSSR, 61:577-580.
- NOVIKOV, G. A., A. E. AIRAPETJANTZ, Y. B. PUKINSKY, P. P. STRELKOV, AND E. K. TIMOFEEVA. 1970. The mammals of the Leningrad region. Izdatelstvo Leningradskogo Universitet, 302 pp.
- NYHOLM, E. S. 1959. Stoats and weasels and their winter habitats. Suomen Riista, 13:106-116.
- . 1968. Ecological observations on the snow hare (*Lepus timidus* L.) on the islands of Krunnit and in Juusamo. Suomen Riista, 20:15-31.
- OGNEV, S. I. 1922. Nekotorye dannye po sistematike russkikh zaitsev. Biologicheskije Izvestiya, 1:106.
- . 1929. Zur systematik der russischen Hasen. Zoologische Anzeiger, Leipzig, 84:69-83.
- . 1940. Mammals of the USSR and adjacent countries. IV. Rodents. Izvestii Akademii Nauk SSSR, Moscow, Leningrad, 429 pp.
- OHTAISHI, N., N. NACHIYA, AND Y. SHIBATA. 1976. Age determination of the hare from annual layers in the mandibular bone. Acta Theriologica, 21:168-171.
- OSMOLOVSKAYA, V. I. 1980. Importance of snow covering and conifer harvest on the life of mammals and birds in the Moscow area, Russian SFSR, USSR. Bulletin Moskovskogo Obshchestra Ispyatelai Prirody, 85:135-148.
- PALLAS, P. S. 1778. Novae species quadrupedum e glirium ordine. Wolfgangi Waltheri, Erlangae, 388 pp.
- PAROVSHCHIKOV, V. Y. 1961. The feeding habits of pine martens in the vicinity of Archangel. Zoologicheskii Zhurnal, 40:1112-1115.
- PEHRSON, Å. 1981. Winter food consumption and digestibility in caged mountain hares. Pp. 732-742, in Proceedings of World Lagomorph Conference (K. Myers and C. D. MacInnes, eds.). Guelph, Ontario, 983 pp.
- . 1983a. Digestibility and retention of food components in caged mountain hares (*Lepus timidus* L.) during the winter. Holarctic Ecology, 6:395-400.
- . 1983b. Maximal winter browse intake in captive mountain hare. Finnish Game Research, 41:45-55.
- . 1983c. Caecotrophy in caged mountain hares (*Lepus timidus*). Journal of Zoology (London), 199:563-574.
- . 1984. Faecal nitrogen as an index of hare browse quality. Canadian Journal of Zoology, 62:510-513.
- PEHRSON, Å., AND B. LINDLÖF. 1984. Impact of winter nutrition on reproduction in captive mountain hares (*Lepus timidus*) (Mammalia: Lagomorpha). Journal of Zoology (London), 204:201-209.
- PICOZZI, N. 1978. Dispersion, breeding and prey of the hen harrier *Circus cyaneus* in Glen Dye, Kincardineshire. Ibis, 120:498-509.
- PULLIANEN, E. 1972. Nutrition of the arctic hare (*Lepus timidus*) in northeast Finland. Annales Zoologici Fennici, 9:17-22.
- . 1981. A transect survey of small land carnivore and red fox populations on a subarctic fell in Finnish forest Lapland over 13 winters. Annales Zoologici Fennici, 18:270-278.
- . 1983. The refuge theory and habitat selection in the mountain hare on a subarctic fell in Finnish forest Lapland. Finnish Game Research, 41:39-44.
- RAITIS, T., AND A. ERMALA. 1972. Internal parasites in the snow hare (*Lepus timidus*). Suomen Riista, 24:82-87.
- RITCHIE, J. 1926. Abnormal colouration in Scottish mountain hares. Scottish Naturalist, 1926:11-15.
- . 1929. The spread of the mountain hare in the Scottish Lowlands and Border Country. Scottish Naturalist, 1929:169-175.
- ROBINSON, T. J., F. F. B. ELDER, AND J. A. CHAPMAN. 1983. Karyotypic conservation in the genus *Lepus* (order Lagomorpha). Canadian Journal of Genetics and Cytology, 25:540-544.
- ROSEF, O., B. GONDROSEN, G. KAPPERUD, AND B. UNDERDAL. 1983. Isolation and characterization of *Campylobacter jejuni* and *Campylobacter coli* from domestic and wild mammals in Norway. Applied Environmental Microbiology, 46:855-859.
- ROUSI, M., J. HÄGGMAN, AND J. P. BRYANT. 1987. The effect of bark phenols upon mountain hare barking of winter-dormant Scots pine. Holarctic Ecology, 10:60-64.
- ROSSOLIMO, O. L. 1979. A study of geographical variation in the skull of *Lepus timidus* L. Sbornik Trudor Zoologicheskogo Muzeya Moskovskogo Universiteta, 18:325-350.
- RUKOVSKY, N. N., AND A. G. KUPRIYANOV. 1972. Some peculiarities of distribution and ecology of *Canis lupus* in the Onega Peninsula. Zoologicheskii Zhurnal, 51:1592-1596.
- SALOMONSEN, F. 1939. Moults and sequence of plumages in the rock ptarmigan (*Lagopus mutus* (Montin)). Videnskabelige Meddelelser fra Dansk naturhistorisk Forening i Kjobenhavn, 103:1-491.
- SCHNEIDER, E. 1976. Der Zeitige Kenntnisse uber das Paarungsverhalten des Feldhasen. Pp. 41-57, in Ecology and management of European hare populations (Z. Pielowski and Z. Pucek, eds.). Polish Hunting Association, Warsaw, 286 pp.
- SCHRÖDER, J., T. SOVERI, H. A. SUOMALAINEN, L.-A. LINDBERG, AND W. VAN DER LOO. 1987. Hybrids between *Lepus timidus* and *Lepus europaeus* are rare although fertile. Hereditas, 107:185-189.
- SEISKARI, P. 1957. Winter home range of the snow hare. Suomen Riista, 16:101-108.
- . 1963. Summer food of *Lepus timidus*. Suomen Riista, 16:46-55.
- SHIBATA, Y., AND T. YAMAMOTO. 1980. A study on the population dynamics of *Lepus timidus ainu* 1. Age distributions and life table. Bulletin of the Forestry and Forest Products Research Institute, 309:13-22.
- SIIVONEN, L. 1972. Suyomen nisäkkäät 2. Otava, Helsinki, 435 pp.
- SOKOLOV, V. S., M. E. KRYUKOVA, AND L. N. SKURAT. 1987. Changes in the fine structure of sebaceous glands in the specific inguinal gland of the arctic hare (*Lepus timidus*) during mating season. Doklady Akademii Nauk, SSSR, 290:718-719.
- SOSNINA, E. F., AND E. N. NOVOZHILOVA. 1985. Lice of hares from the fauna of the USSR. Parazitologiya (Leningrad), 19:290-295.
- SOVERI, T., AND M. AARNIO. 1983. Measuring body condition of hares during the winter. Finnish Game Research, 41:21-28.
- SPERBER, I. 1974. Food utilization of *Lepus timidus* in the winter. Proceedings of the International Congress for Game Biologists, 11:175-177.

- SULKAVA, S. 1966. Feeding habits of the eagle owl (*Bubo bubo*) in Finland. Suomen Riista, 18:145-156.
- . 1967. Zur Nahrung des Steinadlers, *Aquila chrysaetos*, in Finnland südlich vom Rentierzuchtgebiet. Aquilo Serie Zoologica, 5:1-13.
- SULKAVA, S., K. HUHTALA, AND P. RAJALA. 1984. Diet and breeding success of the golden eagle in Finland 1958-82. Annales Zoologici Fennici, 21:283-286.
- THIRGOOD, S. J., AND R. HEWSON. 1987. Shelter characteristics of mountain hare resting sites. Holarctic Ecology, 10:297-298.
- THOMPSON, H. V. 1957. Mammal and bird pests on the land. Transactions of the International Union of Game Biologists, 3:57-59.
- TOLONEN, A. 1982. The food of the mink (*Mustela vison*) in north-eastern Finnish Lapland in 1967-76. Suomen Riista, 29:61-65.
- VAN DER MERWE, M., AND P. A. RACEY. 1982. Abdominal foetus in the hare (*Lepus timidus scoticus*). Journal of Zoology (London), 197:309-311.
- . 1991. Body composition and reproduction in mountain hares (*Lepus timidus scoticus*) in north-east Scotland. Journal of Zoology (London), 225:676-682.
- VERKAIK, A. J., AND R. HEWSON. 1986. Moults and ranks in male mountain hares (*Lepus timidus*). Journal of Zoology (London), 207:628-630.
- VUOLANTO, S. 1972. Some aspects of the results of game marking with wing-tags in Finland in 1962-69. Suomen Riista, 24:57-63.
- WAHLIN, B. J. O. 1950. Hare damage and protection. Svensk Jakt, 88:306-308.
- WALHOVD, H. 1965. Age criteria of the mountain hare (*Lepus timidus* L.) with analyses of age and sex ratios, body weights and growth in some Norwegian populations. Papers of Norwegian State Game Research Institute, 22:1-57.
- WALKER, J., AND J. S. FAIRLEY. 1968. Winter food of Irish hares in County Antrim, Northern Ireland. Journal of Mammalogy, 49:783-785.
- WATSON, A. 1963. The effect of climate on the colour of mountain hares in Scotland. Proceedings of the Zoological Society of London, 141:823-835.
- WATSON, A., AND R. HEWSON. 1973. Population densities of mountain hares (*Lepus timidus*) on western Scottish and Irish moors and on Scottish hills. Journal of Zoology (London), 170:151-159.
- WEBB, C. S. 1955. A hare about the house. Hutchinson and Co., London, 72 pp.
- WILLGOHS, J. F. 1961. The white-tailed eagle *Haliaeetus a. albicollis* (L.) in Norway. Universitetet i Bergen Årbok, Naturvit, Ser. 12:1-212.
- WILSON, D. E., AND D. M. REEDER. 1993. Mammal species of the world. A taxonomic and geographic reference. Smithsonian Institution Press, Washington, D.C., 1206 pp.
- YALDEN, D. W. 1984. The status of the mountain hare, *Lepus timidus*, in the Peak District. The Naturalist, Leeds, 109:55-59.
- YURGENSON, P. B. 1955. Ecology of the lynx in the forests of the central zone of the USSR. Zoologicheskii Zhurnal, 34:609-620.

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