

Mustela erminea. By Carolyn M. King

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Mustela erminea Linnaeus, 1758
Ermine

- Mustela Erminea* Linnaeus, 1758:46. Type locality "Europa and Asia frigidior"; restricted to Uppsala, Sweden, by some later revisors, to central Europe by Cabrera, 1913.
- Mustela Cigognanii* Bonaparte, 1838:37 (spelled *Cicognanii* on p. 38). Type locality "North America," restricted to United States (Hall, 1951:118, and earlier authors).
- Mustela Richardsonii* Bonaparte, 1838:38. Type locality "North America," probably Fort Franklin, Canada (Hall, 1951:110).
- Mustela pusilla* DeKay, 1842:34. Type locality not given, by implication New York state.
- Putorius kaneii* Baird, 1857:172. Type locality "Arikamitchichi, in Behring Straits."
- Putorius ermineus ferghanae* Thomas, 1895:452. Type locality "Ferghana"; treated as species *levis ferghanae* by Satunin, 1911; according to Ognev, 1935:35.
- Putorius hibernicus* Thomas and Barrett-Hamilton, 1895:374. Type locality "Enniskillen," Co. Fermanagh, Ireland.
- Putorius sreatori* Merriam, 1896:13. Type locality "Mount Vernon, Skagit Valley, Washington."
- Putorius arcticus* Merriam, 1896:15. Type locality "Point Barrow, Alaska."
- Putorius haidarum* Preble, 1898:169. Type locality "Massett (Graham Island), Queen Charlotte Islands," British Columbia.
- Putorius (Arcotale) muricus* Bangs, 1899:71. Type locality "Echo, El Dorado Co., California."
- Putorius microtis* Allen, 1903:563. Type locality "Shesley, British Columbia."
- Putorius audax* Barrett-Hamilton, 1904:392. Type locality "Discovery Bay, North Greenland."
- Mustela whiteheadi* Wroughton, 1908:852. Type locality "Kagan Valley," Hazara, Northern India.
- Mustela lynxii* Hollister, 1912:5. Type locality "Tapacha, Altai Mountains, Siberia."
- Mustela nippon* Cabrera, 1913:392. Type locality "Sinano, Hon-do," Japan.
- Mustela kaneii* Allen, 1914:58; variant spelling of *kaneii* Baird.
- M. e. gulosa* Hall, 1945a:84. Type locality "Trout Lake, Klickitat County, Washington" (7).
- M. e. haidarum* (Preble, 1898), see above (12).
- M. e. haiderica* (Thomas and Barrett-Hamilton, 1895), see above (21).
- M. e. initis* Hall, 1944:37. Type locality "Saook Bay, Baranof Island, Alaska" (17).
- M. e. invicta* Hall, 1945a:75. Type locality "Benawah, Benawah County, Idaho" (5).
- M. e. kadiacensis* (Merriam, 1896:16). Type locality "Kadiak Island, Alaska" (18).
- M. e. kaneii* (Baird, 1857), see above (*baturini* Ognev, *digna* Hall, *kaneii* Allen, *kamtschatica* Dybowski, *naumovi* Yurgenson, *orientalis* Ognev, *sibirica* Dybowski, and *transbaikicalica* Ognev are synonyms; 28).
- M. e. karagimensis* Yurgenson, 1936:240. Type locality Karaginsk Island, off northeast coast of Kamtschatka (29).
- M. e. lynxii* Hollister, 1912, see above (32).
- M. e. minima* (Cavazza, 1913:194). Type locality "Monte Rosa, sui Monti d'Ossola, al Nord della Valtellina," Switzerland (24).
- M. e. mongolica* Ognev, 1928:18. Type locality Dundu-Saichan, Mongolian Altai (31).
- M. e. muricus* (Bangs, 1899), see above (*leptus* Merriam a synonym; 3).
- M. e. nippon* Cabrera, 1913, see above (34).
- M. e. olympica* Hall, 1945a:81. Type locality "near head of Soleduc [=Soulduc] River, 4,500 feet elevation, Olympic Mountains, Clallam County, Washington" (8).
- M. e. polaris* (Barrett-Hamilton, 1904:393). Type locality Gap Valley, "latitude 82°N, longitude 59°20'W., in Hall Land, in the very far north of Greenland" (20).
- M. e. richardsonii* Bonaparte, 1838:38, see above (*imperii* Barrett-Hamilton, *microtis* Allen, and *mortigena* Bangs are synonyms; 4).
- M. e. riciniae* (Miller, 1907:395). Type locality "Islay House, Island of Islay, Scotland" (23).
- M. e. sarlov* Hall, 1944:35. Type locality "Mole Harbor, Admiralty Island, Alaska" (16).
- M. e. seclusa* Hall, 1944:39. Type locality "Port Santa Cruz, Sumez Island, Alaska" (14).

CONTEXT AND CONTENT. Order Carnivora, Family Mustelidae, Genus *Mustela*, Subgenus *Mustela*, with about 13 species. The species *M. erminea* has 20 recognized subspecies in the New World (Hall, 1951) and a smaller number in the Old World (Heptner et al., 1967; Corbet, 1978, recognized only three subspecies in Eurasia). The taxonomic treatment of subspecies in the Old and New Worlds do not appear to be equivalent; further revision is needed.

- M. e. aestiva* Kerr, 1792:181. Type locality Germany (*algericus* Thomas, *alpestris* Burg, *giganteus* Burg, and *major* Nilsson are synonyms). Locality numbered (26) in Fig. 3.
- M. e. alascensis* (Merriam, 1896:12). Type locality "Juneau, Alaska" (15).
- M. e. anguinae* Hall, 1932:417. Type locality "French Creek, Vancouver Island, British Columbia" (10).
- M. e. arctica* (Merriam, 1896), see above (*audax* Barrett-Hamilton a synonym; 19).
- M. e. bangsi* Hall, 1945b:176. Type locality "Elk River, Sherburne County, Minnesota" (2).
- M. e. calandri* Hall, 1944:38. Type locality "Kasaan Bay, Prince of Wales Island, Alaska" (13).
- M. e. cigognanii* Bonaparte, 1838:37, see above (*pusilla* DeKay a synonym; 1).
- M. e. erminea* Linnaeus, 1758, see above (*hyberna* Kerr, *herminea* Oken, and *maculata* Billberg are synonyms; 25).
- M. e. fallenda* Hall, 1945a:79. Type locality "Huntingdon, British Columbia" (9).
- M. e. ferghanae* (Thomas, 1895), see above (*shnitnikovi* Ognev, and *whiteheadi* Wroughton are synonyms; 33).



FIGURE 1. *Mustela erminea* from northern North America, from files in Department of Mammalogy, American Museum of Natural History (photographer unknown).

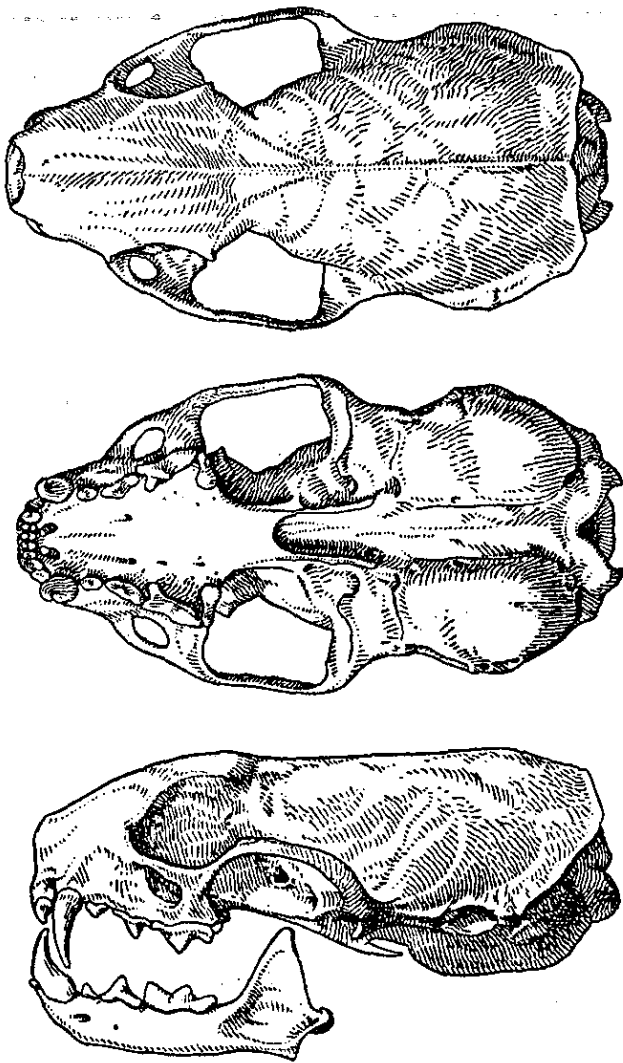


FIGURE 2. Cranium of *Mustela erminea* (from Heptner et al., 1967), in dorsal, ventral, and lateral views, and mandible in lateral view. Greatest length of skull is approximately 53 mm.

- M. e. semplei* Sutton and Hamilton, 1932:79. Type locality "Coral Inlet, South Bay, Southampton Island," Canada (*labiata* Degeborl a synonym; 11).
M. e. stabilis Barrett-Hamilton, 1904:394. Type locality "Blandford, Dorset," Great Britain (22).
M. e. streator (Merriam, 1896), see above (6).
M. e. teberdina Kornejev, 1941. Type locality Teberdina region, Caucasus, U.S.S.R. (*balcarica* Baziev a synonym; 30).
M. e. tobolica Ognev, 1922:112. Type locality Tara, West Siberian Territory (*ognevi* Yurgenson, *birulai* Martino, and *martinoi* Ellerman and Morrison-Scott are synonyms; 27).

DIAGNOSIS. *Mustela erminea* differs from *M. nivalis* (including *rixosa*) in having a bushy black tip on the tail; tail length more than 25% of the length of head and body in North America (Hall, 1951) or more than 33% in the USSR (Heptner et al., 1967); and, in regions where the two are sympatric, larger size.

In regions where both *M. erminea* and *M. frenata* occur, the tail of *M. erminea* is less than 44% of length of head and body; the postglenoidal length of skull is more than 46% of condylobasal length in males and more than 48% in females; and *M. erminea* is smaller. There is great geographical and individual variation in size.

GENERAL CHARACTERISTICS. The ermine shows the typical weasel form, with a long body and short legs; a long neck supporting a rather flat triangular head; bright black eyes, slightly protruding; rounded ears; and long whiskers (Fig. 1). The pelage is reddish brown above and creamy white below in summer, white in winter. The soles of the feet are totally covered with dense hair in

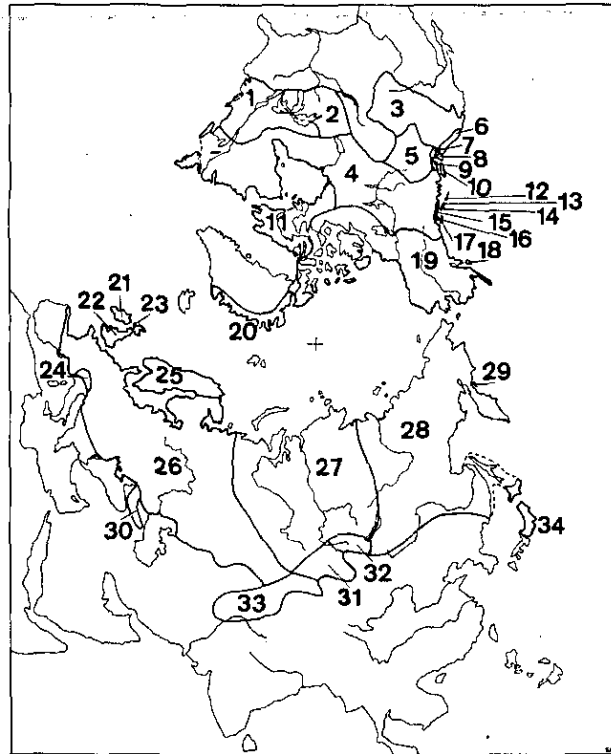


FIGURE 3. Map showing the Holarctic (circumpolar) geographical distribution of the species *Mustela erminea* and its subspecies (numbers are referred to in the list of subspecies in text).

winter, and even in summer only the relatively small toepads (five on each foot) are exposed. The tail is 30 to 45% of the length of the head and body and has 16 to 19 caudal vertebrae. The skull has a long braincase, a short face, greatly inflated tympanic bullae, and the palate extends behind the upper molars (Fig. 2). Males have a baculum or os penis, which develops a distinct head at the proximal end at sexual maturity. Mean body weights of adult males in various European countries range from 208 to 283 g; in Britain ca. 320 g; in New Zealand (imported from Britain) 285 to 356 g; in Ireland 233 to 365 g; in Russia 134 to 191 g (smaller in the north); and in North America 56 to 206 g (smaller in the south) (Deansley, 1935; Fairley, 1981; Hall, 1951; Heptner et al., 1967; King and Moody, 1982; Kratochvil, 1977). The different patterns of size variation in the Palearctic and Nearctic need further investigation. Current explanations (Kratochvil, 1977; MacNab, 1971; Petrov, 1962) are unsatisfactory.

Secondary sexual dimorphism in size is pronounced. The basilar length of the skull in males in North America is about 9 to 24% greater than in females of the same populations (Hall, 1951). Dimorphism in body weight is even greater (40 to 80%). Sexual dimorphism in size probably evolved as a consequence of the different roles played by males and females in reproduction (Erlinge, 1979a; Moors, 1980). Females raise their young alone and smaller females are more efficient in hunting favored small prey, and have smaller absolute (but not relative) energy requirements; males are polygynous, and larger males are presumed to have an advantage in obtaining mates.

There is some geographic variation in color pattern. The brown upperparts are all of one color, but they may vary from deep reddish brown to a light sandy brown; the pale underparts may vary from dead white through cream to yellow. Among the North American subspecies, there are no white facial markings, as in some subspecies of *M. frenata*, but *M. erminea* varies more than does *frenata* in the extent of white fur on the belly.

Variation in the skulls of ermine was analyzed in detail by Kopein (1969), Kratochvil (1977), Petrov (1956) and Yurgenson (1933).

DISTRIBUTION. The ermine has a circumboreal range throughout the Holarctic (Fig. 3). In the 1880s, ermine were introduced from Britain to New Zealand (Gibb and Flux, 1973).

FOSSIL RECORD. Hall (1951) stated that no fossil *Mus-*

tela were known before the Pleistocene period, and that *M. erminea* was the most generalized and the nearest to the stem form from which all the living weasels ascended. The ancestry of Recent *M. erminea* can be traced back to *M. plioerminea* from the Astian (=late Pliocene) period in central Europe, about four million years ago (Kurtén, 1968). In the early middle Pleistocene, *M. plioerminea* was replaced by *M. palerminea*, which was common until the Cromerian interglacial, about 0.7 million years ago. The Recent *M. erminea* is the direct descendant of *M. palerminea*, and differs only slightly. From this European origin, *M. erminea* or its predecessors crossed the Bering Bridge into North America, where the earliest known remains are of Illinoian (penultimate glaciation) age (Kurtén, 1966). The Illinoian fauna of Conard Fissure, Arkansas, contains both *M. e. angustidens* and *M. frenata gracilis*. No subspecies of *M. erminea* now occur nearer than about 640 km north of Conard Fissure. After the retreat of the most recent glaciers, some ermine remained stranded on isolated high mountaintops in the Great Basin (Brown, 1971), and some moved northward to meet others invading from ice-free refuges to the north (Macpherson, 1965).

Fossil deposits containing remains of ermine in North America were listed by Kurtén and Anderson (1980), and in Britain by Stuart (1964). Fossil *M. erminea* and *M. palerminea* from cold phases of the Pleistocene tend to be smaller than those from warmer phases or the present day (Kurtén, 1960; Wojcik, 1974).

FORM AND FUNCTION. The dental formula is $i\ 3/3, c\ 1/1, p\ 3/3, m\ 1/2$, total 34, and the dentition is highly specialized for a carnivorous diet.

There are two complete molts a year, starting on the head and sweeping down the flanks to the venter in spring and vice versa in autumn (illustrated by van Soest and van Bree, 1969). In northern populations, the autumn molt is to white (except for the black tail tip); in the south, the winter coat is brown, but it is denser and may be paler than in summer. In the intermediate zone, winter fur may be white, brown or piebald; the white or piebald animals are more often females than males (Flintoff, 1935; Hall, 1951; King and Moody, 1982; Müller, 1970; in Yorkshire, North America, New Zealand, and Germany, respectively). Hutchinson and Parker (1978) suggested that this was because winter whitening in ermine is controlled by a sex-linked genetic polymorphism. Whitening persists for several generations in ermine translocated from constantly snowy to mild environments (Rothschild and Lane, 1957). The proximate control of the molt cycle of ermine is photoperiod, modifiable by temperature, and mediated by hormonal mechanisms (Rust, 1965). The preparatory or anagen phase of the spring molt is initiated by increasing daylength (Bissonnette and Bailey, 1944; Gaiduk, 1977), but shedding of the old winter fur is delayed if the temperature is low (Rust, 1962). Hence, in years with a particularly late or cold spring, animals do not lose their winter coats too early. In autumn, temperature controls whether the new hair grows brown or white. Production of brown hair depends on the pituitary hormone melanocyte-stimulating hormone (MSH), but the synthesis of MSH is inhibited in cold climates in autumn (Rust and Meyer, 1969). In Scotland, the proportion of ermine (sex unknown) turning white was correlated with minimum temperatures and with number of days of snowfall and duration of snow cover (Hewson and Watson, 1979); and in New Zealand (males only), with minimum temperature and number of days of ground frost, though not with either snowfall or duration (King and Moody, 1982). In the USSR, ermines do not turn white in regions where stable snow cover lasts for less than 40 days per year (Gaiduk, 1977).

The long, thin shape of the ermine and its small size considerably increase the cost of thermoregulation, especially in cold climates. Mean body temperature is 39 to 40°C, and is independent of ambient temperatures measured over the range -10 to 30°C (Casey and Casey, 1979). The pelage is short and not a significantly better insulator in winter than in summer. The ratio of surface to volume is high, even at rest, because weasels in general cannot curl up into a sphere, only a flattened disc (Brown and Lasiewski, 1972). Weasels therefore lose heat at a greater rate than do other mammals of similar body mass. Ermine at rest in low temperatures must have a thickly insulated nest, which they take over from recent prey and improve by lining with fur of voles (Chappell, 1980; Erlinge, 1979b; Fitzgerald, 1981).

The active life and high oxygen demands of ermine require efficient cardiac and respiratory systems. The heart is large relative to body weight, especially in northern populations (Kopein, 1967a), and the load on the heart and lungs and the expenditure of energy are greater than in *M. vison* of the same weight, though of different ages (Segal, 1975). Tumanov and Levin (1974) gave the average pulse rate at 3 months of age as 402 beats/min in males and 421

in females, and respiration rates at 6 months of age in both sexes, as 86 to 100 breaths/min. Segal (1975) gave slightly different figures, controlled for temperature.

The structure of the eyes and the visual abilities of the ermine were investigated by Gewalt (1959). The relative proportion of rods to cones was about 14:1; the ratio of the inner to outer nuclear layers about 1:3.4. A single male ermine tested could distinguish red, yellow, blue, and green from shades of grey of the same brightness. Ermine are active both day and night (Erlinge, 1979b). The tapetum (eyeshine) is vivid green, and the pupil is a horizontal slit (pers. observ.). Casua! observations of ermines hunting suggest that both hearing and olfaction are keen.

The structure of the anal glands was described by Stubbe (1972). Holocrine and apocrine secretory glands discharge into paired storage sacs, which are encased in muscular husks and open by sphincters into the anus. Both sets of muscles are under voluntary control. Stubbe (1970) regarded the anal glands of *Mustela* as the most advanced of a series of four types distinguishable in the Mustelidae. The three major chemical components of the musk of male ermine are sulfur-containing thietanes and dithiolanes (Crump, 1980); female stoats also produce two additional compounds not found in males.

The histological details of the reproductive organs were described by Deanesly (1935), Danilov and Tumanov (1972 and 1975) and Gulamhusein and Tam (1974). Most females have 8 or 10 nipples.

ONTOGENY AND REPRODUCTION. Ovulation must be induced by the stimulus of copulation; artificial insemination was unsuccessful, even after injection of gonadotropin (Rowlands, 1972). Corpora lutea are not found in unmated females. Statements in the literature, that spontaneous ovulation occurs throughout the year, derive from Deanesly's (1935) misinterpretation of the corpora lutea of delay, corrected later (Deanesly, 1943).

Mean ovulation rate is 9 to 10, but up to 19 ova may be released at one time both in Britain (Deanesly, 1935; Rowlands, 1972) and New Zealand (King and Moody, 1982). In New Zealand there was also a significant inverse correlation between the number of corpora lutea counted on each side. Ovulation rate may be increased by abundant supplies of rodent prey at the time of mating, but ovulation rate and productivity are not correlated (King, 1981).

The fertilized ova develop to the blastocyst stage in about 14 days, and remain free in the uterus for 9 to 10 months thereafter (Wright, 1942). Ovariectomy during delay stimulates mitotic activity in the blastocysts after 1.5 to 3 weeks, but after 3.5 to 9 weeks the blastocysts deteriorate, perhaps because their increased activity cannot be sustained without support from the ovary (Shelden, 1972). Administration of exogenous steroids failed to prevent deterioration (Shelden, 1973). Both sexes are reproductively quiescent during winter. Implantation is probably stimulated by increasing daylength in spring, and can be induced out of season by changes of the photoperiod over captive animals (Rowlands, 1974), though not by injections of gonadotropins or steroids (Shelden, 1973). Natural implantation is heralded by an increase in the size of the corpora lutea from about 0.7 or 0.8 mm to 1.3 mm in ermine from Britain (Deanesly, 1935), and from 0.48 mm to 0.87 mm in ermine from North America (Wright, 1963), and by a rise in the level of plasma progesterone (Gulamhusein and Hawley, 1974). Blastocysts space themselves between the two horns of the uterus, and may migrate from one to the other before implantation. Active gestation from implantation to parturition takes 4 weeks (Rowlands, 1972), giving a total gestation of about 280 days (range in seven complete observations by Müller (1970), 223 to 378 days, $\bar{X} = 283$). Mean number of embryos found by Deanesly (1935), King and Moody (1982), and Rowlands (1972), was 9, but 25 to 40% of females contained some resorbing embryos.

Stubbe (1973) concluded, from various sources, that the number of young born per litter ranged from 4 to 13. Litters of up to 18 have been recorded (Heptner et al., 1967), but 4 to 8 is the usual number, with equal sex ratio (Müller, 1970). In both New York and in Germany, litters averaged 6 (Hamilton, 1933; Müller 1970; based on nine litters each). Reproductive success is strongly influenced by food supplies prior to parturition (Erlinge, 1981; King, 1981; Vershinin, 1972). The single litter is born in spring, most often in April in the Northern Hemisphere and October in New Zealand.

Newborn Eurasian ermine (adult females >150 g) weigh about 3 g (range 2.7 to 4.2) (Müller, 1970; Tumanov et al., 1970); the small American forms weigh less (e.g., *M. e. cicognanii*, adult female 54 g, newborn young 1.7 g) (Hamilton, 1933). Neonates are blind and naked, though very soon they are covered with a coat of fine, white hair. At week 3, a prominent dark mane of dense fur

develops on the neck (illustrated by Bishop, 1923). The function of this mane is unknown, but Stubbe (1973) mentioned "special nape glands" found in this area by unidentified Soviet workers.

The physical development of the young was described by East and Lockie (1965), Hamilton (1933), Müller (1970), and Tumanov et al. (1970). The milk teeth appear at about week 3; the eyes open at weeks 4 to 6 (females first), the black tail tip appears at weeks 6 to 7; solid food is taken after week 4 or 5, though lactation may continue until weeks 7 to 12. At weeks 6 to 8, the young will play outside the nest, and at months 2.5 to 3, when their permanent dentition is complete, they begin attempts to kill small rodents. Typical prey-killing behavior is unlearned, and fully established by month 3 (Gossow, 1970). Growth of juveniles differs in various subspecies (East and Lockie, 1965; Hamilton, 1933; Müller, 1970; Tumanov and Levin, 1974). Females reach adult size at about month 6; males are not fully grown until sexually mature at one year (Deanesly, 1935; King and Moody, 1982).

In the northern subspecies at least, small juveniles left alone in low temperatures enter a temporary, reversible cold rigor if their body temperature drops below 10 to 12°C. Tumanov and Levin (1974) found that the body temperature of 3-day-old young separated from their mother normally varied between 25 and 31°C, and reached 38 to 40° (as in adults) only when their fur was well grown at about day 30. Segal (1975) stated that juveniles were unable to maintain full thermoregulation over a range of temperatures down to 0°C until days 60 to 70.

In temperate climates, adult females have a post-partum estrous, and young females are usually fertilized before weaning, or possibly even before their eyes are open (Hamilton, 1958; Müller, 1970; Rowlands, 1974), apparently by the same adult male who serves the adult female. However, there is a rapid turnover of resident males (Erlinge, 1979a; Simms, 1979b), and no permanent pair bond, so there is little chance that he is mating with his own young. By the end of the summer, virtually all females of all ages are fertilized (King and Moody, 1982; Wright, 1963). Kopein (1965) stated that in Yamal-Nenets region (68° to 73°N) there were two periods of estrous in ermine: a summer one, leading to a delay in implantation of about 9 months, and a spring one, leading to direct implantation and parturition after 6 weeks, but the evidence is not conclusive.

Determination of sex and reproductive condition is straightforward, but determination of age is not, since the methods proposed so far have not been adequately calibrated against reference stock of known age. Methods include toothwear (Stroganov, 1937); relative width of canine pulp cavity, in dead (Kopein, 1965, 1967b) or live (Debrot and Mermod, 1978) ermine; closure of cranial sutures (Hansson, 1970); various combinations of characters of skull, baculum, and lateral suprascapular tubercle (Fog, 1969; van Soest and van Bree, 1970; Stubbe, 1969; Vershinin, 1972). Up to eight layers have been seen in the canine cementum (Grue and Jensen, 1979; Jensen, 1978; Kukarcev, 1978; van Soest and van Bree, 1970), which agrees roughly with Stroganov's (1937) estimate of 6 to 7 years as the maximum age infrequently attained by wild ermine, although in none of these studies was any individual known to have lived that long. The permanent dentition is in place too early (at about 2.5 months) to be useful for determining age.

Kopein (1967b) estimated the average individual lifespan in the far north as 1 to 1.5 years; Simms (1979b) found that few resident ermine held their home ranges for more than a year. Mortality is probably related most directly to food supplies, though ermine may be killed by raptors and cats occasionally (Gaughan, 1950; Hall, 1951; Stubbe, 1973); Powell (1982) suggested that the black tail-tip evolved to divert the strike of raptors attacking fleeing ermines in the open.

ECOLOGY. Ermine are specialist predators of small, warm-blooded vertebrates, preferably mammals of the size of rabbits or water voles and smaller. In severe climates, ermine, especially females, frequently hunt under snow and may live almost entirely on small rodents and lemmings (Aspivov and Popov, 1940; Fitzgerald, 1977; Lavrov, 1956; Nasimovich, 1949; Simms, 1978, 1979a; Vershinin, 1972). In parts of Eurasia, water voles (*Arvicola* sp.) are the chief prey (Debrot, 1981; Erlinge, 1979b, 1981; Klimov, 1940). When ermines were first introduced to the island of Terschelling (Netherlands), they lived largely on watervoles (van Wijngaarden and Bruijns, 1961). In diverse habitats in temperate climates, ermine take various prey species in different proportions (Brugge, 1977; Day, 1968; Fairley, 1971; Howes, 1977; Potts and Vickerman, 1974). Heptner et al. (1967) summarized several Russian studies not available in English. In New Zealand (voles absent) ermine frequently add insects to their diet of *Mus musculus*, rats, lagomorphs, and birds (King and Moody, 1982); during a decline

of vole populations in Lapland, ermine ate many juniper fruits and berries (Nasimovich, 1949). Osgood (1936) observed a pair of ermine carrying earthworms to their young. They often remove eggs (Morris, 1976; Myrberget, 1972) and chicks (Clowes, 1933; Hussell, 1974) from the nests of birds. Some studies suggested positive selection of certain prey (e.g., fat, hibernating *Zapus*; Northcott, 1971) and avoidance of others (e.g., shrews are rarely found among food remains of Eurasian ermine, although North American ermine eat at least some shrews; Aldous and Manweiler, 1942; Hamilton, 1928). Females generally eat smaller prey (Moors, 1980). Daily food requirements of captive European stock, in temperate conditions and fed on whole small mammals, averaged 19 to 32% of body weight per day in males and 23 to 27% in females (Müller, 1970).

Ermine are regarded by some people as useful exterminators of mice around farms (Stubbe, 1973; Criddle and Criddle, 1925), and they may have a substantial effect on the population dynamics of boreal rodents (Fitzgerald, 1977, 1981). Use of ermine for biological control of rodents succeeded on the small (100 km²) island of Terschelling (van Wijngaarden and Bruijns, 1961), although not in an unenclosed forest in Canada (Sullivan and Sullivan, 1980). Ermine also failed to control rabbits in the two main islands of New Zealand, of 114,000 and 157,000 km² (Gibb and Flux, 1973).

The local distribution of ermine is broadly related to that of small rodents and lagomorphs. In the Holarctic, ermine tend to avoid dense forest and deserts, and settle in successional or forest-edge habitats, in scrub, alpine meadows, marshes, riparian woodlands, hedgerows, and riverbanks rich in small mammals, especially *Microtus* and *Arvicola* (Erlinge, 1977a, 1977b, 1981; Fitzgerald, 1977; Heptner et al., 1967; Simms, 1979a; Vaisfeld, 1972). In New Zealand, ermine are common in all kinds of native forest (King and Moody, 1982). Ermine are well adapted to snowy environments and range to above treeline in alpine areas. Ermine live year-round at 2,000 to 3,000 m or more on lower-latitude mountain ranges such as the Sierra Nevada (Fitzgerald, 1977) and the Caucasus, Altai, and Tien Shan (Heptner et al., 1967). Ermine are able to burrow into soft snow or run on the surface if it becomes compacted or frozen, and are able to enter the subnivean runways of many small mammals, so snow presents little obstacle to the distribution, hunting, or movements of the small northern ermine (Formosov, 1946; Simms, 1979a). In addition, snow provides vital insulation against extremes of air temperature (Chappell, 1980). In northern Kazakhstan between 1959 and 1963, movements of ermine above the snow were curtailed at low temperatures (Kraft, 1966).

Males and females live separately for most of the year. Home ranges of males are larger and may include the ranges of one or more females, but exclude adjacent males. Females exclude each other from their ranges and avoid the male on whose range they live (Powell, 1979). The distribution of individuals is greatly affected by dominance relationships. Adult males dominate both females and juvenile males during most of the year. Resident individuals dominate intruders, so excursions onto the ground occupied by a neighbor of the same sex occur only in the absence of the owner (Erlinge, 1977a, 1977b, 1977c; Vaisfeld, 1972). Ranges are marked by scent from the anal glands, and subdominant individuals exposed to fresh scent marks attempt to retreat or escape (Erlinge, 1977a). Home ranges have been measured by snow-tracking (Heptner et al., 1967; Nasimovich, 1949; Nyholm, 1959; Vaisfeld, 1972), trapping (Lockie, 1966; Simms, 1979b), and radiotelemetry (Erlinge, 1977a, 1977b, 1979b). Where prey is abundant, ranges are small. Estimates for individual males vary from 4 to 200 ha, most often from 10 to 40 ha. Individual ranges contain several nests, which the owner visits in turn, repeatedly visiting favored hunting areas near each base and then moving on, often along regular routes used by successive owners of the same ground (Musgrove, 1951; Nyholm, 1959). Regular visits to all parts of its range allow a resident to patrol its boundaries and maintain fresh scent marks in the course of foraging and exploring (Erlinge, 1977a). Distance travelled in a single hunt averages 1.3 km and ranges up to 8 km. Time spent hunting and distance travelled decrease when prey density is high. In spring and summer, young and adult males become more active; some establish or extend breeding territories, others, especially juvenile males, disperse over considerable distances, presumably in search of breeding territories. One tagged ermine moved 35 km in Alaska between August 1960 and March 1961 (Burns, 1964).

The density and structure of ermine populations are unstable, because lifespans are short and reproductive capacity is high (King and Moors, 1979b). Populations are greatly influenced by fluctuations in the supply of prey, especially of small mammals. In England, the sudden removal of rabbits by myxomatosis from 1953 to 1955 decimated populations of ermines (Hewson, 1972; Jeffries and Pendlebury, 1968; King and Moors, 1979a). Estimates of population

density have ranged from 1 per 17 ha (Simms, 1979b), to 1 per 50 ha (Heptner et al., 1967).

Factors determining the variations in numbers of ermine in central European Russia were summarized by Aspisov and Popov (1940) and Lavrov (1941) as: 1) population density of small mammals and water-voles; 2) the level of spring floods; 3) meteorological factors such as spring and summer temperatures, depth of snow, unfavorable conditions such as drought and glazed frost; 4) harmful events such as fires, draining of marshes and clearing of scrub, and over-trapping; 5) helminth infestations and epizootics such as tularemia. Of these, population density of prey was considered by far the most important.

Present methods of obtaining population data are unsatisfactory in various ways. Snow-tracking (Teplov, 1952) may not directly reflect numbers, gives no physical information about the animals, and cannot be used in summer or in mild climates. Trapping (alive or dead) has provided most of the knowledge we have about the biology of ermine, but catches are liable to misrepresent the populations in various ways (King, 1980a; King and Edgar, 1977). At least some individual ermine may learn to avoid traps (Cahn, 1936).

Most collections of ermine show an excess of males (60 to 65%) and juveniles (up to 90%). The former is often an artifact of trapping, because males have larger home ranges and hunt less often in tunnels than females, and therefore have a greater opportunity to find traps (King, 1975a; Teplov, 1948). Snow-tracking may reveal an equal sex ratio or even an excess of females (Nyholm, 1959). The sex ratio at birth is 1:1 (Kopein, 1970; Müller, 1970). The proportion of juveniles varies from year to year with the reproductive success of the previous season (King, 1981; Kukarcev, 1978); occasionally, no juveniles survive at all. In generalized collections, pooling material from several years, the proportion of young ermine (variously defined) has been estimated to range from 37 to 90% (Fog, 1969; Kopein, 1967b; Kukarcev, 1978; Petrov, 1956; van Soest and van Bree, 1970; Stroganov, 1937; Stubbe, 1969). Results from some other studies not available in English were summarized by Heptner et al. (1967) and Stubbe (1973). Population turnover is rapid.

The only parasite of ermine investigated in any detail is the nematode, *Skrjabinylus nasicola*, which often causes considerable distortion of the nasal sinuses, possibly leading to pressure on the brain. Rates of infestation in Britain, continental Europe, and Russia are generally 20 to 70% (Hansson, 1968, 1970; Lavrov, 1944; Popov, 1943; van Soest et al., 1972); they average 10% (range, 0 to 37%) in New Zealand (King and Moody, 1982), and often range up to 100% in North America (Dougherty and Hall, 1955). Obligate intermediate hosts are terrestrial mollusks, which ermine rarely eat. The hypothesis that shrews often act as carrier hosts (Hansson, 1967) is supported by the increase in incidence of skrjabinylus in Newfoundland *M. erminea* since the introduction of shrews (Jennings et al., 1982); however, other intermediates must be possible, because the parasites survive in New Zealand where shrews are absent (King, 1974). Some authors have claimed that infestation adversely affected numbers, skull size, body weight and fertility, and that fur harvests in seasons following widespread infestation were reduced (Lavrov, 1944; Popov, 1943; van Soest et al., 1972). However, controlled comparisons among 1,492 ermine from New Zealand produced no evidence that infested individuals were smaller or lighter than uninfested ones (King and Moody, 1982). Lavrov (1944) and Vershinin (1972) listed various other parasites and diseases (e.g., tularemia) of ermine in the USSR.

BEHAVIOR. Ermine typically move rapidly, investigating every hole and crevice, and often stop to survey the surroundings by raising the head or standing upright on the hindlegs. They may glide along with the body extended almost straight, taking many rapid steps with the short legs, or if alarmed, they gallop with great leaps, with the back arched. They swim well (King and Moors, 1979a), and easily climb trees to great heights, where they visit the nests of birds and squirrels.

Radiotracking studies in Sweden showed that ermine were active for short periods (usually for 10 to 45 min, but up to 4 h), alternating with rest periods, more or less regularly every 3 to 5 h throughout the 24-h period (Erlinge, 1979b).

Erlinge et al. (1974) and Nams (1981) observed the behavior of ermine hunting rodents in large enclosures. Surplus prey are cached and defended from other ermine (Heptner et al., 1967). Caches are an important means of storing energy for ermine, which must avoid obesity in order to retain the ability to enter rodent tunnels (Simms, 1979a). Hunting in the wild has been observed infrequently and by chance, e.g., hares and pikas followed by scent (Dixon, 1931; Ward, 1936), insects located by sound (Willey, 1970), and fish snatched from a stream (Feuer, 1958). Ermine regularly

kill prey several times their own weight, always by an accurately delivered bite to the neck. However, Hewson and Healing (1971) suggested that the neck of a rabbit was too well fleshed for the teeth of an ermine to penetrate far, and that rabbits attacked by ermine usually died of shock. Rabbits have been observed to act in a panic-stricken way and to lie down squealing as the ermine approached (Forsyth, 1967). Prey are gripped at the nape, enfolded with the forelegs, and scratched with the hind claws. The ermine licks blood from wounds first; this habit may have given rise to the false idea that ermine "suck the blood" of their prey. Ermine kill whenever given the opportunity and cache what is not immediately required (Gossow, 1970; Wüsthube, 1960; Müller, 1970). Field studies by Erlinge (1979a) and Simms (1979b) showed that the male usually avoids the nest area and does not regularly support the family with food. The male may consort with families when the adult female and her female young are in estrous, and at these times he might present food to the adult female, because she is dominant over him at this time (Erlinge, 1977c).

Nests are made in hollow trees, rock piles or burrows, often commandeered from prey. A breeding den was described by Bishop (1923). Various galleries, mostly 300 mm below ground, contained food remains, and the nest was lined with rat fur, grass and leaves.

Mating behavior, observed in captive ermine by Müller (1970), was less vigorous and prolonged than in *M. frenata*. The male grabs the female by the scruff of the neck and may drag her about; she usually remains passive, as when being carried by her mother. The copulations Müller observed (all fertile) lasted from 2 to 20 min and were often repeated (one pair mated five times in an hour). This relatively extended procedure may be needed to induce ovulation in the female. The baculum of the male permits the prolonged intromission required.

Erlinge (1977c) observed a dominance hierarchy among captive ermine, and described offensive and defensive reactions. Vocalizations and play behavior in captive animals were described by Gossow (1970), and Wüsthube (1960). Ermine are characteristically curious, and may be called up to within a few meters of an observer standing still and making squeaking noises (Feuer, 1958).

GENETICS. The karyotype of *M. erminea cicognanii* was described by Meylan (1967). The diploid number of chromosomes was 44, consisting of 10 pairs of biarmed autosomes and 11 pairs of uniarmed autosomes. The X was metacentric and the Y was minute; the structure of the Y was difficult to determine, although Meylan (1967) stated that it was probably biarmed.

Wu and Chang (1973) reported on artificial hybridizations between ermines and ferrets, *M. putorius furo*. Sperm of ermine fertilized 78% of the 86 ferret eggs counted. Implantation occurred at 13 to 14 days, and a single live foetus, nearly fullgrown (2.7 g) was found in one of three ferrets after 42 days gestation. However, there was a high rate of embryonic mortality (by days 24 to 28 only 18% of 39 implantation sites contained foetuses), possibly because of chromosome incompatibility (2n of ferrets is 40), and no young were born from another three animals kept until day 54. Ermine eggs were fertilized by spermatozoa of ferrets but their development was not observed.

REMARKS. Alternative English names are "stoat," used in Britain and New Zealand, and "short-tailed weasel" used in North America.

Most of the Russian language papers cited in the bibliography are available as English translations (King, 1975b, 1980b); the paper by Nyholm (1959), originally published in Finnish, appears in English in King (1975b).

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