Mustela nivalis. By Steven R. Sheffield and Carolyn M. King

Mustela nivalis Linnaeus, 1766

Least Weasel

Mustela nivalis Linnaeus 1766:69. Type locality "Province of Vesterbotten, Sweden."

Mustela vulgaris Erxleben, 1777:471. Type locality "near Leipzig, Germany."

Mustela boccamela Bechstein, 1801:395. Type locality "Sardinia."

Mustela gale Pallas, 1811:94; renaming of *vulgaris*.

Mustela minor Nilsson, 1820:35; renaming of *nivalis*.

Mustela subpalmata Hemprich and Ehrenberg, 1833:2. Type locality "Cairo, Egypt."

Putorius minutus Pomel, 1853:51. Type locality "Augvergne, near Paris, France."

Putorius numidicus Pucheran, 1855:393. Type locality "Tangier, Morocco."

Foetorius pusillus Fatio, 1869:332. Type locality "Switzerland" (not of DeKay, which is *Mustela erminea*).

Mustela stoliczkana Blanford, 1877:260. Type locality "Yarkand, East Turkestan, China."

Putorius rixosus Bangs, 1896:21. Type locality "Osler, Saskatchewan, Canada."

Mustela nikolskii Semenov, 1899:14. Type locality "Simferopol, Crimea, USSR."

Putorius allegheniensis Rhoads, 1900:751. Type locality "Beallsville, Washington County, Pennsylvania."

Mustela (Ictis) dombrowskii Matschie, 1901:231. Type locality "Siulnita, Rumania."

Putorius (Arctogale) pygmaeus Allen, 1903:176. Type locality "Gizhiga, north coast of Okhotsk Sea, eastern Siberia, USSR."

Mustela russelliana Thomas, 1911:168. Type locality "Tatsienlu, Szechuan, China."

Mustela campestris Jackson, 1913:124. Type locality "Beemer, Cuming County, Nebraska."

Mustela punctata Domaniewski, 1926:55. Type locality "Darasun, eastern Transbaikalia, USSR."

Mustela trettaui Kleinschmidt, 1937:11. Type locality "Germany."

Mustela hungarica Vasarhelyi, 1942:221. Type locality "Hungary" (not *Mustela eversmanni hungarica* Ehik, 1932).

Mustela vasarhelyi Kretzoi, 1942:349 (new name for *M. hungarica* Vasarhelyi, 1942, preoccupied).

CONTEXT AND CONTENT. Order Carnivora, Family Mustelidae, Subfamily Mustelinae, Genus *Mustela*, Subgenus *Mustela*, with 17 extant species in the genus and five in the subgenus (Nowak, 1991). While some recognize four subspecies in the Nearctic (Hall, 1951, 1981; Swenk, 1926) and up to 17 subspecies in the Palaearctic (Ellerman and Morrison-Scott, 1966; Frank, 1985; Heptner, 1967), Corbet (1978) recognizes one Nearctic and five Palaearctic subspecies. We accept the four Nearctic subspecies of Hall (1981), and four of the five Palaearctic subspecies listed by Corbet (1978). We split the fifth into two, since a definable boundary exists between two distinct but interfertile forms (*M. n. nivalis* and *M. n. vulgaris*) in southern Sweden (Stolt, 1979). The geographical distributions and synonyms of these two subspecies are not clearly definable from present data. The subspecies of *M. nivalis* include:

M. n. allegheniensis Rhoads, 1900:751, see above.

M. n. boccamela Bechstein, 1801:395, see above (*albipes* Mina Palumbo, *alpinus* Burg, *corsicanus* Cavazza, *fulva* Mina Palumbo, *iberica* Barrett-Hamilton, *italicus* Barrett-Hamilton, *meridionalis* Costa, and *siculus* Barrett-Hamilton probably are synonyms).

M. n. campestris Jackson, 1913:124, see above.

M. n. eskimo Stone, 1900:44. Type locality "Point Barrow, Alaska."

M. n. namiyei Kuroda, 1921:209. Type locality "Awomori, Honshu, Japan" (*yesoidsuna* Kishida is a synonym).

M. n. nivalis Linnaeus, 1766:69, see above (*caraftensis* Kishida, *dinniki* Satunin, *kamtschatica* Dybowski, *kerulenica* Bannikov, *minor* Nilsson, *mosanensis* Mori, *punctata* Domaniewski, *pygmaea* Allen, *russelliana* Thomas, *stoliczkana* Blanford, and *typicus* Barrett-Hamilton probably are synonyms).

M. n. numidica Pucheran, 1855:393, see above (*africana* Gray, *atlas* Barrett-Hamilton, and *galinthias* Bate are synonyms).

M. n. rixosa Bangs, 1896:21, see above.

M. n. subpalmata Hemprich and Ehrenberg, 1833:2, see above.

M. n. vulgaris Erxleben, 1777:471, see above (*caucasica* Barrett-Hamilton, *dombrowskii* Matschie, *gale* Pallas, *heptneri* Morozova-Turova, *hungarica* Vasarhelyi, *major* Fatio, *minutus* Pomel, *monticola* Cavazza, *nikolskii* Semenov, *pallida* Barrett-Hamilton, *pusillus* Fatio, *trettaui* Kleinschmidt, and *vasarhelyi* Kretzoi probably are synonyms).

DIAGNOSIS. *Mustela nivalis* is the smallest member of the Order Carnivora. *M. nivalis* differs from *M. erminea* and *M. frenata* by the absence of a black tip on the tail; smaller size in regions of sympatry; length of tail ≤25% of the head and body length in North America (Hall, 1951) or <33% in the USSR (Heptner, 1967); basilar length of skull (<32.5 mm in males, <31.0 mm in females) less than in shortest skull of *M. frenata* and *M. erminea* in regions of sympatry (Hall, 1951); <17 caudal vertebrae; pelage of North American forms fluoresces under UV light (Latham, 1953); and baculum is straight with a hook-like tip instead of sigmoidally recurved (King, 1989b). The ratio of palatine length to smallest palatine width also is suggested to discriminate between *M. nivalis* and *M. erminea* (Reumer, 1988).

GENERAL CHARACTERS. *Mustela nivalis* has a long slender body and short limbs; a long neck and a flat, narrow head; large, black eyes; relatively large, rounded ears; and long vibrissae (Fig. 1). Summer pelage is about 10 mm in length and generally is chocolate brown on the dorsal side. The white underparts often have brown spots or blotches. The line of demarcation between the upper-brown and the lower-white colors is straight in most forms (a Type I, *M. n. nivalis* pattern) and irregular in some European and American forms (a Type II, *M. n. vulgaris* pattern; Frank, 1985; King, 1989b). Winter pelage is ca. 15–16 mm in length and is entirely white in northern populations, but remains brown in southern populations. The feet, each with five digits, have sharp non-retractable,

FIG. 1. The least weasel, *Mustela nivalis*, in summer pelage (from captive population, Department of Biology, University of Arkansas–Little Rock). Photograph by G. Heidt.
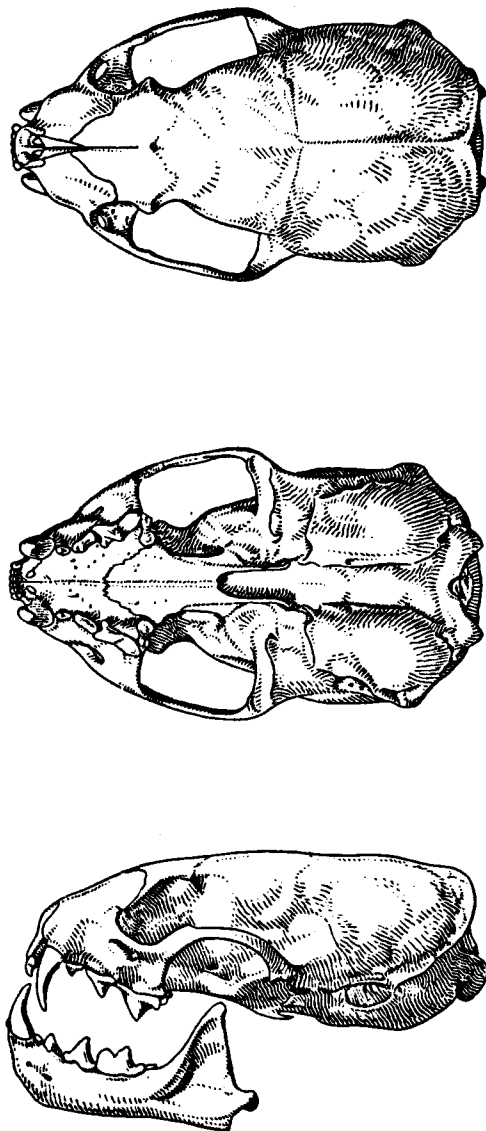
FIG. 2. Cranium of *Mustela nivalis* in dorsal, ventral, and lateral views, and mandible in lateral view from the Zoological Institute, Academy of Sciences of the USSR, Moscow (from Novikov, 1956). Greatest length of cranium is approximately 35 mm (52 mm for the species).

curved claws, and the soles, except the pads, are fully furred. Number of vertebrae averages 44, including 7 C, 14 T, 6 L, 3-4 S, and 14-15 Ca (Hall, 1951). The skull has a long braincase, short rostrum, and greatly inflated tympanic bullae. The palate extends behind the upper molars and its width is approximately equal to the distance between the tympanic bullae (Fig. 2). The baculum completely ossifies by 3 months of age, and develops an excrescence at the proximal end at sexual maturity (Heidt, 1970).

Extensive individual and geographic variation exists in many characters in relation to gender, age, and season, including pelage color, position of the demarcation line between brown and white fur, molt patterns, dentition, lengths of tail and hind foot, relative skull measurements, and body size (Hall, 1951; King, 1989b). The upper pelage varies from deep-rusty brown to pale-sandy tan; the white underparts vary from pure white to yellow. The irregular demarcation line and variable brown patches on the venter of *M. n. vulgaris* are individually unique and the pattern is maintained through successive molts, useful for individual identification after 4 months of age (Linn and Day, 1966). Ranges of body mass of adult males are: 30-100 g in North America, 55-202 g in the UK, 33-108 g in Sweden, 40-220 g in Czechoslovakia, 36-250 g in the USSR, 72-185 g in New Zealand, and 125-250 g in Africa (Hall, 1951; Heptner, 1967; King, 1989b; Kratochvil, 1977; Stolt, 1979). Patterns of
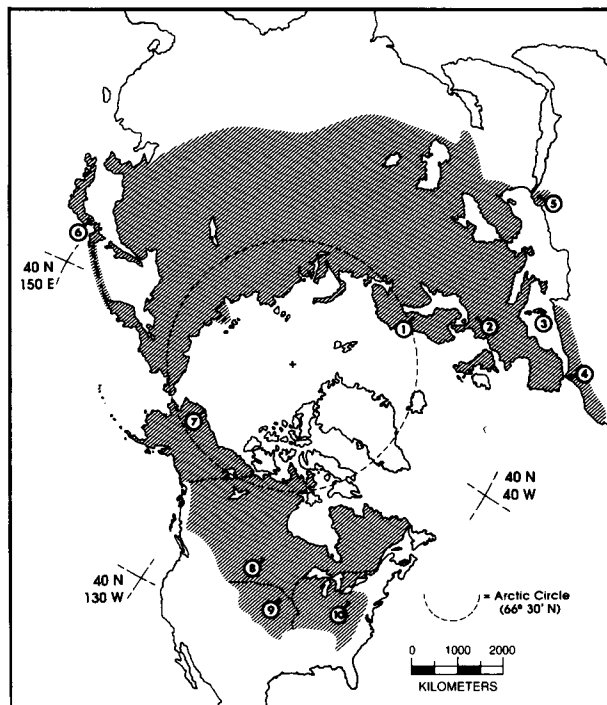

FIG. 3. Geographic range of *Mustela nivalis* (New Zealand not shown). Numbers of Palaearctic type localities and Nearctic subspecies with type localities are given: 1, *M. n. allegheniensis*; 2, *M. n. boccamela*; 3, *M. n. campestris*; 4, *M. n. eskimo*; 5, *M. n. namiyei*; 6, *M. n. nivalis*; 7, *M. n. numidica*; 8, *M. n. rixosa*; 9, *M. n. subpalmata*; 10, *M. n. vulgaris*. (Modified from Corbet, 1978; Hall, 1981; and King, 1989b.)

geographic variation in size throughout its range are complex; smaller forms are found in the Alps, northern Europe, eastern Siberia, and North America, whereas larger forms are found in southern and western Europe, reaching maximum size in Egypt (Corbet, 1978; King, 1989b). In North America, variation in body size is not consistently related to latitude, longitude, or the presence or absence of *M. erminea* or *M. frenata* (Holmes, 1988; Ralls and Harvey, 1985). Others suggest that at least some size variation in *M. nivalis* reflects competitive interactions and character displacement with *M. erminea* and *M. frenata* (Dayan et al., 1989; Simms, 1979). Body size and skull measurements increase from north to south in Eurasia (Heptner, 1967; Kratochvil, 1977; Morozova-Turova, 1965; Reichstein, 1957).

Sexual dimorphism in size is pronounced, more so in the larger subspecies (King, 1989b). In the UK and southern Sweden, males usually are ca. 10-20% longer than females and ca. 100% heavier; however, in northern Sweden males are 12% longer but only about 50% heavier (Stolt, 1979). Skulls of adult males are larger, stronger, and broader than those of females, with the sagittal and occipital crests more strongly developed. The variability with age in skull size and shape is greater in males than in females. Sexual dimorphism in weasels may be a consequence of the different energy budgets of the two genders, which are determined by the different roles they play in reproduction (Erlinge, 1979; Moors, 1980; Sandell, 1984), a polygynous mating system favoring large males, or the abundance of prey during the period of rapid growth in young weasels (Hayward, 1983; Powell, 1979; Ralls and Harvey, 1985). Larger males have a presumed advantage in obtaining mates, whereas smaller size in females favors greater hunting efficiency, a vital advantage when rearing young. Good nutrition during the period of rapid growth increases adult size much more in males than in females (King, 1989b).

DISTRIBUTION. *Mustela nivalis* has a circumboreal range throughout the Holarctic (Fig. 3). In 1885, *M. nivalis* was introduced from the UK to New Zealand (King, 1984b). This weasel also was introduced to Malta, Crete, the Azore Islands, and apparently to the island of Sao Tomé (west Africa; Corbet, 1978; Miller, 1912). In North America, many recent range extensions of *M. nivalis* have

been reported, particularly along the southern and western boundaries.

FOSSIL RECORD. The ancestry of Recent *M. nivalis* can be traced back to *M. praenivalis* from the early Villifranchian (=late Pliocene) and Biharian (=early Pleistocene) in central Europe (Savage and Russell, 1983). This primitive weasel was probably derived from *M. pliocaenica*, a Ruscinian (=middle Pliocene) form (Kurtén, 1968). The transition from *M. praenivalis* to *M. nivalis* was gradual (Kurtén, 1968). Specimens from the early and early-middle Pleistocene, 0.75–1.5 × 10⁶ years ago, are mostly classified as *M. praenivalis*, while those from the late-middle Pleistocene to the present, <0.43 × 10⁶ years ago, are regarded as *M. nivalis*. *M. nivalis* is common in cave deposits from late Pleistocene faunas in Europe (Kurtén, 1968). In the UK, it is associated with temperate forests and large numbers of small rodents in deposits of interglacial Cromerian age (Stuart, 1982).

From its European origin, *M. nivalis* emigrated across the Bering land bridge into North America during the late Rancholabrean (=late Pleistocene), probably during the Wisconsinan glaciation (Kurtén and Anderson, 1980). The presence of both *M. erminea* and *M. frenata* in North America at least since the late Irvingtonian (=middle Pleistocene) probably influenced the North American dispersal of *M. nivalis* (Hall, 1951; Kurtén and Anderson, 1980). *M. nivalis* also is known from the late Pleistocene in Africa and Asia, and from 10 sites of Rancholabrean age in North America (Kurtén and Anderson, 1980; Savage and Russell, 1983). Fossil remains of *M. nivalis* from outside its present range have been found in late Pleistocene localities in Israel (Dayan and Tchernov, 1988), Jordan (Boessneck, 1977), and North America (Hall, 1951).

FORM AND FUNCTION. The dental formula is i 3/3, c 1/1, p 3/3, m 1/2, total 34. The highly specialized dentition includes shearing carnassials for a completely carnivorous diet.

There are two complete molts per year, each starting on the head and dorsum and moving down the flanks to the venter in spring, and vice-versa in autumn (King, 1979). At high latitudes, local populations consistently molt to white in winter, with few brown or mottled-white and brown individuals, and do so earlier in the year than at lower latitudes (Ognev, 1935). In the UK and western Europe, the spring molt lasts from March to May, and summer pelage occurs from May to September. The autumn molt lasts from September to November, the brown winter pelage occurs from November to March (King, 1979). Individual molts are completed in about 3 weeks. The seasonal molting cycle is controlled by photoperiod and mediated by hormonal mechanisms. Breeding females may molt later in the spring than inactive females, perhaps because estrogen interferes with the molt process (King, 1979). However, females have enough energy for both the molt and pregnancy simultaneously, since pregnant females resume molting after estrus. There is no change in thermal conductance associated with seasonal molt (Casey and Casey, 1979); the advantage of the white winter pelage, therefore, is concealment, not insulation (Chappell, 1980).

Mustela nivalis generally has greater surface to volume ratios and shorter fur than other mammals of similar mass, and is unable to assume a spherical resting posture, due to its long, thin shape. As a result, basal metabolic rate (BMR) and mass-specific rates of heat loss are high, increasing the cost of thermoregulation, especially in cold climates (Brown and Lasiewski, 1972). The shape and size of *M. nivalis* is presumably a compromise between energy conservation and predation efficiency; although its shape is metabolically inefficient, it allows them to enter the burrows and subnivean habitat of its prey (Brown and Lasiewski, 1972; King, 1989a). Mean body temperature averages 36.6°C at rest and 39.5°C when active, independent of ambient temperatures ranging from −10 to 30°C. There is virtually no thermal neutral zone (Casey and Casey, 1979). Adults can maintain normal body temperatures with thermoneutral resting metabolic rates at ambient temperatures to −20°C (Chappell, 1980). Individual *M. nivalis* weighing 38–70 g have a BMR of 12.96–19.74 kcal/day (Casey and Casey, 1979). The resting BMR of a 65-g weasel living at −20°C is 98 kcal/day, equal to about two 50-g lemmings/day (MacLean et al., 1974). However, when weasels can use lemming nests to maintain a microclimate of ≥0°C, resting BMR decreases significantly and much less food is required (MacLean et al., 1974). The average daily metabolic requirement is about three to four times the BMR over the entire year and may at times reach up to six times the BMR, which approaches the maximum for small mammals (Chappell, 1980). The energy metab-

olism for winter thermoregulation (15 ml O₂ g⁻¹ h⁻¹) is twice that in summer (7.5 ml O₂ g⁻¹ h⁻¹; Casey and Casey, 1979). *M. nivalis* tolerates typical arctic subnivean conditions (ambient and ground temperatures from 0 to −20°C), but to maintain a positive energy balance depends heavily upon efficient foraging strategies and access to insulated lemming nests (Chappell, 1980).

Maintenance requirements for captive *M. nivalis* are about 1 g food (wet weight)/h, and the maximum rate of food consumption is 1.9 g/h; a 50–60 g weasel in North America must eat 40–60% of its body mass daily (Gillingham, 1984; Llewellyn, 1942; Short, 1961). The larger *M. nivalis* in Scotland requires 33 (East and Lockie, 1964) to 35% of its body mass daily (Moors, 1977). Stomach capacity is about 10 g (Heptner, 1967) and captives average 9–10 meals, each of a few grams, in 24 h (Gillingham, 1984). Meals average 203 min (range, 138–270 min) to pass through the gut (Short, 1961).

Cardiac and respiratory systems of *M. nivalis* are highly efficient as required in an active small mammal with high O₂ demands. Rate of O₂ consumption is greatest during the spring and summer, and is greater in the smaller females (Tumanov and Levin, 1974). The pulse rate is 483–516 beats/min at 1 month of age and 451–468 beats/min at 3 months; respiration rate is 110–124 breaths/min at 1 month of age and 96–104 breaths/min at 6 months (Tumanov and Levin, 1974).

Hearing range of *M. nivalis* extends from 51 Hz to 60.5 kHz, with a region of best hearing extending from 1 to 16 kHz and highest sensitivity at 2 kHz (Heffner and Heffner, 1985, 1987). Auditory and visual cues are thought to be important in hunting prey (Heidt, 1972; Herter, 1939). The sight of moving prey elicits an immediate attack, but a stationary rodent is not readily detected, even if the weasel passes close to it (Heidt, 1972). *M. nivalis* can differentiate between estrous and diestrous odors of its prey and selects estrous scents, suggesting that olfaction is keen and also is an important cue in prey identification (Cushing, 1984, 1985).

Anal glands of *M. nivalis* include holocrine and apocrine secretory glands that discharge into paired storage sacs, which are encased in muscular husks and open by sphincters into the anus (Stubbe, 1970, 1972). Both sets of muscles are under voluntary control and anal gland secretions are routinely deposited with the feces to serve as a territory marker. These secretions contain thietanes and dithiacyclopentanes, sulfur-containing compounds that may be an effect of the defense function of the anal gland secretion (Brinck et al., 1983).

The abdominal mammary glands have four pairs of mammae, inconspicuous in non-parous females (Heidt, 1970). The ovaries are small and compact, enlarging from ≤11 mg during anestrus to 24–48 mg during pregnancy (Deanesly, 1944). Uteri of immature weasels weigh 0.015–0.040 g and, as first estrus nears, the uterus grows to 0.12 g, the glands enlarge and thicken, and the stroma becomes more edematous. The uterus regresses to ca. 0.07 g during lactation and regresses to 0.02–0.05 g during anestrus (Deanesly, 1944). There are no seminal vesicles or obvious prostate gland in males. The testes descend at an early age and remain in the scrotum throughout life (Hill, 1939). The corpora penis is thick and averages 14 mm in length. It is encased in an integumentary sheath which is largest in diameter subdistally, especially at its dorsoventral diameter (ca. 3.5 mm—Long, 1969).

ONTOGENY AND REPRODUCTION. Ovulation is induced by the stimulus of copulation. Mean ovulation rate is 7.1 (range, 4–11) in the UK (Deanesly, 1944). Fertilized ova develop to the blastocyst stage and implant after 10–12 days (Heidt, 1970). Blastocysts are spaced within the bicornuate uterus, reaching equal distribution between the two horns by migrating from one to the other (Deanesly, 1944). Implantation is direct, without the significant delay seen in *M. erminea* and *M. frenata*. Both *M. nivalis* and *M. erminea* are thought to have derived from a common ancestor with delayed implantation, but that, in the process of evolving into a specialist predator of rodents, *M. nivalis* abandoned delayed implantation, achieving a more opportunistic life history strategy (Heidt, 1970; King, 1983a, 1984a, 1989b; Powell, 1985; Sandell, 1984; Stenseth, 1985).

Active gestation from implantation to parturition takes about 25 days, giving a total gestation of 34–37 days (East and Lockie, 1965; Hartman, 1964; Heidt, 1970; Heidt et al., 1968). Mean number of embryos is 6.4 (range, 6–7) and 5.6 (4–7) in the U.K. (Deanesly, 1944; King, 1980c), 7.1 (4–10) in northwestern USSR (Danilov and Tumanov, 1975), 9.7 (3–16) in northern Alaska (Fitz-

gerald, 1981), and 12.0 (5–19) in Mongolia (Heptner, 1967). The number of young born/litter averages 4.4 (range, 4–5) in Finland (Blomquist et al., 1981), 4.5 (3–6) in New Zealand (Hartman, 1964), 4.8 (1–6) in temperate North America (Heidt, 1970), and 5.0 (2–7) in Scotland (East and Lockie, 1964, 1965). Litters from high arctic regions tend to be larger than those from temperate regions when small rodents are plentiful; records of up to 15 young from Pt. Barrow, Alaska are known (Fitzgerald, 1981).

Breeding may continue throughout the year in North America, central Europe, and parts of the USSR, but is concentrated in spring and late summer (Danilov and Tumanov, 1972; Frank, 1974; Heidt, 1970; Heptner, 1967; Stubbe, 1969). In the arctic, when small rodents are abundant, *M. nivalis* breeds during winter under the snow (Fitzgerald, 1981; MacLean et al., 1974). In the UK, the breeding season generally is from March to August (Deanesly, 1944); estrus is curtailed and the testes regress between August and February (Hill, 1939). Two litters per year are common in the wild, although mortality often is high in the second. There is an important difference in breeding cycles between *M. n. nivalis* and *M. n. vulgaris*. In three consecutive years, a captive, feral-born Scandinavian *M. n. nivalis* came into post-partum estrus at 5 weeks, so that most of the second pregnancy was already completed during the rearing of the first litter (Frank, 1974). *M. n. vulgaris* does not return to estrus until the first litter is weaned at 10–11 weeks (Deanesly, 1944). The ability to come into post-partum estrus probably evolved to increase productivity when prey are plentiful (King, 1989b). Since breeding in *M. n. nivalis* is independent of season, this ability is not an adaptation to the short summer of northern latitudes as hypothesized by Frank (1974). A third litter is possible in captivity and perhaps in the wild during population peaks of small rodents (Frank, 1974; Hartman, 1964).

Newborn *M. nivalis* in North America (adult females >60 g) weigh from 1.1 to 1.7 g ($\bar{X}$ = 1.4 g; Heidt, 1970). At birth, the altricial young are wrinkled, pink, naked, blind, and deaf. By day 4, fine white hair completely covers the body; gray pigmentation begins to show on the dorsum by day 6 and, by day 10–11, clear demarcation is seen between the pigmented dorsal and unpigmented ventral sides. At day 11, deciduous canines erupt, followed by incisors at day 12–13 and premolars at day 18. At day 18, the dorsum is brown and the venter white. Ears open between days 21–28 and eyes open between days 26–30. By day 30, permanent canines start emerging, followed by permanent incisors at day 32–33, and aggressive play behavior is first seen. The permanent dentition is complete by days 40–42. Weaning is initiated at ca. day 32 and continues until days 42–56. The young begin to eat meat as early as day 18; actions leading up to killing begin at about day 32–38, but the young are unable to kill until days 38–42. By day 40, the typical mustelid locomotion is acquired and, by day 49, all young are adept at killing small mice. From about week 6, males are noticeably larger and heavier than females. By days 49–56, all four standard body measurements reach adult dimensions, and by day 60, the skull (except the sagittal crest) completes growth in both sexes. Adult body mass is attained between weeks 12–15 (Heidt, 1970; Heidt et al., 1968). Young of the larger British form (adult females >80 g) weigh 2.0–4.0 g ($\bar{X}$ = 3.0 g) by day 1 (East and Lockie, 1965). Thereafter, they develop in much the same way as North American *M. nivalis*, but reach each stage slightly later. Family groups break up by 9–12 weeks (East and Lockie, 1964, 1965; Hartman, 1964).

Spring-born females of *M. n. vulgaris* are sexually mature at about 3 months and, if small rodents are abundant, may produce young in their first summer (Deanesly, 1944; King, 1980c, 1983a), while adult females produce a second litter. However, young of summer and autumn litters grow more slowly and do not reach sexual maturity until the following spring (Hill, 1939; King, 1980c). These differences in growth rate and age at sexual maturity make age determination in live animals nearly impossible and add to the already extensive geographical variation in body size (King, 1989b).

Two characteristics of *M. nivalis* confound the determination of reproductive condition from carcasses: the corpora lutea persist for some time after parturition (Deanesly, 1944) and placental scars are rapidly lost (Heidt, 1970). Permanent dentition is in place too early to be of use in aging. The date-skull-baculum method, developed from known-aged material (King, 1980b), classifies by year class and date, not by absolute age. Accuracy of this method decreases rapidly after 8–9 months; it can be applied only to large, dated, homogeneous samples and is not applicable to populations that have

no defined breeding season. Other methods of age determination use wear of canine teeth, cementum annuli, closure of cranial (nasal) sutures, development of the sagittal crest, mass and morphology of the baculum, development of the lateral suprasesamoid tubercle, and various combinations of these (Fog, 1969; Hansson, 1968; King, 1980b; Lockie, 1966). These methods may be used to rank individuals by age and then into relative age groups, but the resulting age structures cannot be compared since they are not based on known-aged material and represent unknown chronological intervals. Counting cementum annuli provides the best age estimate, but calibration with teeth from known-aged weasels is needed (Jensen, 1978).

Annual survival rate of *M. nivalis* on British game estates is estimated at 20% for males and 25% for females (King, 1980c). Life expectancy is <1 year from independence, though a few individuals live into their 3rd year. The proportion of weasels <1 year old ranges from 59 to 84% and the mean age is from 0.79 to 1.16 years. Mean annual mortality of both genders and all ages is 75–90% and general mean age at death is 0.88 year (0.86 in males, 0.93 in females; King, 1980c; Stubbe, 1969). In captivity, *M. nivalis* lives 7–10 years (Frank, 1974; Hill, 1939).

ECOLOGY. *Mustela nivalis* is a specialist predator of small mammals, especially microtine rodents and other mice. The proportions of different small rodent species in the diet roughly reflects their relative abundances throughout the year (Erlinge, 1975). In Europe, *Microtus agrestis*, *M. arvalis*, *Clethrionomys glareolus*, *Apodemus sylvaticus*, and *Lemmus lemmus* are preyed upon (Barbu, 1968; Brugge, 1977; Day, 1968; Delattre, 1983, 1984; Erlinge, 1974, 1975; King, 1980a; Korpimäki and Norrdahl, 1987; Moors, 1975; Tapper, 1979). In the USSR, *M. agrestis*, *M. oeconomus*, *M. brandti*, *Arvicola terrestris*, *C. glareolus*, *Clethrionomys rutilus*, and *Lemmus sibiricus* are preyed upon (Heptner, 1967; Nasimovich, 1949; Novikov, 1956; Ognev, 1935; Parovshchikov, 1963; Stroganov, 1962). In North America, *Microtus pennsylvanicus*, *M. ochrogaster*, *C. rutilus*, *C. gapperi*, *Peromyscus leucopus*, *P. maniculatus*, *Reithrodontomys megalotis*, *Sigmodon hispidus*, *Dicrostonyx rubricatus*, *D. hudsonius*, and *L. sibiricus* are preyed upon (Criddle, 1947; Hall, 1951; Polderboer, 1942). In New Zealand, where microtines are absent, *Mus musculus* is taken, but *M. nivalis* has not done well there and survives only at low densities (King, 1984b). Diet analyses suggest a specialization by *M. nivalis* on intermediate-sized small rodents even when larger rodents are abundant in the laboratory (Derting, 1989) and in the field (Goszczynski, 1977; Hall, 1951; King, 1980a; Parovshchikov, 1963; Tapper, 1979). Intermediate-sized inactive or non-aggressive small rodents are more vulnerable to predation than relatively larger, aggressive, active small rodents (Derting, 1989). This apparent specialization on readily available intermediate-sized small rodents may be a major factor limiting the geographic range of *M. nivalis* (Simms, 1979). *M. nivalis* is susceptible to secondary poisoning from rodenticides; adults eating 20–30 g of food/day may receive a lethal exposure if prey are contaminated with 1.0–1.5 ppm of warfarin (Townsend et al., 1984).

When small rodents are scarce, *M. nivalis* takes birds' eggs and nestlings and young lagomorphs, especially in late winter, spring, and early summer (King, 1980a; Moors, 1975, 1977; Tapper, 1979). Moles, shrews, squirrels, chipmunks, hamsters, gerbils, house mice, rats (*Rattus* sp.), insects (mostly beetles), lizards, frogs, salamanders, fish, worms, and carrion are taken occasionally (Brugge, 1977; Hall, 1951; Ognev, 1935; Parovshchikov, 1963; Tapper, 1979). Shrews are caught less frequently than expected from their local abundance and are rarely eaten (Brugge, 1977; Korpimäki and Norrdahl, 1987; Parovshchikov, 1963). In the arctic, *M. nivalis* occasionally is known to scavenge carcasses of brown lemmings, *L. sibiricus* (Mullen and Pitelka, 1972). Male *M. nivalis* readily shift to larger prey such as birds, lagomorphs, and water voles, while females continue to search for short-tailed voles (Erlinge, 1974, 1975). This segregation results from a difference in hunting behavior and size of the two genders; females spend more time hunting in tunnels and generally take smaller prey than do males (Erlinge, 1975; King, 1980a). In arctic regions, birds' eggs and nestlings frequently are taken during the summer; the rest of the year is spent hunting under the snow, searching for vole and lemming nests in the subnivean environment (Fitzgerald, 1981; MacLean et al., 1974; Nasimovich, 1949). In these regions, there are few alternative prey available in winter, so voles and lemmings are systematically

hunted into their last refuges. This heavy predation on voles and lemmings may cause pronounced microtine population fluctuations (Henttonen et al., 1987; Pearson, 1966; Sonerud, 1988). By contrast, predation by least weasels on any particular rodent population in temperate areas is relatively slight, although the total pressure exerted by all local predators together may be heavy and continuous (King, 1985, 1989b). *M. nivalis* can cause ecological and behavioral alterations in their prey populations either by their presence or just their odor, including decreased population density and altered daily activity patterns and space use (Jedrzejewski and Jedrzejewska, 1990; King, 1989b; Stoddart, 1976).

Mustela nivalis is preyed upon by almost any larger predator, including raptors, snakes, man, and larger carnivores, including foxes, domestic cats and dogs (Fitzgerald, 1981; Handley, 1949; Heptner, 1967; King, 1980c; Lokemoen and Higgins, 1972; Svendsen, 1982), and even its close relatives *M. frenata* (Polderboer et al., 1941) and *M. erminea* (Erlinge and Sandell, 1988). In the UK, *M. nivalis* in woodlands are more active by day than by night when they would be exposed to predation by tawny owls, *Strix aluco* (King, 1975a). The white winter pelage of northern *M. nivalis* provides camouflage against the snow. The black tail tip of *M. erminea* and *M. frenata* is a predator-deflection spot, and its absence in *M. nivalis* is due to their very short tails; a black tail tip would be too close to the body to misdirect predators (Powell, 1982). It is unclear whether predation on *M. nivalis* has any significant effect on their numbers. Avian predators are thought to exert a substantial impact on *M. nivalis* populations during the decline phase of the northern vole cycle (Korpimäki and Norrdahl, 1989a, 1989b), but peak numbers of *M. nivalis* associated with vole peaks are short-lived and decline with the voles even in the absence of avian predators (King, 1983a, 1983b, 1989b).

Long-term coexistence between *M. nivalis* and *M. erminea* may result through an unstable balance of competitive advantages determined by the environment (Erlinge and Sandell, 1988; King and Moors, 1979b; Powell and Zielinski, 1983). Differences between the two species in body size, foraging and breeding strategies, and social dominance give *M. erminea* superiority in interference and *M. nivalis* superiority in exploitation. When there is sufficient prey, the two species can coexist and have little effect on each other's distributions even at the local level (Andersen, 1978; Pounds, 1981). When prey numbers are low, only one species survives, and size distribution of available prey determines which species disappears and which one remains. In sympatry, *M. nivalis* and *M. erminea* are thought to hunt different prey in different habitats (Simms, 1979). However, coexistence mediated by this or any other means can only be temporary, interrupted by periods of local extinction and recolonization (Powell and Zielinski, 1983).

Habitat selection by *M. nivalis* is determined by the local distribution of small rodents. Throughout its range, it is found in open forests, farmlands and cultivated fields, grassy fields and meadows, riparian woodlands, hedgerows, alpine meadows and forests, scrub, steppe and semi-deserts, prairies, and coastal dunes (Heptner, 1967; King, 1989b; Nyholm, 1959; Polder, 1968; Svendsen, 1982). Deep, dense forests and sandy deserts, which lack food and/or cover, are avoided. On the periphery of its range in North America, *M. nivalis* is usually observed in riparian habitats, suggesting that dispersal occurs through these habitats and across adjacent agricultural lands. Foraging individuals avoid open spaces, where they are most vulnerable to predation by raptors, and concentrate their activity along protected edges. In farmlands, *M. nivalis* is generally restricted to hedgerows, fencelines, and piles of cutover brush (Moors, 1975; Polder, 1968; Pounds, 1981), whereas in open steppe they remain under long grass (Heptner, 1967). *M. nivalis* lives year-round at high elevations (to 3,660 m) on low-latitude mountain ranges such as the Caucasus, Alps, Tien Shan, Altai, Atlas, and Appalachians. They are well-adapted to tundra and snowy environments and range above treeline in arctic and alpine areas. Snow presents little obstacle to the distribution, hunting, or movements of *M. nivalis* (Erlinge, 1974; Simms, 1979).

Males and females live separately for most of the year, except during the breeding season. Home ranges of males are larger (0.6–26.2 ha) than females and can include one or more female home ranges (0.2–7.0 ha), but exclude adjacent males (King, 1973, 1975a; Lockie, 1966; Moors, 1975; Nyholm, 1959; Polderboer, 1942; Pounds, 1981). When population density is high, individual ranges of males are largely exclusive. When density is low, overlapping of individual ranges of males is tolerated, but neighbors are temporally

separated in overlap zones (King, 1975a; Lockie, 1966; Powell, 1979). Vacated home ranges are usurped either by adjacent residents or by immigrating non-residents (King, 1975a). Size of home range depends upon habitat, population density, season, gender, and prey density. Females spend more time hunting in rodent tunnels (Erlinge, 1974) and can therefore live on disproportionately small home ranges (King, 1980a).

Although widely distributed, *M. nivalis* is considered rare in North America. In Eurasia, it is relatively common, but not often seen. Local densities of 0.2–1.0/ha occur in favored habitats or when prey are abundant (Erlinge, 1974; Fitzgerald, 1981; Lockie, 1966; Nyholm, 1959). Over wider areas, average density may be as low as 1–7/100 ha (Goszczynski, 1977). North American populations of least weasels may occur at higher densities than Eurasian populations due to their smaller body size. Populations fluctuate both seasonally and annually, especially in northern regions, where the 3–4 year population fluctuations of microtines are both affected by *M. nivalis* (along with *M. erminea*) and also cause instability of *M. nivalis* populations (Andersson and Erlinge, 1977; Henttonen et al., 1987; MacLean et al., 1974). Local disappearance of *M. nivalis* is common when small rodents are scarce, but their high dispersal rate and colonization capacity allows recolonization of vacated areas when small rodents increase in number. *M. nivalis* adjusts its reproductive effort to the local density of small rodents (Andersson and Erlinge, 1977; Heptner, 1967; King and Moors, 1979a; MacLean et al., 1974). The rapid buildup in numbers of *M. nivalis* on the North American tundra during a microtine peak indicates that when food is plentiful, nearly all females breed, and the number of live births and survivorship of the young increase greatly (MacLean et al., 1974). This response is rapid because of early sexual maturity, relatively short lifespan, and high reproductive capacity in *M. nivalis* (King, 1983a). Because producing and rearing young increases energy requirements of females by up to 10% during gestation and up to 100% during lactation (Hayward, 1983), a minimum density of 10–15 voles/ha is necessary for reproductive success (Delattre, 1984; Erlinge, 1974; Tapper, 1979). In years when prey are scarce, spring-born females delay their first breeding attempt until the following spring, many adult females produce no young, and *M. nivalis* becomes scarce (Erlinge, 1974; MacLean et al., 1974; Tapper, 1979). The variable reproductive performance of adult females is an important component of the numerical response (Tapper, 1979), but the two key factors are that the extra food decreases the high juvenile mortality and increases fecundity by allowing the production of extra litters, both by adults and by spring-born females. This capacity of *M. nivalis* is unique among the Mustelidae (King, 1983b). The amplitude of population fluctuations in *M. nivalis* is therefore high. Population irruptions have been documented throughout its range, involving sudden large increases in numbers of up to 10-fold concurrently or within 9 months of a population peak of small rodents and lasting 6–18 months (Delattre, 1983; Heptner, 1967; Jeffries and Pendlebury, 1968; King, 1980c; Lokemoen and Higgins, 1972; Swanson and Fryklund, 1935; Swenk, 1926; Tapper, 1979). The proportion of juveniles in a sample varies among years depending on the reproductive success of the previous season(s); the greatest part of the population at any one time (68–86%, $\bar{X} = 75\%$) is composed of young-of-the-year (King, 1980c).

The sex ratio among trapped *M. nivalis* favors males by about 3:1, varying from 1.9:1 to 6.2:1 (King, 1975b). The sex ratio at birth is 1:1, and King (1975b) found no differential mortality between the genders, so normal sex ratios probably are closer to 1:1. This discrepancy in sex ratio probably is due to sampling bias (Buskirk and Lindstedt, 1989; King, 1975b). However, studies using closely spaced traps have found that females can sometimes be genuinely scarce (King, 1975b). Males may be more abundant in declining populations because the larger size of their home range includes a wider variety of habitats and a greater utilization of alternative prey makes them less vulnerable to food shortages (Erlinge, 1974; Lockie, 1966).

Ectoparasites found on *M. nivalis* include the acarine genera *Ceratophyllus, Nearctopsylla, Neotrichodectes, Megabothris, Ctenophthalmus, Hystricopsylla, Malaraeus, Rhadinopsylla, Peromyscopsylla, Dasypsyllus, Palaeopsylla, Amalareus, Dermacentor, Ixodes,* and *Latrilichus,* and the insect genus *Trichodectes* (King, 1976, 1989b; Mardon and Moors, 1977; Svendsen, 1982). Endoparasites recorded for *M. nivalis* include the nematode genera *Skrjabingylus, Trichinella, Capillaria, Dracunculus, Filaroides, Physaloptera,* the trematode genus *Alaria,* and the cestode

genus *Taenia* (Svendsen, 1982). The most significant and best documented of these is *Skrjabingylus nasicola* (Dougherty and Hall, 1955; Duncan, 1976; Hansson, 1967, 1968, 1974; King, 1977; Lewis, 1978; van Soest et al., 1972), which is found as an adult in the nasal and frontal sinuses of *M. nivalis*. When numerous, these worms may cause considerable distortion, lesions, and perforations in the frontal bones, which can lead to pressure on the brain (King, 1977). External inspection of skulls and comparisons with a standardized scale of damage are an indirect but reliable means of measuring the incidence and degree of damage caused by skrjabingylosis (King, 1977; Lewis, 1978). Infestation rates range from 43 to 100% in the UK (King, 1977), 20–60% in continental Europe and the USSR (Hansson, 1968; Lewis, 1978; van Soest et al., 1972), and 5–50% in the USA (Dougherty and Hall, 1955). Woodmice, *A. sylvaticus*, but not bank voles, *C. glareolus*, fed infected slugs, act as paratenic hosts of *S. nasicola* and induce skrjabingylosis when fed to healthy *M. nivalis* (Weber and Mermod, 1983).

BEHAVIOR. The least weasel typically moves quickly and tirelessly, investigating every hole and crevice along its regular hunting routes, and frequently stands upright on the hind legs looking and listening for prey and predators (King, 1989*b*). It typically moves in bounds averaging 12–32 cm or a series of jumps (Heptner, 1967; King, 1989*b*), and can move rapidly (1.3 km in 55 min— Moors, 1975). *M. nivalis* will climb trees to explore the nests of birds and squirrels (Novikov, 1956), and is an able but slow swimmer (Stroganov, 1962; Svendsen, 1982).

Active both day and night throughout the year, *M. nivalis* enters traps at any time, but more often during the day (King, 1975*a*; Moors, 1975). Timing and extent of daily activity are related to the activity patterns and abundance of its prey (Erlinge, 1974; Heptner, 1967; Zielinski, 1988). Foraging activity is synchronized with the time of day that prey are most vulnerable and, if prey are abundant, hunting will be confined to a relatively small area or may be curtailed, especially if ambient temperatures are low. In captivity, *M. nivalis* dramatically increases its activity in response to food deprivation (Price, 1971).

Killing behavior is innate; young separated from their mothers and litter mates before their eyes opened kill mice at 50–60 days of age with no previous experience (Heidt, 1970). Young that observe their mother killing prey may increase their killing efficiency at earlier ages (East and Lockie, 1964; Heidt, 1970; Heidt et al., 1968). Nestling weasels show aggressive behavior (chirps and thrusts) towards mice as early as 32 days of age but do not harm the mice (Heidt, 1970). Young weasels spend much time play-fighting and play-mating (Gossow, 1970; Heidt et al., 1968).

Mustela nivalis responds to movements of prey as stimulus for attack (Powell, 1978). Killing behavior is independent of satiation, and *M. nivalis* will kill moving prey continually until too exhausted to kill more (Heidt, 1972). The killing bite is delivered at the nape of the neck, and penetrates the base of the skull or throat area (Heidt, 1972; Llewellyn, 1942). *M. nivalis* begins feeding by eating the brain and head, then, unless already well fed, proceeds posteriorly (Heidt, 1972). The anterior portion of the cranium, including toothrow, feet, and stomach, usually are not eaten (MacLean et al., 1974). Prey caching is well documented (Heptner, 1967; Oksanen, 1983; Parovshchikov, 1963; Polder, 1968; Polderboer et al., 1941), especially in winter and in colder climates where cached prey does not spoil. The cache site may be a side burrow off the home burrow or near a kill. Excess killing and prey caching is thought to be an adaptive strategy in *M. nivalis*; it is the smallest member of its predator guild, has high energy requirements, and is unable to defend stocks of prey within its home range from larger predators except by storing prey in caches inaccessible to them (Oksanen, 1983). *M. nivalis* takes 5–10 meals/day; since most prey are large enough to require >1 day to be consumed, some caching may always be necessary (Gillingham, 1984).

Dens are not permanent but are usurped from prey, usually in a burrow, rock pile, or other well-concealed site, and the grassy nests inside are improved by lining them with fur plucked from prey (Criddle, 1947). Nests often contain numerous prey carcasses and uneaten parts of prey, especially skulls, and feces are piled up outside (Criddle, 1947; MacLean et al., 1974). Within its home range, each resident makes use of several dens or other temporary shelters from where it can hunt, rest, hide from predators, or escape inclement weather (King, 1989*b*).

Dominance relations, scent marking, and food supply determine the maintenance and stability of home ranges (Powell, 1979). Individual ranges are defined by scent marking (Lockie, 1966; Stubbe, 1972) and maintained by dominance relationships (Erlinge, 1974). For most of the year, females defend their ground against other females and males against other males. Males are dominant over females outside the breeding season and have relatively free access to ground occupied by a female, although the two avoid each other (Erlinge, 1974; Lockie, 1966). However, in the late stages of pregnancy and during lactation, dominance relationships are reversed and females defend their ranges against males and other females (Lockie, 1966). Residents of all sex–age classes are dominant over introduced members of the same sex–age class and, in enclosure experiments, consistent rank orders are formed (Erlinge, 1974). A dominant male will utter short, sharp, threatening sounds and violently attack a less dominant male, which remains passive, sometimes uttering squeals as it flees. When a dominant male is removed from his territory, a less dominant male will expand its range over central parts of the dominant male's territory (Erlinge, 1974; Gossow, 1970). During the breeding season, males travel widely, extending and overlapping their movements in search of receptive females (Erlinge, 1974; Lockie, 1966; Moors, 1975). Females, however, maintain well-defined ranges during the breeding season. By late summer and autumn, stable and well-defined home ranges are again established for the winter and include young-of-the-year (Erlinge, 1974; Moors, 1975). The entire range is regularly hunted in a rotational manner, thereby minimizing the time spent in any one area (King, 1980*c*, 1989*b*). This space-use pattern may have evolved in response to evasiveness of prey. Time spent hunting and distance traveled decrease when prey density is high (King, 1989*b*).

Mating behavior in captive *M. nivalis* is initiated when an estrous female allows a male to approach, and vigorous struggling and fighting ensue before the male can grab the female by the scruff of the neck before copulation (East and Lockie, 1965; Hartman, 1964; Heidt et al., 1968). Copulations last from 20 s to 48 min (Heidt et al., 1968) and from 65 to 90 min (East and Lockie, 1965), and are repeated over several days. This prolonged coitus is necessary to induce ovulation in the female. The mating system is thought to be promiscuous, and males take no direct part in rearing of the young (King, 1989*b*).

Vocalizations in captive animals consist of a repertoire of five different sounds, including a chirp, a hiss, a trill, a squeal, and a squeak (Gossow, 1970; Heidt and Huff, 1970; Heidt et al., 1968; Huff and Price, 1968). The young are vociferous at birth, making high-pitched, short-bursted squeaking sounds which are replaced by chirps when the eyes open (Heidt and Huff, 1970). Within 2–5 days after the eyes open, the chirp becomes adultlike and the adult hiss is well developed. The trill does not appear until 35–50 days of age (Heidt and Huff, 1970).

GENETICS. The karyotype of *M. nivalis* has a diploid number of 42 chromosomes and a fundamental number of 70 (Mandahl and Fredga, 1980; Wurster-Hill, 1973). Chromosomes consist of 26 metacentric and submetacentric elements and 14 acrocentric and subacrocentric elements. The X is a medium-sized submetacentric and the Y is a small metacentric. Both *M. n. nivalis* and *M. n. vulgaris* have 2n = 42 and identical karyotypes, with identical morphology of the individual chromosome pairs and good agreement with respect to the chromosome banding patterns (Mandahl and Fredga, 1980).

No detectable genetic variability was found after examining 21 enzyme loci using starch gel electrophoresis of liver and muscle tissue of 13 *M. nivalis* (Simonsen, 1982). Pigmentation pattern is controlled by one gene with two alleles and the Type I pattern is considered recessive and ancestral (closer to *M. erminea*) to the Type II pattern (Frank, 1985). An artificial hybridization between *M. nivalis* and a forest polecat, *M. putorius furo* (2n = 40), has been reported (Robinson, 1972).

REMARKS. *Mustela* is from the Latin *mustel* meaning weasel and the specific name, *nivalis*, is from the Latin *nix*, genitive *nivis*, meaning snow or snowy (Jaeger, 1955). This refers to the white winter coat worn by the more northern populations. *M. nivalis* is commonly known as least weasel in North America and weasel in the Palaearctic region and New Zealand. Great taxonomic confusion has existed for a long time regarding the status of this species and its subspecies designations, particularly in Europe (Beaucournu and Grulich, 1968; Corbet, 1978; Douma-Petridou and Ondrias, 1986;

Frank, 1985; Reumer, 1988). *M. nivalis* and a form called *M. rixosa* are still considered by some as separate species. Pronounced sexual dimorphism, great geographic and individual variability, differential growth rates between individuals of the first and subsequent litters of the year, extensive geographic range, and tendency of older taxonomic studies to analyze only a few and usually isolated traits contribute to the confusion (King, 1989b). The first evidence that *M. nivalis* is a Holarctic species was given by Allen (1933), although the subspecies *pygmaea* was made a subspecies of *M. rixosa* by Kuroda (1921). The use of the name *nivalis* in place of *rixosa* for all least weasels was first advocated by Reichstein (1957).

We thank S. Anderson for his assistance with the synonymy and literature cited portions of this account, and E. Anderson, G. Heidt, J. Lackey, R. Powell, H. Thomas, and P. Youngman for helpful comments on the manuscript. Special thanks to G. Heidt for the use of the photograph in Fig. 1.

LITERATURE CITED

ALLEN, G. M. 1933. The least weasel: a circumboreal species. Journal of Mammalogy, 14:316–319.

ALLEN, J. A. 1903. Report on the mammals collected in northeastern Siberia by the Jesup North Pacific Expedition, with itinerary and field notes, by N.G. Buxton. Bulletin of the American Museum of Natural History, 19:101–184.

ANDERSEN, J. 1978. Maengdemaessige forhold i forekomsten af brud (*Mustela nivalis*) i forhold til laekat (*Mustela erminea*) i Danmark. Natura Jutlandica, 20:123–128.

ANDERSSON, M., AND S. ERLINGE. 1977. Influence of predation on rodent populations. Oikos, 29:591–597.

BANGS, O. 1896. A review of the weasels of eastern North America. Proceedings of the Biological Society of Washington, 10:1–24.

BARBU, P. 1968. Systématique et écologie de la belette *Mustela nivalis* L., provenant de quelques forêts des districts D'Ilfov et de Prahova-Roumanie. Travaux du Museum d'Histoire Naturelle "Grigore Antipa" (Bucharest), 8:991–1002.

BECHSTEIN, J. M. 1801. Gemeinnutzige Naturgeschichte Deutschlands I. Second ed. Leipzig (not seen, cited in Miller, 1912).

BEAUCOURNU, J. C., AND I. GRULICH. 1968. A propos de la belette de Corse. Mammalia, 32:341–371.

BLANFORD, W. T. 1877. On an apparently undescribed weasel from Yarkand. Journal of the Asiatic Society of Bengal, 46:259–261.

BLOMQUIST, L., P. MUURONEN, AND V. RANTANAN. 1981. Breeding the least weasel (*Mustela rixosa*) in Helsinki Zoo. Zoologische Garten (Neue Folge), Jenaische, 51:363–368.

BOESSNECK, J. 1977. Funde vom mauswiesel, *Mustela nivalis* Linne, 1766, auf dem Tell Hesbon, Jordanien. Säugetierkundliche Mitteilungen, 25:44–48.

BRINCK, C., S. ERLINGE, AND M. SANDELL. 1983. Anal sac secretion in mustelids: a comparison. Journal of Chemical Ecology, 9:727–745.

BROWN, J. H., AND R. C. LASIEWSKI. 1972. Metabolism of weasels: the cost of being long and thin. Ecology, 53:939–943.

BRUGGE, T. 1977. Prooidierkeuze van wezel, hermelijn en bunzing in relatie tot geslacht en lichaamsgrootte. Lutra, 19:39–49.

BUSKIRK, S. W., AND S. L. LINDSTEDT. 1989. Sex biases in trapped samples of Mustelidae. Journal of Mammalogy, 70:88–97.

CASEY, T. M., AND K. K. CASEY. 1979. Thermoregulation of arctic weasels. Physiological Zoology, 52:153–164.

CHAPPELL, M. A. 1980. Thermal energetics and thermoregulatory costs of small arctic mammals. Journal of Mammalogy, 61:278–291.

CORBET, G. B. 1978. The mammals of the Palaearctic Region: a taxonomic review. Cornell University Press and British Museum of Natural History, London, 314 pp.

CRIDDLE, S. 1947. A nest of the least weasel. The Canadian Field-Naturalist, 61:69.

CUSHING, B. S. 1984. A selective preference by least weasels for oestrous versus dioestrous urine of prairie deer mice. Animal Behaviour, 32:1263–1264.

———. 1985. Estrous mice and vulnerability to weasel predation. Ecology, 66:1976–1978.

DANILOV, P. I., AND I. L. TUMANOV. 1972. [Male reproductive cycles in the Mustelidae.] Zoologicheskii Zhurnal, 51:870–881 (in Russian).

———. 1975. [Female reproductive cycles in the Mustelidae.]

Byulleten' Moskovskoyo Obshchestva Ispytatelei Prirody, Otdel Biologicheskii, 80:137–145 (in Russian).

DAY, M. G. 1968. Food habits of British stoats (*Mustela erminea*) and weasels (*Mustela nivalis*). Journal of Zoology (London), 155:485–497.

DAYAN, T., AND E. TCHERNOV. 1988. On the first occurrence of the common weasel (*Mustela nivalis*) in the fossil record of Israel. Mammalia, 52:165–168.

DAYAN, T., D. SIMBERLOFF, E. TCHERNOV, AND Y. YOM-TOV. 1989. Inter- and intraspecific character displacement in mustelids. Ecology, 70:1526–1539.

DEANESLY, R. 1944. The reproductive cycle of the female weasel (*Mustela nivalis*). Proceedings of the Zoological Society of London, 114:339–349.

DELATTRE, P. 1983. Density of weasel (*Mustela nivalis* L.) and stoat (*Mustela erminea* L.) in relation to water vole abundance. Acta Zoologica Fennica, 174:221–222.

———. 1984. Influence de la pression de prédation exercée par une population de belettes (*Mustela nivalis* L.) sur un peuplement de Microtidae. Acta Oecologica/Oecologia Generalis, 5:285–300.

DERTING, T. L. 1989. Prey selection and foraging characteristics of least weasels (*Mustela nivalis*) in the laboratory. The American Midland Naturalist, 122:394–400.

DOMANIEWSKI, J. 1926. Neue säugetierformen aus nordasien. Annales Zoologici Musei Polonici Historiae Naturalis, 5:52–56.

DOUGHERTY, E. C., AND E. R. HALL. 1955. The biological relationships between American weasels (genus *Mustela*) and nematodes of the genus *Skrjabingylus* Petrov 1927 (Nematoda: Metastrongyliidae), the causative organisms of certain lesions in weasel skulls. Revista Iberica de Parasitologia (Grenada), Tomo Extraordinaro, 1955:531–576.

DOUMA-PETRIDOU, E., AND J. C. ONDRIAS. 1986. Contribution to the taxonomy and geographical distribution of the weasel *Mustela nivalis* on the southern Balkan peninsula. Säugetierkundliche Mitteilungen, 33:235–243.

DUNCAN, N. 1976. Theoretical aspects concerning transmission of the parasite *Skrjabingylus nasicola* (Leuckart 1842) to stoats and weasels. Mammal Review, 6:63–74.

EAST, K., AND J. D. LOCKIE. 1964. Observations on a family of weasels (*Mustela nivalis*) bred in captivity. Proceedings of the Zoological Society of London, 143:359–363.

———. 1965. Further observations on weasels (*Mustela nivalis*) and stoats (*Mustela erminea*) born in captivity. Proceedings of the Zoological Society of London, 147:234–238.

ELLERMAN, J. R., AND T. C. S. MORRISON-SCOTT. 1966. The checklist of Palearctic and Indian mammals, 1758 to 1946. Second ed. British Museum of Natural History, London, 810 pp.

ERLINGE, S. 1974. Distribution, territoriality, and numbers of the weasel *Mustela nivalis* in relation to prey abundance. Oikos, 25:308–314.

———. 1975. Feeding habits of the weasel *Mustela nivalis* in relation to prey abundance. Oikos, 26:378–384.

———. 1979. Adaptive significance of sexual dimorphism in weasels. Oikos, 33:233–245.

ERLINGE, S., AND M. SANDELL. 1988. Coexistence of stoat, *Mustela erminea*, and weasel, *M. nivalis*: social dominance, scent communication, and reciprocal distribution. Oikos, 53:242–246.

ERXLEBEN, J. C. P. 1777. Systema regni animalis per classis, ordines, genera, species, varietates, cum synonymia et historia animalium. Classis I, Mammalia. Impensis Weygandiansis, Leipzig, 636 pp.

FATIO, V. 1869. Faune des Vertébrés de la Suisse. Vol. I. Histoire Naturelle des Mammifères. H. Georg, Genève, 410 pp.

FITZGERALD, B. M. 1981. Predatory birds and mammals. Pp. 485–508, *in* Tundra ecosystems: a comparative analysis (L. C. Bliss, J. B. Cragg, D. W. Heal, and J. J. Moore, eds.). Cambridge University Press, Cambridge, 813 pp.

FOG, M. 1969. Studies on the weasel (*Mustela nivalis*) and the stoat (*Mustela erminea*) in Denmark. Danish Review of Game Biology, 6:1–14.

FRANK, F. 1974. Wurfzahl und wurffolge beim nordischen wiesel (*Mustela nivalis rixosa* Bangs, 1896). Zeitschrift für Säugetierkunde, 39:248–250.

————. 1985. Zur evolution und systematik der kleinen wiesel (*Mustela nivalis* Linnaeus, 1766). Zeitschrift für Säugetierkunde, 50:208–225.

GILLINGHAM, B. J. 1984. Meal size and feeding rate in the least weasel (*Mustela nivalis*). Journal of Mammalogy, 65:517–519.

GOSSOW, H. 1970. Vergleichende verhaltensstudien an Marderartigen. I. Uber lautausserungen und zum beuteverhalten. Zeitschrift für Tierpsychologie, 27:405–480.

GOSZCZYNSKI, J. 1977. Connections between predatory birds and mammals and their prey. Acta Theriologica, 22:399–430.

HALL, E. R. 1951. American weasels. University of Kansas Publications, Museum of Natural History, 4:1–466.

————. 1981. The mammals of North America. Second ed. John Wiley & Sons, New York, 2:601–1181 + 90.

HANDLEY, C. O., JR. 1949. Least weasel, prey of barn owl. Journal of Mammalogy, 30:431.

HANSSON, I. 1967. Transmission of the parasitic nematode *Skrjabingylus nasicola* (Leuckart 1842) to species of *Mustela* (Mammalia). Oikos, 18:247–252.

————. 1968. Cranial helminth parasites in species of Mustelidae. I. Frequency and damage in fresh mustelids from Sweden. Oikos, 19:217–233.

————. 1974. Seasonal and environmental conditions affecting the invasion of mustelids by larvae of the nematode *Skrjabingylus nasicola*. Oikos, 25:61–70.

HARTMAN, L. 1964. The behavior and breeding of captive weasels (*Mustela nivalis* L.). New Zealand Journal of Science, 7:147–156.

HAYWARD, G. F. 1983. The bioenergetics of the weasel, *Mustela nivalis*. Ph.D. dissert., Oxford University, Oxford, 258 pp.

HEFFNER, R. S., AND H. E. HEFFNER. 1985. Hearing in mammals: the least weasel. Journal of Mammalogy, 66:745–755.

————. 1987. Localization of noise, use of binaural cues, and a description of the superior olivary complex in the smallest carnivore, the least weasel (*Mustela nivalis*). Behavioral Neuroscience, 101:701–708.

HEIDT, G. A. 1970. The least weasel *Mustela nivalis* Linnaeus. Developmental biology in comparison with other North American *Mustela*. Publications of the Museum, Michigan State University Biological Series, 4:229–282.

————. 1972. Anatomical and behavioral aspects of killing and feeding by the least weasel, *Mustela nivalis* L. Proceedings of the Arkansas Academy of Science, 26:53–54.

HEIDT, G. A., AND J. N. HUFF. 1970. Ontogeny of vocalization in the least weasel. Journal of Mammalogy, 51:385–386.

HEIDT, G. A., M. K. PETERSON, AND G. L. KIRKLAND, JR. 1968. Mating behavior and development of least weasels (*Mustela nivalis*) in captivity. Journal of Mammalogy, 49:413–419.

HEMPRICH, F. G., AND C. G. EHRENBERG. 1833. Seu icones et descriptiones corporum naturalium novorum aut minus cognitorum, quae ex itineribus per Libyam, Aegyptum, Nubium, Dongalum, Syriam, Arabiam et Habessiniam. Symbolae Physicae, I. Mammalia, 3, part 2 (not seen, partially cited in Ellerman and Morrison-Scott, 1966).

HENTTONEN, H., T. OKSANEN, A. JORTIKKA, AND V. HAUKISALMI. 1987. How much do weasels shape microtine cycles in the northern Fennoscandian taiga? Oikos, 50:353–365.

HEPTNER, V. G. 1967. [The mammals of the Soviet Union. Sirenia and Carnivora (V. G. Heptner and N. P. Naumov, eds.)]. Gustav Fischer, Jena, 2:5–1004 (in Russian).

HERTER, K. 1939. Psychologische untersuchungen an einem mauswiesel (*Mustela nivalis* L.). Zeitschrift für Tierpsychologie, 3:249–263.

HILL, M. 1939. The reproductive cycle of the male weasel (*Mustela nivalis*). Proceedings of the Zoological Society of London, 109:481–512.

HOLMES, T., JR. 1988. Sexual dimorphism in North American weasels with a phylogeny of the Mustelidae. Ph.D. dissert., The University of Kansas, Lawrence, 324 pp.

HUFF, J. N., AND E. O. PRICE. 1968. Vocalizations of the least weasel, *Mustela nivalis*. Journal of Mammalogy, 49:548–550.

JACKSON, H. H. T. 1913. Two new weasels from the United States. Proceedings of the Biological Society of Washington, 26:123–124.

JAEGER, E. C. 1955. A source-book of biological names and terms.

Third ed. Charles C Thomas Publisher, Springfield, Illinois, 323 pp.

JEDRZEJEWSKI, W., AND B. JEDRZEJEWSKA. 1990. Effect of a predator's visit on the spatial distribution of bank voles: experiments with weasels. Canadian Journal of Zoology, 68:660–666.

JEFFRIES, D. J., AND J. B. PENDLEBURY. 1968. Population fluctuations of stoats, weasels, and hedgehogs in recent years. Journal of Zoology (London), 156:513–517.

JENSEN, B. 1978. Resultater af fangst med kassefaelder. Natura Jutlandica, 20:129–136.

KING, C. M. 1973. A system for trapping and handling live weasels in the field. Journal of Zoology (London), 171:458–464.

————. 1975a. The home range of the weasel *Mustela nivalis* in an English woodland. The Journal of Animal Ecology, 44:639–668.

————. 1975b. The sex ratio of trapped weasels *Mustela nivalis*. Mammal Review, 5:1–8.

————. 1976. The fleas of a population of weasels in Wytham Woods, Oxford. Journal of Zoology (London), 180:525–535.

————. 1977. The effects of the nematode parasite *Skrjabingylus nasicola* on British weasels *Mustela nivalis*. Journal of Zoology (London), 182:225–249.

————. 1979. Moult and color change in English weasels (*Mustela nivalis*). Journal of Zoology (London), 189:127–134.

————. 1980a. The weasel *Mustela nivalis* and its prey in an English woodland. The Journal of Animal Ecology, 49:127–159.

————. 1980b. Age determination in the weasel (*Mustela nivalis*) in relation to the development of the skull. Zeitschrift für Säugetierkunde, 45:153–173.

————. 1980c. Population biology of the weasel *Mustela nivalis* on British game estates. Holarctic Ecology, 3:160–168.

————. 1983a. The life history strategies of *Mustela nivalis* and *M. erminea*. Acta Zoologica Fennica, 174:183–184.

————. 1983b. Factors regulating mustelid populations. Acta Zoologica Fennica, 174:217–220.

————. 1984a. The origin and adaptive advantages of delayed implantation in *Mustela erminea*. Oikos, 42:126–128.

————. 1984b. Immigrant killers: introduced predators and the conservation of birds in New Zealand. Oxford University Press, Auckland, 224 pp.

————. 1985. Interactions between woodland rodents and their predators. Symposia of the Zoological Society of London, 55:219–247.

————. 1989a. The advantages and disadvantages of small size to weasels, *Mustela* species. Pp. 302–334, *in* Carnivore behavior, ecology, and evolution (J. L. Gittleman, ed.). Cornell University Press, Ithaca, New York, 624 pp.

————. 1989b. The natural history of weasels and stoats. Christopher Helm Publishers, London, 253 pp.

KING, C. M., AND P. J. MOORS. 1979a. The life history tactics of mustelids and their significance for predator control and conservation in New Zealand. New Zealand Journal of Zoology, 6:619–622.

————. 1979b. On co-existence, foraging strategy, and biogeography of weasels and stoats (*Mustela nivalis* and *M. erminea*) in Britain. Oecologia (Berlin), 39:129–150.

KLEINSCHMIDT, O. 1937. Das mauswiesel schlesiens. Falco, 33:10–12.

KORPIMÄKI, E., AND K. NORRDAHL. 1987. Low proportion of shrews in the diets of small mustelids in western Finland. Zeitschrift für Säugetierkunde, 52:257–260.

————. 1989a. Avian predation on mustelids in Europe 1: occurrence and effects on body size variation and life traits. Oikos, 55:205–215.

————. 1989b. Avian predation on mustelids in Europe 2: impact on small mustelid and microtine dynamics — a hypothesis. Oikos, 55:273–276.

KRATOCHVIL, J. 1977. Sexual dimorphism and status of *Mustela nivalis* in central Europe (Mammalia, Mustelidae). Acta Scientiarum Naturalium Academiae Scientiarum Bohemoslovacae (Brno), 11:1–42.

KRETZOI, M. 1942. Praokkupierte und durch ältere zu ersetzende Säugetiernamen. Földtani Közlönyi (Budapest), 72:345–349.

KURODA, N. 1921. On three new mammals from Japan. Journal of Mammalogy, 2:208–211.

KURTÉN, B. 1968. Pleistocene mammals of Europe. Weidenfeld and Nicholson, London, 317 pp.

KURTÉN, B., AND E. ANDERSON. 1980. Pleistocene mammals of North America. Columbia University Press, New York, 443 pp.

LATHAM, R. 1953. Simple method for identification of least weasel. Journal of Mammalogy, 34:385.

LEWIS, J. W. 1978. A population study of the metastrongylid nematode *Skrjabingylus nasicola* in the weasel *Mustela nivalis*. Journal of Zoology (London), 184:225–229.

LINN, I., AND M. G. DAY. 1966. Identification of individual weasels *Mustela nivalis* using the ventral pelage pattern. Journal of Zoology (London), 148:583–585.

LINNAEUS, C. 1766. Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Twelfth edition. Laurentii Salvii, Uppsala, 1:1–532.

LLEWELLYN, L. M. 1942. Notes on the Alleghenian least weasel in Virginia. Journal of Mammalogy, 23:439–441.

LOCKIE, J. D. 1966. Territory in small carnivores. Symposia of the Zoological Society of London, 18:143–165.

LOKEMOEN, J. T., AND K. F. HIGGINS. 1972. Population irruption of the least weasel *Mustela nivalis* in east central North Dakota. The Prairie Naturalist, 4:96.

LONG, C. A. 1969. Gross morphology of the penis in seven species of the Mustelidae. Mammalia, 33:145–160.

MACLEAN, S. F., JR., B. M. FITZGERALD, AND F. A. PITELKA. 1974. Population cycles in arctic lemmings: winter reproduction and predation by weasels. Arctic and Alpine Research, 6:1–12.

MANDAHL, N., AND K. FREDGA. 1980. A comparative chromosome study by means of G-, C-, and NOR-bandings of the weasel, the pygmy weasel, and the stoat (*Mustela*, Carnivora, Mammalia). Hereditas, 93:75–83.

MARDON, D. K., AND P. J. MOORS. 1977. Records of fleas collected from weasels (*Mustela nivalis* L.) in northeast Scotland (Siphonaptera: Hystricopsyllidae and Ceratopsyllidae). Entomologist's Gazette, 28:277–280.

MATSCHIE, P. 1901. Über rumänische Säugethiere. Sitzungsberichte der Gesellschaft Naturforschender Freunde zu Berlin, 1901:220–238.

MILLER, G. S., JR. 1912. Catalogue of the mammals of western Europe. British Museum of Natural History, London, 1019 pp.

MOORS, P. J. 1975. The food of weasels (*Mustela nivalis*) on farmland in northeast Scotland. Journal of Zoology (London), 177:455–461.

———. 1977. Studies on the metabolism, food consumption, and assimilation efficiency of a small carnivore, the weasel (*Mustela nivalis* L.). Oecologia (Berlin), 27:185–202.

———. 1980. Sexual dimorphism in the body size of mustelids (Carnivora): the roles of food habits and breeding systems. Oikos, 34:147–158.

MOROZOVA-TUROVA, L. G. 1965. [Geographic variation in weasels in the Soviet Union.] Pp. 265–279, *in* [Game and fur animals: their biology and commercial exploitation (D. P. Dement'ev et al., eds.)]. Moscow (in Russian).

MULLEN, D. A., AND F. A. PITELKA. 1972. Efficiency of winter scavengers in the arctic. Arctic, 25:225–231.

NASIMOVICH, A. A. 1949. [The biology of the weasel in Kola Peninsula in connection with its competitive relations with the ermine.] Zoologicheskii Zhurnal, 28:177–182 (in Russian).

NILSSON, S. 1820. Skandinavisk Fauna. Första Delen. Däggande Djuren, Lund, 419 pp.

NOVIKOV, G. A. 1956. [Carnivorous mammals of the fauna of the U.S.S.R.] Zoological Institute of the Academy of Sciences of the U.S.S.R., 62:134–138. English Translation. 1962. Israel Program for Scientific Translations, 284 pp.

NOWAK, R. M. 1991. Walker's mammals of the world. Fifth ed. The Johns Hopkins University Press, Baltimore, 2:643–1629.

NYHOLM, E. S. 1959. Kärpästä ja lumikosta ja niiden talvisista elinpiireistä. Suomen Riista, 13:106–116.

OGNEV, S. I. 1935. [Mammals of the U.S.S.R. and Adjacent Countries. Carnivora. Fissipedia and Pinnipedia, Vol. 3.] English Translation. 1962. Israel Program for Scientific Translations, 641 pp.

OKSANEN, T. 1983. Prey caching in the hunting strategy of small mustelids. Acta Zoologica Fennica, 174:197–199.

PALLAS, P. S. 1811. Sistens omnium animalium in extenso imperio Rossico et adjacentibus maribus observatorum recensionem, domicilia, mores et descriptiones, anatomen atque icones plurimorum. Zoographia Rosso-Asiatica, 1:1–568.

PAROVSHCHIKOV, V. Y. 1963. [A contribution to the ecology of *Mustela nivalis* Linnaeus, 1766 of the Arkhangel'sk north.] Vestnik Ceskoslovenske Spolecnosti Zoologicke, 27:335–344 (in Russian).

PEARSON, O. P. 1966. The prey of carnivores during one cycle of mouse abundance. The Journal of Animal Ecology, 35:217–233.

POLDER, E. 1968. Spotted skunk and weasel populations den and cover usage in northeast Iowa. Transactions of the Iowa Academy of Science, 75:142–146.

POLDERBOER, E. B. 1942. Habits of the least weasel (*Mustela rixosa*) in northeastern Iowa. Journal of Mammalogy, 23:145–147.

POLDERBOER, E. B., L. W. KUHN, AND G. O. HENDRICKSON. 1941. Winter and spring habits of weasels in central Iowa. The Journal of Wildlife Management, 5:115–119.

POMEL, M. 1853. Catalogue méthodique et desriptif des vertébrés fossiles découverts dans le bassin hydrographique supérieur de la Loire et surtout dans la vallée de son affluent principal l'Allier. J.-B. Baillière, Paris, 193 pp.

POUNDS, C. J. 1981. Niche overlap in sympatric populations of stoats (*Mustela erminea*) and weasels (*Mustela nivalis*) in northeast Scotland. Ph.D. dissert., University of Aberdeen, Aberdeen, 326 pp.

POWELL, R. A. 1978. A comparison of fisher and weasel hunting behavior. Carnivore, 1:28–34.

———. 1979. Mustelid spacing patterns: variations on a theme by *Mustela*. Zeitschrift für Tierpsychologie, 50:153–165.

———. 1982. Evolution of black-tipped tails in weasels: predator confusion. The American Naturalist, 119:126–131.

———. 1985. Possible pathways for the evolution of reproductive strategies in weasels and stoats. Oikos, 44:506–508.

POWELL, R. A., AND W. J. ZIELINSKI. 1983. Competition and coexistence in mustelid communities. Acta Zoologica Fennica, 174:223–227.

PRICE, E. O. 1971. Effects of food deprivation on activity of the least weasel. Journal of Mammalogy, 52:636–640.

PUCHERAN, J. 1855. Notes mammalogiques. Revue et Magasin de Zoologie, series 2, 7:392–394.

RALLS, K., AND P. H. HARVEY. 1985. Geographic variation in size and sexual dimorphism of North American weasels. Biological Journal of the Linnean Society, 25:119–167.

REICHSTEIN, H. 1957. Schädelvariabilität europäischer mauswiesel (*Mustela nivalis* L.) und hermaline (*Mustela erminea* L.) in beziehung zu verbreitung und geschlecht. Zeitschrift für Säugetierkunde, 22:151–182.

REUMER, J. W. F. 1988. Een bruikbaar onderscheid tussen deschedels van de wezel (*Mustela nivalis*) in de hermelijn (*Mustela erminea*). Dieren, 5:106–108.

RHOADS, S. N. 1900. A new weasel from western Pennsylvania. Proceedings of the Academy of Natural Sciences of Philadelphia, 52:751–754.

ROBINSON, R. 1972. Hybridisation among the Mustelidae. Carnivore Genetics Newsletter, 2:91–92.

SANDELL, M. 1984. To have or not to have delayed implantation: the example of the weasel and the stoat. Oikos, 42:123–126.

SAVAGE, D. E., AND D. E. RUSSELL. 1983. Mammalian paleofaunas of the world. Addison-Wesley Publishing Company, Reading, Massachusetts, 432 pp.

SEMENOV, A. 1899. [Some reflections on the past history of the flora and fauna of the Crimea.] Zapiski Imperatorskago Akademiya Nauk, Series 8, 8:1–19 (in Russian).

SHORT, H. L. 1961. Food habits of a captive least weasel. Journal of Mammalogy, 42:273–274.

SIMMS, D. A. 1979. North American weasels: resource utilization and distribution. Canadian Journal of Zoology, 57:504–520.

SIMONSEN, V. 1982. Electrophoretic variation in large mammals. II. The red fox *Vulpes vulpes*, the stoat *Mustela erminea*, the weasel *Mustela nivalis*, the polecat *Mustela putorius*, the pine marten *Martes martes*, the beech marten *Martes foina*, and the badger *Meles meles*. Hereditas, 96:299–305.

SONERUD, G. A. 1988. What causes extended lows in microtine cycles? Analysis of fluctuations in sympatric shrew and micro-

tine populations in Fennoscandia. Oecologia (Berlin), 76:37–42.

STENSETH, N. C. 1985. Optimal size and frequency of litters in predators of cyclic prey: comments on the reproductive biology of stoats and weasels. Oikos, 45:293–296.

STODDART, D. M. 1976. Effect of the odour of weasels (*Mustela nivalis* L.) on trapped samples of their prey. Oecologia (Berlin), 22:439–441.

STOLT, B.-O. 1979. Colour pattern and size variation of the weasel *Mustela nivalis* L. in Sweden. Zoon, 7:55–61.

STONE, W. 1900. Report on the birds and mammals collected by the McIlhenny expedition to Pt. Barrow, Alaska. Proceedings of the Academy of Natural Sciences of Philadelphia, 52:4–49.

STROGANOV, S. U. 1962. [Carnivorous mammals of Siberia.] Academy of Sciences of the U.S.S.R., Siberian Branch. English Translation. 1969. Israel Program for Scientific Translations Ltd., 522 pp.

STUART, A. J. 1982. Pleistocene vertebrates in the British Isles. Longman, London, 212 pp.

STUBBE, M. 1969. Populationsbiologische untersuchungen an *Mustela*-arten. Hercynia, 6:306–318.

———. 1970. Zur evolution der analen markierungsorgane bei musteliden. Biologisches Zentralblatt, 89:213–223.

———. 1972. Die analen markierungsorgane der *Mustela*-arten. Zoologische Garten (Neue Folge), Leipzig, 42:176–188.

SVENDSEN, G. E. 1982. Weasels, *Mustela* sp. Pp. 613–628, *in* Wild mammals of North America: biology, management, and economics (J. A. Chapman and G. A. Feldhamer, eds.). The Johns Hopkins University Press, Baltimore, 1147 pp.

SWANSON, G., AND P. O. FRYKLUND. 1935. The least weasel in Minnesota and its fluctuations in numbers. The American Midland Naturalist, 16:120–126.

SWENK, M. H. 1926. Notes on *M. campestris*, and on the American forms of least weasel. Journal of Mammalogy, 7:313–330.

TAPPER, S. C. 1979. The effect of fluctuating vole numbers *Microtus agrestis* on a population of weasels *Mustela nivalis* on farmland. The Journal of Animal Ecology, 48:603–617.

THOMAS, O. 1911. The Duke of Bedford's zoological exploration of eastern Asia. XIII. On mammals from the provinces of Kansu and Sze-chwan, western China. Proceedings of the Zoological Society of London, 81:158–180.

TOWNSEND, M. G., P. J. BUNYON, E. M. ODAM, P. I. STANLEY, AND H. P. WARDALL. 1984. Assessment of secondary poisoning hazard of warfarin to least weasels. The Journal of Wildlife Management, 48:628–632.

TUMANOV, I. L., AND V. G. LEVIN. 1974. [Age and seasonal changes in some physiological characters in the weasel (*Mustela nivalis* L.) and ermine (*Mustela erminea* L.).] Vestnik Zoologii, 2:25–30 (in Russian).

VAN SOEST, R. W. M., J. VAN DER LAND, AND P. J. H. VAN BREE. 1972. *Skrjabingylus nasicola* (Nematoda) in skulls of *Mustela erminea* and *Mustela nivalis* (Mammalia) from the Netherlands. Beaufortia, 20:85–97.

VASARHELYI, S. 1942. *Mustela hungarica* nov. sp., eine neue wieselart der ungarischen säugetierfauna. Zoologische Anzeiger, 137:221–226.

WEBER, J.-M., AND C. MERMOD. 1983. Experimental transmission of *Skrjabingylus nasicola*, parasitic nematode of mustelids. Acta Zoologica Fennica, 174:237–238.

WURSTER-HILL, D. H. 1973. Chromosomes of eight species from five families of Carnivora. Journal of Mammalogy, 54:753–760.

ZIELINSKI, W. J. 1988. The influence of daily variation in foraging cost on the activity of small carnivores. Animal Behaviour, 36:239–249.

S. R. SHEFFIELD, DEPARTMENT OF ZOOLOGY, OKLAHOMA STATE UNIVERSITY, STILLWATER, OKLAHOMA 74078, USA, AND C. M. KING, ROYAL SOCIETY OF NEW ZEALAND, P.O. BOX 598, WELLINGTON, NEW ZEALAND.