

SNOW VOLE - *Chionomys nivalis* (Martins 1842)

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1. Systematic status

Class:	Mammals	Sub-family:	Arvicolinae
Order:	Rodentia	Genus:	<i>Chionomys</i>
Family:	Arvicolidae*	Species:	<i>nivalis</i>

* family Muridae according to Musser & Carleton (1992)

Terra typica: Faulhorn, Bernese Oberland (Switzerland): *Arvicola nivalis* (Rev. zool., p.331).

French: Campagnol des neiges; *German*: Schneemaus; *Italian*: Arvicola delle nevi; *Spanish*: Topillo nival.

Species belonging to the genus *Chionomys*:

<i>C. nivalis</i>	Southern and Central Europe, Asia Minor
<i>C. gud</i>	Caucasus and N.E. Asia Minor
<i>C. roberti</i>	N.E. Asia Minor and W. Caucasus

Comments

Miller (1908) regarded *Chionomys* as a sub-genus, status retained by the major later authors (Ellerman & Morisson Scott 1951; Corbet 1978; Honacki *et al.* 1982; Krapp 1982). However, biochemical data support the hypothesis of a generic isolation (Gromov & Polyakov 1977; Pavlinov & Rossolimo 1987) of *Chionomys* from *Microtus* (*sensu stricto*) (Chaline & Graf 1988); moreover, the calculated genetic distance between *Microtus* and *Chionomys* is even larger than it is between *Microtus* and *Arvicola* (Graf & Scholl 1975; Graf 1982). DNA hybridization confirms the distance between *C. nivalis* and the *Microtus* voles (Catzefflis *in litt.*).

Suranomys Chaline, 1974, sometimes considered as a junior synonym of *Chionomys*, refers to fossil *Microtus* previously included in the *Chionomys* lineage (Nadachowski 1990).

2. Origins and distribution

2.1. Origins

Paleontologists generally agree that the family Arvicolidae originated about 5 million years ago, and since that time has exhibited a great homogeneity. Major changes are documented by fossil material, mainly cheek teeth (M_1 and M^3), and are confirmed by biochemical data

(Chaline & Graf *op. cit.*). One case of disagreement concerns the origin of *Chionomys*.

The former hypothesis (Chaline 1974) was that, in the Early Pleistocene, the *Mimomys* lineage (*M. newtoni* - *tornensis*) gave birth to *Allophaiomys pliocaenicus* (1.8-1.9 million years ago), the ancestor of the genus *Microtus* (*sensu lato*); *Allophaiomys* is treated in most cases as a subgenus of *Microtus*. From the Northern Eurasian steppes, *A. pliocaenicus* migrated to Western Europe, Central Asia and Northern America. Microtine voles, that are now widely holarctic distributed, differentiated in at least 15 lineages issued from successive cladogeneses. The *Chionomys* lineage split from *Microtus* lineages, namely *Microtus oeconomus*, sometimes between 0.6 and 1 million years ago. *Chionomys roberti-gud* probably appeared and evolved in the Near East or Caucasus whereas *C. nivalis* would result from a mountain reclusion during the Günz-Mindel interglacial in Alps, Carpathians and Pyrenees (Chaline & Mein 1979).

Nevertheless, the primitive carotype of *C. nivalis* suggests an early differentiation (Chaline & Matthey 1971). Moreover, if biochemical data support the view that the various lineages of *Microtus* share a recent common ancestor (1.6 to 2 million-year old), they also indicate that the snow voles differentiated earlier, 2.4

million years ago (Chaline & Graf *op. cit.*). So *Chionomys* would originate from an unknown asian *Mimomys* ancestor, although there is no fossil evidence. The first unquestionable fossils of *C. nivalis* (Nadachowski 1991, 1992) are recorded from the Isle of Chios, Greece (Middle Pleistocene?, Storch 1975), they become abundant in the Upper Pleistocene (Nadachowski & Baryshnikov 1991). Former fossils (e.g. Hinton 1907a, b) traditionally included in this group belong to *M. agrestis (nivaloides)* and *M. oeconomus (nivalinus, malei)* (Nadachowski 1991, 1993). Since that time the snow vole exhibits gradial changes in dental pattern in some regions, while in other areas the evolution is not observed. It is also possible that a lineage may have undergone an increased (decreased) rate of genetic differentiation relative to other lineages (Chaline & Graf *op. cit.*).

2.2. Distribution and subspecific taxonomy

Middle and late Pleistocene climatic fluctuations played an important role in changing the geographic range of the species. During glacial and stadial periods, when most of the mountains were covered with ice, *Chionomys nivalis* moved to lowland regions (Nadachowski 1991), always near the mountains (Terzea 1972). After the retreat of the ice-sheets, mountainous regions

were colonized by animals living in adjoining areas; then the range of the snow vole was fragmented into isolated populations and dramatic changes occurred in the smallest ones (e.g. the population of Tatra Mountains could be regarded as a distinct species on dental morphology basis, Nadachowski 1992).

During the Würm glaciation, *C. nivalis* was widely distributed in Central and Western Europe, particularly during the coldest periods (Terzea *op. cit.*). At the end of the Würm it became sporadic where a suitable pebbly habitat was preserved. Nowadays, snow voles are widespread in the mountains of Europe (Fig. 1) from Spain to the Tatra Mountains, the Carpathians and the Balkans, but its range extends in W. Caucasus, Asia Minor, Palestine and Iran (Corbet 1978). Several lowland populations are also recorded in southern Europe: Spain, (mediterranean) France, Italy, Balkan peninsula.

Because of the fragmentation of the mountain habitat and the polymorphism of the species, many forms have been described. If Corbet (1978, 1984) recognizes only 4 subspecies, 16 were listed by Ellerman & Morrison-Scott (*op. cit.*), 21 by Kratochvíl (1981) and 13 by Krapp (*op. cit.*). On the basis of M^3 and M_1 morphology, Nadachowski (1991, 1992) differentiate 6

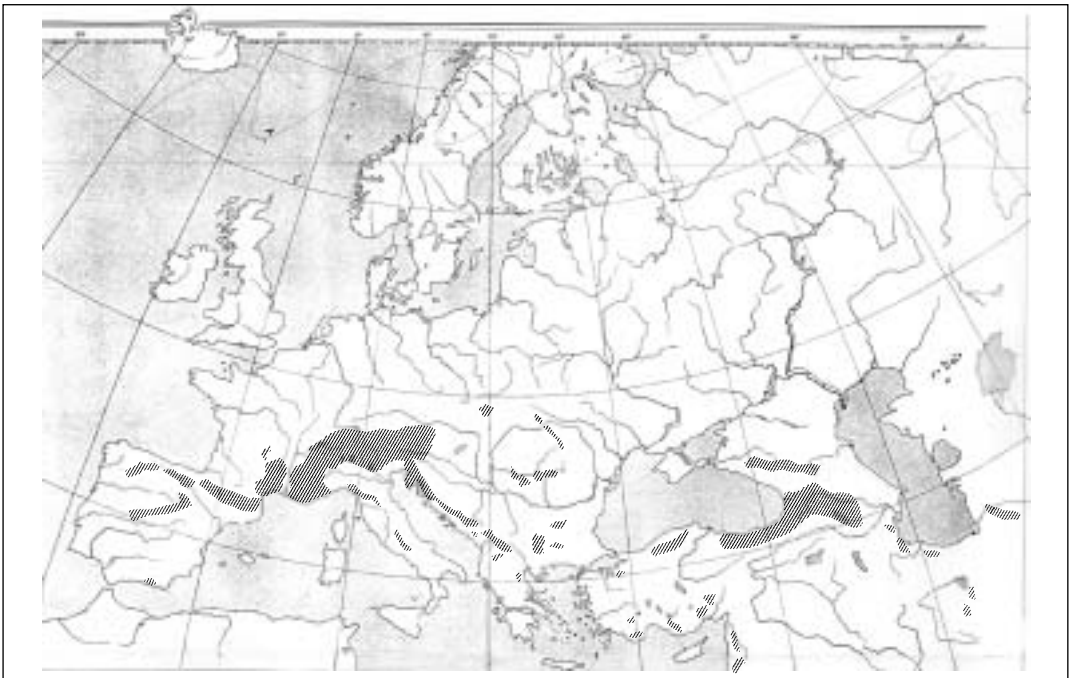


Fig. 1: Distribution of *Chionomys nivalis*.

groups: (i) "lebrunii" including: - *C. nivalis abulensis* (Morales Agacino, 1936), Northern Spain - *C. nivalis aquitanius* (Miller, 1908), Pyrenees - *C. nivalis lebrunii* (Crespon, 1844), Southern France and Massif Central - *C. nivalis leucurus* (Gerbe, 1852), Southern French Alps; (ii) western "nivalis" including: - *C. nivalis nivalis* (Martins, 1842), Central Alps from France to Austria - *C. nivalis wagneri* (Martino, 1940), Juliske Alps - *C. nivalis malyi* (Bolkay, 1925), Slovenia to Macedonia; (iii) eastern "nivalis" including: - *C. nivalis aleco* (Paspalev, Martino & Peshev, 1952), Bulgaria - *C. nivalis ulpius* (Miller, 1908), Carpathians - *C. nivalis loginovi* (Ognev, 1950), Greater Caucasus - *C. nivalis trialeticus* (Schidlovskij, 1919), Transcaucasia - *C. nivalis pontius* (Miller, 1908), northeastern Turkey - *C. nivalis dementievi*, Elbourz Mountains - *C. nivalis hermonis* (Miller, 1908), Lebanon and Palestine; (iv) "mirhanreini" with the sole *C. nivalis mirhanreini* (Schäfer, 1935), Tatra Mountains; (v) "cedrorum" including: - *C. nivalis cedrorum* Spitzenberger, 1973, southern Taurus - *C. nivalis olympius* (Neuhäuser, 1936), northwestern Turkey; and (vi) "spitzenbergerae" with *C. nivalis spitzenbergerae* Nadachowski, 1990, Middle Taurus. Surprisingly, the isolated Sierra Nevada (southern Spain) population (*C. nivalis* spp.) is morphologically close to *C. nivalis nivalis*.

It is noteworthy that southern populations, except *C. nivalis hermonis*, are the most primitive ("lebrunii", "cedrorum" and "spitzenbergerae" groups). During stadial (cool) periods, these populations were not forced to change their habitat contrary to mountain populations that emigrated. These morphological data are supported by preliminary genetic results. Protein electrophoresis (22 loci) emphasizes the homogeneity of the southwestern group ("lebrunii") and its difference from the alpine group ("nivalis") (Graf *op. cit.*). This confirms that southern group issues from the former Southwestern Europe populations whereas Central Alps were colonized by northeastern immigrants. The homogeneity of alpine populations is emphasized by Filippucci *et al.* (1991) on the basis of 34 protein loci, but the other results of these authors disagree with morphological hypotheses: Balkan populations could belong to several subspecies; moreover, Palestine snow voles could be regarded as a distinct species when compared with european populations. Genetic studies on eastern populations are needed to draw conclusions on the subspecific taxonomy of *C. nivalis*.

3. Physical features

The snow vole, larger than microtine voles, is characterized by prominent whiskers (40-50 mm). Ears are rather long, they come out the fur. The pallid tail, bicoloured to uniform, is about half the head-body length. Forehand and hind-foot are longer but narrower than in other arvicolids. Fingers and toes have large callosities (Cantuel 1944). The skull is broad, rather flat, smooth with a wide interorbital region (of same size in young and adults) and low and inconspicuous temporal ridges. Zygomatic arch is rounded, tympanic bullae are rather broad and flat.

3.1. Size, weight

The main measurements increase roughly from the west to the east in the Alps, and according to altitude and latitude over the range. Head-body length: 90-140 mm (maximum 143 mm in the Tatra Mountains); tail length: 47-75 mm (minimum in the Tatra Mountains, maximum in the Pyrenees); hind-foot length: 18-22 mm (maximum 22.4 mm in the Tatra Mountains); ear: 17-18 mm; condylo-basal length: 25.5-31.5 mm (minimum in the Taurus mountain, maximum in the Carpathians); upper molar tooth-row: 5.7-7.5 mm (up to 7.8 mm in Lebanon); diastema: 8.1-10.0 mm; bizygomatic breadth: 15.8-17.5 mm (up to 18.4 mm for an italian specimen); interorbital breadth: 4.0-4.7 mm; weight: 40-62 g (after Miller 1912; Kratochvíl 1956; Kowalski 1957; Dottrens 1962; Kahman & Halbgewachs 1962a; Niethammer 1964; Peshev 1970; Spitzenberger 1971; Felten *et al.* 1973; Vericad & Meylan 1973; Saint Girons 1973; Jones & Carter 1980; Farina & Cenni 1985; Krystufek 1990; Nadachowski 1991).

3.2. Pelt

The coat is dense, variably coloured. The dorsal side is brown, dark brown, brown-grey, or dark grey in the most northern parts of the range, pale grey tinged with brown in the southern parts, and more or less reddish in the mediterranean region. The ventral side is grey to white, the transition of the colour of the back into the ventral side is gradual. The adult moult is sublateral (Le Louarn & Saint Girons 1977). Kahman & Halbgewachs (1962a) distinguished three types of hairs: (i) long (15 mm) and black tactile hairs, (ii) white to brownish guard hairs with black tips, and (iii) short and dense dark underhairs. Guard hairs are thicker than in the other voles; shaft diameter: 13-16 µm (medulla: 10-13 µm); shield diameter: 35-45 µm (medulla: 26-36 µm) (Faliu *et al.* 1980). Cuticular scale

pattern is longitudinal with undulating margins in central shaft, transversal with rippled margins in central shield. Monocellular in the shaft, the medulla becomes multicellular in the shield; medullar cells are isolated. Cross-sections are kidney-shaped with up to 4 cells on the largest sections (Keller 1981).

3.3. Teeth

The dental formula is similar to that of the family (no canines, no premolars): 1/1I, 0/0C, 0/0P, 3/3M. The main specific features concern M_1 and M^3 (Fig.2 & 3). The anterior loop of the first lower molar tends to assume a more or less sharpen arrow-head-like outline owing partly to the general narrowness of the loop (T5 and T6 separated in 70% of specimens,

sue, can be more or less enlarged (Lehman 1969). Tarsal glands were examined by Hrabe (1979), he found from 2 to 6 glands per animal, a single tarsal gland in each inner corner of the eye on the upper and the lower eyelid was noted as the most frequent. Prepuce glands are larger than in other palearctic arviculids (Kratochvíl 1981). According to Lehman & Schaefer (1974), sperm cells are distinctive in the three *Chionomys* species: the front of the head is clearly notched. The baculum has a notched basis with distal appendixes (see Morales Agacino 1936).

3.5. Caryotype

2N=54 (the first caryotype, 2N=56 by Matthey - 1947, 1953 - has not been observed by later

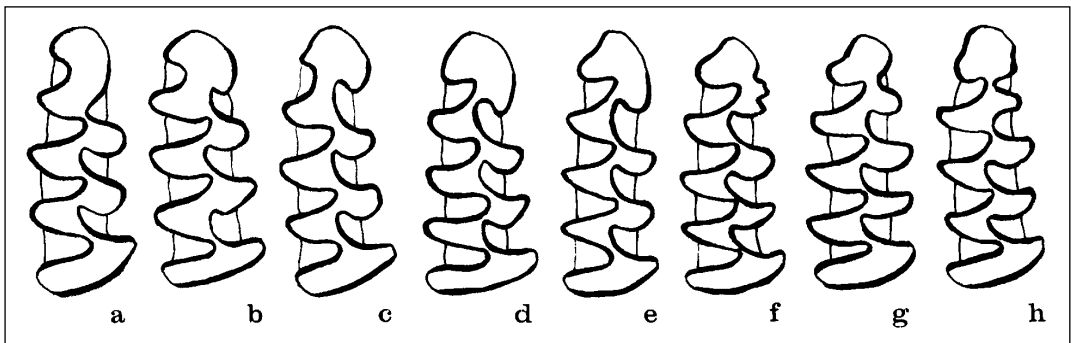


Fig. 2: Morphological variation of M_1 (after Nadachowski 1991); a - Taurus Mts (Turkey); b - Massif Central (France); c - Cordillera Cantabrica (Spain); d - Southern Pyrenees (Spain); e - Central Alps (Switzerland); f - Tatra Mts (Slovakia); g - Southern Alps (France); h - Tatra Mts (Slovakia).

Krystufek *op. cit.*). The predominant morphotype of the third upper molar has only two re-entrant angles on each side (simplex type); the structure is highly variable over the range (Nadachowski 1991), and even over a small area, e.g. in Carpathians (Hamar 1960), or in Austria and Yugoslavia (Krystufek *op. cit.*). This great interpopulation variability in the dental pattern of M_1 and M^3 (also existing in M^2 , Buszko 1974) is most probably connected with the Pleistocene history of the species, namely the isolation of populations during postglacial periods, and different patterns of competition in the mountainous regions (Nadachowski 1992).

3.4. Miscellaneous

Mammæ: 2-2 pectoral, 2-2 inguinal. Lateral sebaceous glands are distributed in two regions: the largest and most active are located on both sides, whereas anal glands, overlaid by fat tis-

authors over the range: Král 1972; Dias de la Guardia *et al.* 1981; Sablina *et al.* 1988; Zagorodnyuk 1990; ...). In Central Europe populations, autosomes are acrocentric (NFa=52), the X-chromosome is submetacentric and the Y-chromosome is a medium-sized acrocentric (Todorovic *et al.* 1971) or a small-sized acrocentric (Zima & Král 1984); no difference has been detected between lowland and altitude populations in Bulgaria, even with C- and G-banding (Peshev & Belcheva 1979). In western populations, the Y-chromosome is the smallest, and Meylan & Graf (1973) described one pair of submetacentric autosomes (NFa =54). One of the smallest pair of autosomes are also submetacentric in the Caucasus (Jacenko 1982 in Zima & Král *op. cit.*). All the results point out the primitive structure of that type of chromosome complement, surprisingly geographic isolation has not been accompanied by chromosome diversification.

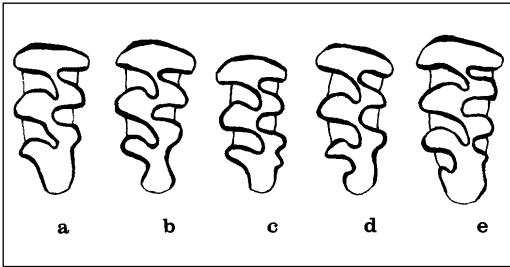


Fig. 3: Morphological variation of M' (after Nadachowski 1991): a - Languedoc (France); b - Cordillera Cantabrica (Spain); c - Southern Alps (France); d - Tatra Mts (Slovakia); e - Central Alps (Austria).

4. Ecology, Ethology and Ecophysiology

4.1 Altitudinal range

The snow vole does not only inhabit high (and snowy) mountains, but also lowlands in the mediterranean region. Its vertical distribution ranges from 30 m above sea level in Croatia (Krystufek & Kovacic 1989) up to more than 4,000 m in the Alps (Zimmermann 1953). Lowland localities have been reported in Spain (250 m, Niethammer 1964), France (250 m, Heim de Balsac 1955; 100 m, Fons & Libois 1977), Italy (200 m, Malec & Storch 1964), Slovenia and Croatia (120 m, Jones & Carter 1980; 30 m, Krystufek & Kovacic *op. cit.*), and Bulgaria (200 m, Peshev 1970). In most part of the range, the upper limit is the height of the highest peaks (e.g. 2,450 m in the Dinarids, Krystufek & Kovacic *op. cit.*; 3,150 m in the Sierra Nevada, Vericad & Meylan *op. cit.*). The highest record, 4,700 m in the Western Alps (Saint Giron *op. cit.*) is probably a consequence of its somewhat sinanthropic way of life in high mountains. In the Alps, the most favourable habitats are located between 2,000 m and 2,400 m (Dottrens 1962; Janeau 1976, 1980), while they range between 1,800 and 2,300 m in the Pyrenees (Leconte 1983), between 1,300 and 1,900 m in the Carpathians (Firchuk 1961), and between 1,200 and 2,000 m in the Tatra Mountains (Kratochvíl 1956). In the Dinarids, any suitable habitat above 550 m could be inhabited by snow voles (Krystufek & Kovacic *op. cit.*).

4.2. Preferred habitat

All the studies about habitat show that snow voles live in rocky environments (scree, rock blocs, moraines, karst cliffs, quarries, river canyons,...), mainly in open habitats (Zimmermann 1953, 1956; Kowalski *op. cit.*; Firchuk *op. cit.*; Kahmann & Halbgewachs

1962a; Saint Giron *op. cit.*; Le Louarn & Janeau 1975; Janeau 1976, 1980; Orsini 1982; Leconte 1983; Krystufek & Kovacic *op. cit.*; Bocchini & Nieder 1994), and eventually close to small rivers (Saint Giron *op. cit.*; Krapp *op. cit.*). The snow vole populations are very rare in mountain forest, in this case they always stand in stony shelters and fissures connected to caves (Janeau 1976, 1980; Leconte 1983; Krystufek & Kovacic *op. cit.*). In mountain areas, snow voles can use the refuges and the sheep-folds (Saint Giron *op. cit.*; Krapp *op. cit.*).

In the Alps, Le Louarn & Janeau (*op. cit.*) and Janeau (1976, 1980) found that the main characteristic of the snow vole biotope is the size of the stones, the best biotope contains stones bigger than 20 cm with some larger blocks. Their studies revealed also that snow voles prefer the areas with sparse vegetation ($\leq 10\%$ of vegetal cover), and south, south-east and south-west exposures (where the snow can melt quickly); the most suitable slopes are 10 to 20% declivous. In the Pyrenees, Leconte (1983) showed that snow voles were trapped in the rocky areas with large blocks covering more than 90% of the ground. Adults, but not young, were trapped more frequently when the blocks were large. There, the underground microclimate is very different from the external mesoclimate: at -1.5 m Leconte (1983) considered only 2 seasons: the first from November to May (temperature around 0° C) and the second from May to November when the temperature is upper than 0° C (around 10° C in July and August). These stable, mainly stenothermal, conditions are the main factors determining the mountain distribution of the snow vole.

In lowlands, snow voles usually inhabit dry and sunny hills wherever the ground is thin and stony, covered with *Quercus ilex* and *Quercus pubescens* garrigue (Genest 1970). They also occupy low wall fences, and sometimes in winter they retreat in houses' annexes (Le Louarn & Saint Giron *op. cit.*).

Despite both its scientific (*Chionomys* = snow mouse in Greek and *nivalis* = snowy in Latin) and its common names, the snow vole is a petricolic (or even trogliphilic) animal.

4.3. Burrows

Snow vole burrows are always located under the stones, for this reason tunnel network is difficult to observe. The opening of the tunnel is always close to a rock. Animals excavate themselves some parts of the tunnel and "chambers" but they often use natural clefts in (and between)

rocks. Küsthardt (1941) described a tunnel of 1.80 m, but the tunnel network could be longer according to direct observations of marked animals (Janeau unpubl. data). A burrow includes (Kahmann & Halbgewachs 1962a) several chambers: one for the nest, one or more to stock dry vegetals (for changing the nest and for feeding), and one or more for faeces.

The hole of the burrow is the main track of snow voles and it is often possible to observe some dry parts of plants closely around (cf. *infra*).

4.4. Space use, social structure and territorial behaviour

The adult female home ranges generally do not overlap (in some cases overlapping can occur but on very small surface). Until the beginning of winter, the young use a small or large part of their mother home range but they sometimes move around. The home range of an adult male can overlap one or more adult female home ranges (Le Louarn & Janeau *op. cit.*). For Nieder & Bocchini (1994), in Northern Apennines, the mean home range is significantly greater for the adult males ($332.4 \text{ m}^2 \pm 20.4$) than for adult females ($207 \text{ m}^2 \pm 183.2$); for the immature individuals, the mean home range ($104.1 \text{ m}^2 \pm 69.95$) is smaller than their mothers' one. These authors did not observe significant density- or season- (reproductive/non-reproductive) related variations in home range. Snow voles often use the same small trails around their burrow, but not in other parts of their home range. They use rock blocks as shelters (Le Louarn & Janeau *op. cit.*) during their travelling.

Snow voles live in small populations more or less scattered depending on the environment. During winter (when the snow covers the ground in upper mountains) some individuals migrate in neighbouring populations (Le Louarn & Janeau *op. cit.*; Leconte 1983). No paper has ascertained large migratory movements.

In the laboratory, Frank (1954) observed agonistic behaviour towards foreign snow voles. Females accept the presence in the burrow of the male and young when a new litter arrives. Faeces and urine droppings in the terrarium would have a marking function.

4.5. Activity rhythm

The daily activity rhythm of the snow vole (observed in captive conditions) shows a polyphasic pattern, with a main period of activity during the night and a second (shorter) peak around 14 h. *In natura*, Le Louarn & Janeau (*op.*

cit.) observed snow voles movements mainly around the sunset, less frequently during the daylight, and rarely during raining time. For Leconte (1983), feeding activities occur mainly at night. Snow voles are active during the whole year (during winter time, they move between the ground and the snow). The time spent daily outside the nest raises 37% in summer and 30% in winter (Bienkowski & Marszalek 1974).

4.6. Foraging

The snow vole foraging was only studied in mountain area: in the Alps (Küsthardt 1925, 1941; Kahmann & Halbgewachs 1962a) and in the Carpathians (Rudyshin 1975). This vole is strictly an herbivorous; according to the plant species it can use the leaves, the stems, the flowers, the seeds and the roots. The main plants it uses change along the year according to their phenology. In July, Rudyshin (*op. cit.*) listed: *Hieracium silvestre*, *Poa annua*, *Deschampsia caespitosa*, *Campanula abietina*, *Poa chaixii*, *Festuca rubra*, *Vaccinium myrtillus*, *Homogyne alpina*, *Fragaria vesca*, *Calamagrostis arundinacea* and in August, Kahmann & Halbgewachs (1962a) recorded: *Crepis blattarioides*, *Carex sempervivum*, *Trifolium pratense*, *Lotus corniculatus*, *Achillea clavata*, *Cirsium sp.*, *Crepis aurea*, *Potentilla aurea*. Küsthardt (1941) mentions that snow voles eat flour worms in laboratory, but no reference exists about insects ingestion *in natura*. Snow voles let parts of plants dry around the burrow before stocking inside (Küsthardt 1925; Hainard 1988; Le Louarn & Janeau *op. cit.*).

In terrarium, the summer daily adults forage intake ranges from 36.5 g to 64.9 g (mean = 51.9 g) of fresh matter corresponding to 5.0 g to 10.4 g (mean = 8.1 g) of dry matter per day (Rudyshin *op. cit.*).

4.7. Metabolism and energy budget

The metabolism and energy budget of the snow vole was studied by Bienkowski & Marszalek (*op. cit.*). In the laboratory, the average daily metabolic rate (ADMR) is 0.410 kcal/g.day at 20° C, that is about 2.5 times the interspecific basal metabolism of Kleiber (1961). The thermoneutral zone is around 20° C; from 20° C to -10° C the resting metabolic rate (RMR) would be multiplied by 2. These data, similar to previous data obtained with the bank vole (*Clethrionomys glareolus*), are a sign of an adaptation to stenothermal conditions.

In the Tatra Mountains, the daily energy budgets (DEB) for summer and winter are similar (summer DEB (kcal/g.day) = 1.26 W -0.264; winter

DEB (kcal/g.day) = 1.24 W -0.264) because of: - a shorter activity time in winter; - a lower cost of maintenance in winter, explained by the relatively constant thermal conditions (in the burrow, *cf. supra*, and outside under the snow) and by the winter reduction or absence of some metabolic expenditures (e.g. reproduction).

5. Life History Traits

5.1. Reproduction and development

The snow vole gestation is about 20 to 22 days long (Frank *op. cit.*; Kahmann & Halbgewachs 1962a). The reproductive period changes according to the climatic conditions, *i.e.* with the altitude: gestant females have been found from the beginning of May to the end of September at 1,500 m (Le Louarn & Janeau *op. cit.*), from June to September between 1,600 to 1,900 m (Kahmann & Halbgewachs 1962a), and from the beginning of June to the end of August between 1,800 to 2,600 m (Le Louarn & Janeau *op. cit.*; Janeau 1976).

Some females born at the beginning of summer are able to have a litter by the end of the season (Frank *op. cit.*; Leconte 1983); males are sexually active only on the next summer (Frank *op. cit.*; Le Louarn & Janeau *op. cit.*; Janeau 1976; Leconte 1983). Females of the overwintered cohort produce normally 2 litters (Le Louarn & Janeau *op. cit.*; Kratochvíl 1981). Martirosyan (1964) recorded up to 3 litters in Armenia, and Kahmann & Halbgewachs (1962a) think that some females could give birth to 4 litters. In the Alps, the number of embryos ranges from 2 to 4 (Dottrens *op. cit.*; Kahmann & Halbgewachs 1962a; Le Louarn & Janeau *op. cit.*), even 5 (Janeau 1976). In the Pyrenees, Saint Girons (*op. cit.*) recorded 6 embryos, and in Armenian, Martirosyan (*op. cit.*) found 9 embryos in one female. The litter size ranges from 1 to 4 young, and the young mortality before weaning is about 1/3 (Le Louarn & Janeau *op. cit.*).

The new-born weights range from 3.2 g to 4.0 g (Frank *op. cit.*). The young open their eyes on the 13th day. The first emergences from the burrow are observed when the young are 2 to 3 weeks old (Le Louarn & Janeau *op. cit.*).

5.2. Population dynamics

In the wild, sex-ratio is balanced at birth (Le Louarn & Janeau *op. cit.*), then longevity is shorter for females than for males. Females rarely survive after the end of their second summer but Bocchini & Nieder (*op. cit.*) have recaptured a 20-month-old female. Males do not live longer than 24 months.

Mortality plus emigration represent 50% per year in a snow vole population in Pyrenean Mountains (Leconte 1983). When migration occurs, between neighbouring populations, the result is usually balanced (Le Louarn & Janeau *op. cit.*; Leconte 1983). An example of the dynamics of a micropopulation is showed in figure 4.

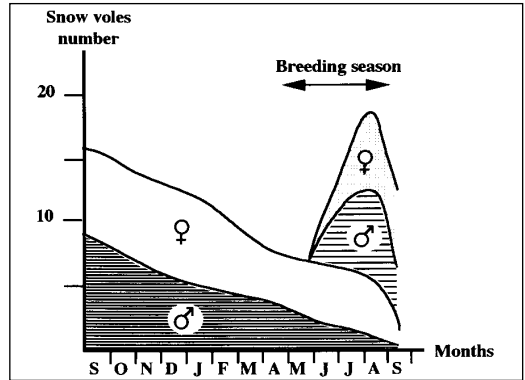


Fig. 4: Annual micropopulation fluctuations recorded in the French Alps (2160 m) by Le Louarn & Janeau (*op. cit.*).

Contributing to the stability of the populations, death rate is not important after the weaning period. Le Louarn & Janeau (*op. cit.*) and Leconte (1983) found a very low level of predation in their study areas.

Populations at low altitude are small and isolated (Leconte 1984) and they have extremely low density. The reverse regularity has been observed with a rise in altitude (Peshev, 1970). The density observed by Nieder & Bocchini (1993), in the Apennines, ranges from 5 to 10 individuals/ha in spring, and from 20 to 40 individuals/ha in autumn. In the Alps, Le Louarn & Janeau (*op. cit.*) have observed 35 individuals/ha in May and 95 individuals/ha in August (in a small microhabitat of 2,000 m²). No outbreak of population has been reported in the literature.

As snow voles use a stable microhabitat and show little density variations, long adult survival, low fertility and delayed sexual maturity, Leconte (1983) and Nieder & Bocchini (1993) suggest that they are more *k*-strategists than the other voles, namely the *Microtus* species.

6. Interactions with other species

6.1. Competition

There is little direct competition between snow voles and other species. In mountain areas,

Alpine marmots (*Marmota marmota*) and, occasionally, Orthoptera and wild ungulates like chamois (*Rupicapra rupicapra*) feed on the same places as snow voles. In rocky forest environment, Leconte (1983) suggests a possible interspecific competition for shelters with the garden dormouse (*Eliomys quercinus*) and with the edible dormouse (*Glis glis*) from May to September.

In the Balkan peninsula, another petricolic rodent, the Martino's vole (*Dinaromys bogdanovi*), prevails over the snow vole in interspecific encounters (Petrov & Todorovic 1982). As a result, in Northern Velebit (Tvrtkovic 1984 in Krystufek & Kovacic *op. cit.*), Martino's vole inhabits rocky environments between 400 and 900 m while the snow vole settles above 900 m. The other voles do not use the same biotopes. The common vole (*Microtus arvalis*), a much more prolific species, occupies pastures; the bank vole (*Clethrionomys glareolus*) is restricted to forests and thick vegetation. Similarly, in lowlands, the mediterranean pine vole (*Microtus duodecimcostatus*), also more vigorous, inhabits all sandy and deep ground habitats (Fons & Saint Girons 1980), and so the snow vole never cohabits with it. The present way of life and distribution of *C. nivalis* could be a consequence of past competition with these voles.

6.2. Prey-predator interactions

The predators recorded in the literature are:

(i) *birds*: - eagle owl *Bubo bubo* (Schäfer 1938; Uttendörfer 1939; Wagner & Springer 1970); - Tengmalm's owl *Aegolius funereus*, (Uttendörfer *op. cit.*; Kahmann & Halbgewachs 1962b); - long-eared owl *Asio otus* (Uttendörfer *op. cit.*); - tawny owl *Strix aluco* (Uttendörfer *op. cit.*); - sparrowhawk *Accipiter nisus* (Uttendörfer *op. cit.*); - barn owl *Tyto alba* (Niethammer *op. cit.*; Heim de Balsac & de Beaufort 1966; Libois *et al.*, 1983; Aulagnier & Rivière 1983); - alpine chough *Pyrrhocorax graculus* (Kahmann & Halbgewachs 1962b); - raven *Corvus corax* (Kahmann & Halbgewachs 1962b).
(ii) *mammals*: - red fox *Vulpes vulpes* (Kahmann & Halbgewachs 1962a); - stoat *Mustela erminea* (Kahmann & Halbgewachs 1962a); - weasel *Mustela nivalis* (Kahmann & Halbgewachs 1962b); domestic cat (Kahmann & Halbgewachs 1962b).
(iii) *snakes*: - common viper *Vipera berus* (Kahmann & Halbgewachs 1962b).

This non-exhaustive list of predators is rather long but, in fact, the predation on snow voles is

very low because their biotope, rocks (and snow in mountains), provides them with many shelters to avoid attacks (e.g. in the diet of lower Eastern Pyrenees barn owls, Libois *et al. op. cit.*) have identified 10, 2, 1 snow voles over respectively 6,047, 1,330, 3,005 voles in only three over 21 sampled locations).

6.3. Parasites and diseases

A large number of ectoparasites have been recorded on snow voles, they differ according to the region and the altitude. The most important are: (i) *fleas*: *Callosopsylla saxatilis*, *Peromyscopsylla spectabilis*, *P. fallax*, *Amphipsylla sibirica*, *A. rossica*, *Rhadinopsylla mesa*, *Ctenophthalmus nivalis*, *C. ubayensis*, *C. orphilus*, *Malaerus penicilliger* (Lahnert 1969; Brelih 1986; Beaucournu & Launay 1990), (ii) *lice*: *Hoplopleura acanthopus*; (iii) *scabs*: *Haemogamasus nidi*, *Hirstionyssus isabellinus*, *H. taticus*, *Laelaps hylaris*, *Trombicula willmanni* (Mahnert 1971), (iv) *ticks*: *Ixodes trianguliceps*. While Kahmann & Halbgewachs (1963b) report that fleas and lice are abundant all over the animals collected in Bavarian Alps, Le Louarn & Janeau (*op. cit.*) and Janeau (1976) have never observed ectoparasites on any snow vole during a 4-years field study in French Alps. Endoparasites are also numerous (i) *nematodes*: *Heligmosomum halli*, *H. skrjabini*, and (ii) *cestodes*: *Paranoplocephala dentata*, *Aprostotandrya macrocephala*, *Taenia martis* (Kahmann & Halbgewachs 1962b; Prokopic & Mahnert 1970). At last, snow voles proved to be infected by blood parasites of the genera *Grahamella*, *Babesia*, *Hepatozoon* and *Trypanosoma* (Mahnert 1970, 1972)

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