Review

Received: 18 July 2015 Revised: 17 December 2015 Accepted article published: 23 December 2015 Published online in Wiley Online Library: 28 January 2016

(wileyonlinelibrary.com) DOI 10.1002/ps.4212

From biology to management of Savi's pine vole (*Microtus savii*)

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Abstract

Savi's pine vole (*Microtus savii*) is a rodent species of the *Cricetidae* family, inhabiting southern European agroecosystems. It is considered to be the main cause of rodent-attributed damage in Italy. To achieve an effective management, detailed knowledge of this species is needed. However, the available information about this species is fragmentary and incomplete. In this paper, the existing knowledge of Savi's pine vole taxonomy, reproduction, population dynamics, habitat and food preferences is reviewed in order to organise available information and identify priority areas of future research. Some of the changes in farming practices that have occurred in recent decades may have increased the impact of Savi's pine vole populations in crop fields. To manage this pest species effectively, an integrated strategy is recommended (involving habitat management, trapping and, when appropriate, the use of rodenticides). The apparent lack of cyclical population outbreaks and the relatively small litter size and long gestation and interpartum period of this species suggest that it could be more manageable than other vole species, while its strict herbivorous diet, stable population size in open habitats and wide distribution seem to indicate it as an ideal model species for risk assessment studies.

Keywords: *Microtus savii*; crop damage; small mammals; agriculture; pest species; Savi's pine vole

1 INTRODUCTION

Fossorial and semi-fossorial species of rodents are important agricultural pests, and voles are especially relevant pests in Asia, Europe and North America.[1] In fact, in past centuries, voles gave rise to famine in Hungary, the Soviet Union and France.[2]

In Italy, the most damage to agricultural activities is caused by *Microtus* voles. Among the Arvicolinae, the genus *Microtus* is the richest in terms of species (62); these species are widespread throughout the holarctic region (Asia, North America and Europe), the only exception being arid areas. Following the definition by Contreras and McNab,[3] voles are considered to be fossorial species that may spend a certain amount of time above ground. Their different degrees of aptitude for underground life may allow a rough distinction among fossorial voles (subgenus *Terricola*, e.g. *M. savii*, *M. multiplex*, *M. subterraneus*) and above-ground-active voles (subgenus *Microtus*, e.g. *M. agrestis*, *M. arvalis*). Voles have a herbivorous diet based mainly on grass, roots and bark, although some species may also consume seeds and invertebrates.[4] Owing to their small size and intense activity levels, voles have a high food intake rate. The common vole (*Microtus arvalis*) is the most abundant wild mammal species in Europe,[5,6] while in Italy it occurs only in the north-east regions. In the other parts of the Italian peninsula and in Sicily, the most widespread species is Savi's pine vole (*Microtus savii*). Savi's pine vole is a fossorial species that nests in a network of tunnels; it is usually found in rural areas, edge clearings of forests, uncultivated fields, meadows and orchards and is held responsible for most of the rodent-attributed damage to agricultural crops.[7] To date, knowledge about this species has been scattered and often based on local studies, despite these voles being considered one of the most important agricultural pest species of the Mediterranean region.

The aim of this review is to summarise the available knowledge about Savi's pine vole. We reviewed taxonomy, distribution, habitat and feeding preferences, breeding biology and social organisation, population dynamics and main predators. We screened the main scientific databases, articles, conference proceedings, books and chapters for publications about this species written in English, French and Italian. We compared the information about Savi's pine vole with that about other vole species, especially regarding breeding biology, fossorial activity and population dynamics. Furthermore, specific attention was paid to the management of Savi's pine vole in agriculture and control strategies.

This review provides a basis for direct further research on optimising plant protection and risk assessment.

2 SAVI'S PINE VOLE

2.1 Taxonomy and morphology

The taxonomic status of *Microtus savii* is still debated. Several subspecies have been described: *M. s. savii* in northern and central Italy (De Sèlys Longchamps, 1838), *M. s. brachycercus* (von

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Lehmann, 1961) in southern Italy and *M. s. nebrodensis* (Minà Palumbo, 1868) in Sicily.[8–12] Two other subspecies, *M. s. tolfetanus* (Contoli, 2003) and *M. s. niethammericus* (Contoli, 2008), have recently been described in a small area of central Italy (Tolfa Hills, near Rome) and in Gargano (Apulia) respectively.[8,10,12] Genetic studies recently addressed the phylogenetic relationships between *M. savii* subspecies.[13–15] There is evidence of a separation between Calabrian populations and the other Italian populations,[12,13] but whether *M. s. brachycercus* should be elevated to the rank of a species is not yet clear. According to Galleni *et al.*,[16,17] morphological, karyological and hybridisation studies suggest that Savi's pine vole is a heterogeneous group at the first stages of speciation, consisting of two different species:[18] *M. savii* in northern and central Italy, and *M. brachycercus* in the south-west. In addition, chromosomal distances revealed differences also between *M. savii nebrodensis* and the group *M. savii savii*–*M. brachycercus*.[12] These data would be in agreement with the genetic divergence of the clade *brachycercus*, which departed from *M. s. savii* only in the Middle Pleistocene (0.3–0.5 million years ago).[12,15]

Regarding Savi's pine vole morphology, some authors argued that the pattern of teeth morphology among the populations of north-central and southern Italy reflects the interaction between morphological and environmental variability.[19] The variability of tooth morphology indeed shows two geographical scales: at a regional level, morphological variability seems to be related to the pressure of climatic conditions, while at a more local scale it may be linked to the fragmentation of areas where small populations undergo ecological isolation, thus developing different morphotypes.[19] At an intraspecific level, north-central and southern populations may be discriminated by the morphology of the first lower molar. Interestingly, the same pattern is also known at an interspecific level within the subgenus *Microtus* (*Terricola*) between northern and southern species in western Europe.[19]

2.2 Distribution and habitat

Savi's pine vole is widespread in the Italian peninsula, and it is also present in a small portion of southern France and Switzerland. The southern part of the Canton Ticino is the northern limit of its distribution range, and the presence of the species is reported at altitudes between 250 and 700 m.[20] In Italy, Savi's pine vole has been found up to an altitude of 2800 m in Gran Paradiso National Park, Valle d'Aosta.[21] It is present in Sicily, but seems to be missing from the slopes of Etna.[8] The north-eastern boundary of the species' distribution range is the Tagliamento river, between Veneto and Friuli Venezia Giulia.

Savi's pine vole occurs in fallow fields, banks of ditches and canals, ecotonal areas, cereals, forage crops and orchards.[22–24] Only occasionally is it found in forests.[23]

Canova[25] reported the presence of Savi's pine vole in reed beds, hedgerows and poplar plantations. In Sicily, the species is found mainly in open hills and plains, steppes, meadows, pastures and cereal crops.[26] In Switzerland, in the southern Ticino, it lives in meadows with deep and permeable soils, in vineyards and orchards of the lowland areas.[20]

Savi's pine vole also occurs in urban areas, but it avoids too hard,[8] dry and rocky soil, preferring deep, moist and well-drained soil.[23,26,27] However, it may also inhabit sandy soils, peat, clay and soils subject to water logging.[22] Savi's pine vole has a polyphasic daily activity rhythm, alternating short rest and activity periods during both day and night. Home range size ranges from 300 m^2 (females) to 450 m^2 (males).[28] The burrow system consists of several chambers, stores and primary and secondary entrance holes connected by a network of corridors up to 40–50 cm deep.[26] Exits are close to the burrow entrance holes that allow voles to feed above ground, mainly on grasses.[22] Nests are often built by modifying pre-existing mole burrows (*Talpa* spp.). Each burrow system consists of several nests that are occupied either simultaneously or successively by several individuals.[28] Individuals who occupy the same tunnels and the same nests do not seem to show a synchronisation of daily activity rhythm.[20] Up to 15 voles use the same nests and share the same area in a colony of closely related individuals.

2.3 Reproductive behaviour and population dynamics

In the Mediterranean area, the Savi's pine vole's breeding season extends from March to November,[20] but it is concentrated especially in spring and summer,[26] sometimes with breaks during the summer months, possibly owing to dryness.[20]

Data from laboratory studies show that females reach sexual maturity at an average age of 50 days, and the first parturition is on average at 73 ± 12 days; the gestation period is 22–24 days,[29] while the interpartum time is on average 30 days. This interval is shorter in spring and winter and longer in summer and autumn, and is not affected by age. The litter size of captive-bred females is on average 2.5 ± 1.1, and is similar to that of females captured in the wild (2.49 ± 0.7).[29]

Furthermore, laboratory data show a reproductive potential of females of 11.8 ± 3.4 litters per year under optimal conditions. The average life expectancy in captivity is less than 2 years (Table 1).[29]

Wild populations consist of promiscuous groups usually formed by 1–3 sexually active females, generally an adult male (in summer), some subadults and several juveniles, but composition may vary.[28] Two or more females can nurse their pups in communal nests, taking parental care in turns. Studies carried out in a population of Viterbo in central Italy have shown that, if the mother leaves the nest,[30] it is immediately replaced by a male, possibly the father, or another adult. This behaviour probably relates to the pups' inability to thermoregulate during the first hours of their life. In the case of danger, females carry the newborns in their mouth to safer places.[30] Female co-nesting is, according to Salvioni,[20] one of the main factors causing the highest population densities.

Numerical fluctuations in Savi's pine vole populations are less significant than in other *Microtus* species. Voles species living at northern latitudes (e.g. field vole) usually show large seasonal fluctuations in population size. In northern and central Europe, the common vole is subject to periodic outbreaks, with cycles of 3–5 years.[31] Savi's pine vole, instead, shows both multiannual and seasonal peaks, but no extreme cyclical population outbreaks.

The availability of food is an important limiting factor. The seasonal population pattern has been studied in Switzerland (Canton Ticino), where the population density has minimum values at the end of the summer (<50 individuals ha^{-1}) and a maximum in spring (>100 individuals ha^{-1}).[20]

After the studies by Salvioni in the 1980s and early 1990s, little research effort has been devoted to this rodent. Recently, a study of population dynamics in Italy has been conducted by our group, and results show population density peaks between August and November.[32] Contoli[8] reported density values ranging from 10 to 100 individuals ha^{-1}, which may sometimes rise up to 1000 individuals ha^{-1}.[8]

2.4 Main predators

The barn owl (*Tyto alba*) is considered to be the main predator of Savi's pine vole in some cultivated areas of central Italy, and it has

Table 1. Activity and reproductive behaviour of captive-bred vole colonies (modified from Caroli *et al.*[29])

Species	Activity	Mating system	Litter size (range)	Litter size (mean)	Age at puberty[a] (days)
M. agrestis	Above ground	Polygamy	2–8	5[74]	21 (F),[74] 42 (M)[76]
M. arvalis	Above ground	Polygamy	1–9	5[29]	13 (F), 21 (M)[29]
M. californicus	Above ground	Polygamy	1–9	5[74]	21 (F), 42 (M)[77]
M. duodecimcostatus	Fossorial	?	1–4	2.5[29]	60 (F)[78]
M. montanus	Above ground	Polygamy	3–9	6[74]	28 (F)[79]
M. multiplex	Fossorial	Monogamy	1–4	2.5[29]	?
M. ochrogaster	Above ground	Monogamy	1–8	4.5[74]	35 (M),[74] 40 (F)
M. oregoni	Above ground	?	1–6	3.5[74]	27 (F), 45 (M)[29]
M. pennsylvanicus	Above ground	Polygamy	2–8	5[74]	26 (F), 35 (M)[74]
M. pinetorum	Fossorial	Monogamy	1–6	3.5[74]	51 (M), 77 (F)[74]
M. savii	Fossorial	?	1–4	2.5[29]	47 (M), 50 (F)[29]
M. subterraneus	Fossorial	Polygamy	1–5	3[29]	60 (F), 90 (M)[29]
Myodes glareolus	Above ground	Polygamy	2–8	5[75]	32 (F), 49 (M)[74]

[a] M – male; F – female.

been hypothesised to be an important factor for biological control of populations.[33] The same conclusion was drawn by Contoli and Sammuri,[34] who studied the diet of barn owls and tawny owls (*Strix aluco*) in the Farma valley (Tuscany). Their study revealed that both species prey upon the same small mammals (representing more than 95% of their diet), although the barn owl was more specialised in the predation of Savi's pine vole, preying on this species at a significantly higher rate (12.5% versus 2.4% for tawny owl). Other studies on barn owl diet showed percentages from 64.2 to 79.4% of rodents in pellets,[35,36] with Savi's pine vole remains accounting for 3.9–39.8%.[35,37]

Other important predators of Savi's pine voles are diurnal raptors, such as kestrel (*Falco tinnunculus*) and common buzzard (*Buteo buteo*),[38,39] and mammals such as weasel (*Mustela nivalis*) and red fox (*Vulpes vulpes*).[22,40,41] Predation by snakes is considered to be rare for Savi's pine vole.[37,42]

2.5 Impact of Savi's pine vole in agroecosystems

Savi's pine vole plays an important role in natural ecosystems. Its burrowing activity can change the soil structure, bringing to the surface the soil collected in depth and mixing up the layers. This can affect the composition of the herbaceous plant communities near the burrows. Moreover, the material that these small rodents carry in and out of their burrows for the construction of nests and as food stocks makes them important agents of seed dispersal of arboreal and herbaceous plant species.[22] However, voles of the genus *Microtus* cause substantial damage to agricultural activities.[22] The strictly herbivorous diet of Savi's pine vole leads to extensive damage to arable crops, in particular in vegetable fields and orchards.[43]

Savi's pine vole feeds on annual and perennial herbaceous plants, both wild and cultivated, preferring the *Graminaceae*, *Leguminosae*, *Chenopodiaceae* and *Compositae*,[21,22,44] mostly within a radius of about 10 cm from the burrow exit hole.[20] During winter, when the grass cover is strongly reduced or covered by snow, Savi's pine voles exploit alternative food sources.[22] In this season, the species causes debarking of trunks and roots just above and below ground level.[45] The reason for this behaviour is probably the search for nutrients present in the phloem. This stripping can remove an entire circular band of bark. Potentially, a single adult vole is able to cause a lethal laceration of a tree in 24 h.[46]

The grass collected at the surface is dragged and eaten in underground tunnels. Thus, during the outbreak periods, Savi's pine vole may cause severe damage to the taproots of sugar beets, and to cereals in their growth and maturation phase.[21] However, the most serious damage is caused to valuable horticultural species such as artichokes (*Cynara cardunculus*), fennel (*Foeniculum vulgare*), lettuce (*Lactuca sativa*), cabbage (*Brassica oleracea*), radicchio (*Cichorium intybus*), parsley (*Petroselinum crispum*), garlic (*Allium sativum*), onion (*Allium cepa*) and chard (*Beta vulgaris*).[21] Santini[21] describes the typical way the artichoke plants are attacked: the vole reaches the base of the plant with a tunnel and then eats the soft and juicy inner tissues, rising inside along the axis of the plant. Within 2 or 3 days, the plant wilts and withers.

The most damaged trees are apple, citrus and, to a lesser extent, olive.[22] In Sicily, the problem of vole infestation in citrus orchards has become more and more relevant, causing a significant decrease in profits.[45] Some damage in Sicilian vineyards was recently reported.[39] In an area of approximately 2 ha, 10–15% of the grapevines were damaged. Probably the lack of herbaceous cover, weeded out since 2006 to avoid drifts, shifted the food selection to the roots of grapevines.

In Monti Cimini (province of Viterbo), in the winter of 1986–1987, in a plot of 4 ha, the species caused the death of 1500 four-year-old apple trees in only 6 days.[46] Infestation of Savi's pine vole also affected northern Italy, with substantial damage on fruit farms.[47] In central Italy, damage caused a remarkable decrease in agricultural production, especially in the province of Pisa. In these regions the most serious damage was detected in horticultural crops, especially in the artichoke. In the province of Latina, artichokes and melons were severely damaged during outbreak years in 1967–1968 and 1970–1971.[43]

The most detrimental infestation of this species ever recorded in Italian history occurred in some areas of the Abruzzo, Molise Apulia and Basilicata regions. The crops damaged were artichokes, grass and cereals.[43]

Santini[48] also mentions other areas affected by this phenomenon, such as citrus orchards of Calabria, Basilicata (Gioia Tauro, Rosarno, Lamezia Terme, the Plain of Sybaris and the Ionian coast) and south-eastern Sicily (between the provinces of Catania and Ragusa). Latian apple orchards were damaged by this species

(100 ha),[48] helped by the permanent grass cover maintained within plant rows according to new agricultural practices.

D'Errico *et al.*[49] report damage to asparagus, artichoke, iris, hyacinth and tulip cultivation in Campania that caused total yield loss. Furthermore, the environmental changes produced by modern farming techniques (see below) played an important role in this scenario, creating optimal conditions for feeding and reproduction and encouraging population growth.[45]

2.6 Impact of agriculture on Savi's pine vole

Recent changes in the agricultural environment and farming practices have favoured fluctuations in rodent populations in crop fields.[47,50] The permanent grass cover maintained within orchard rows provides food throughout the year. In particular, it allows voles to extend their reproductive activity beyond the usual seasonal limit.[46] In a study conducted in apple orchards of the Cimini hills (Viterbo), about 20% of adult females continued to breed even in autumn and winter.[46] Herbaceous vegetation provides optimal habitat for this species in forage crops, horticulture and orchards.[22] In citrus and apple orchards,[46,50] the replacement of the traditional surface irrigation method (application of water by flooding the entire field) with drip irrigation (sprinklers above canopy or microsprinklers under canopy) leads to a growth of herbaceous cover throughout the year that supports Savi's pine vole population growth. In fact, given the burrowing habits of Savi's pine vole, periodic flooding by surface irrigation is a limiting factor for population growth.[22,50]

Conversely, the mechanisation of agricultural practices in orchards and arable fields that occurred in the second half of the twentieth century has reduced vole damage, because deep tillage prevents the establishment of stable populations. Ecotonal, marginal environments, not subjected to tillage and thus providing shelter for voles, are nowadays greatly reduced.[22]

2.7 Savi's pine vole management

Although Savi's pine vole populations do not go through cycles like other voles (e.g. common vole, field vole), the densities reached and the damage they can cause to vegetable crops and fruit trees may often require an appropriate control strategy. Many studies have been carried out worldwide to identify the best methods to manage vole populations,[1] such as tunnel fumigation,[51] use of repellents in both agriculture and forestry,[52–56] use of natural predators, parasites and pathogens,[57] diversionary feeding[58,59] and barriers and fences.[60,61] However, rodenticides[62] and traps are still the most used techniques.[61,63,64] Both anticoagulants and acute rodenticides (e.g. aluminium phosphide) have been used against voles in Europe. In general, control strategies adopted against other European pest voles are also suitable for implementation against Savi's pine voles, despite the latter being more fossorial. However, in Italy, Savi's pine vole management has been carried out mainly via trapping and poisoning, but the latter method was the most popular, and the most used compound was chlorophacinone.[22] The common practice was to deploy the bait with the rodenticide inside the tunnel entrances, avoiding scattering it on the soil and thus reducing the risk for non-target species.[48] However, in 2007, EU registration of chlorophacinone for use in plant protection ceased. In 2008, a new Italian ministerial regulation prohibited the use of any rodenticide bait outside special containers, strongly limiting (if not actually prohibiting) vole control by rodenticides.

Traps may reduce the number of individuals during outbreaks to supplement the use of toxic baits.[46,48] Capizzi and Santini[22] reported that good control of a Savi's pine vole outbreak was achieved by massive trapping only. Traps should be placed close to the tunnel exits. Santini[46] reported the removal of 90% of voles in 3–4 days. Galliano *et al.*[47] integrated the use of traps with rodenticide baits on two fruit farms in the province of Cuneo. Firstly, they used traps to identify the species responsible for the damage and its distribution. Secondly, they applied chlorophacinone at bait points in two separate treatments. This led to a 95% reduction in vole density. In addition, the reduction of potential habitat is useful. Farmers should cut the grass frequently and mow between the trees. Tillage is also important for the destruction of underground tunnels.[7] Moreover, using barn owls and other biological methods has been suggested as profitable, especially where the use of rodenticide is forbidden or strongly limited legally.[65] As there is no single technique that is efficient, economical and safe for non-target species, it is necessary to adopt both preventive (limiting the availability of food resources and burrowing activity) and control strategies (i.e. trapping and/or application of rodenticides).[22,46,48]

3 DISCUSSION

The literature on Savi's pine vole provides an overview of the knowledge about this species. The ongoing taxonomic debate poses problems for assessing the species' distribution. For the time being, it is appropriate to refer to the 'Savii group'. If some taxa are to be elevated to species level, the economic importance of each of them should be reassessed (e.g. see the damage by *M. s. nebrodensis* to orchards in Sicily, as well as damage by *M. s. brachycercus* in Calabria).[22]

Given Savi's pine vole's widespread distribution in Italy and its opportunistic habitat preferences,[8,23] it can be stated that the species can flexibly adapt to cultivated areas. It is not a species of conservation concern, being listed as LC (least concern) in the IUCN Italian Red List.[66] There is no evidence for an increasing relevance as pest, even though Savi's pine vole is actually considered to be a serious local pest in specific crops.

Although this species is no longer subject to control interventions as in past decades, it could be relevant as a target species for the analysis of ecological processes. In fact, stable populations in open habitats (including those intensively cultivated) with a strictly herbivorous diet seem to be an ideal target for this kind of study, with the potential for almost immediate response to experimental treatments.

Compared with other voles, fossorial species such as Savi's pine vole are less prolific than species that are active above ground (Table 2) such as the common vole. Litter size is comparable with that of other fossorial voles such as Mediterranean pine vole, Woodland vole and European pine vole. The small litter size and the long mean gestation time and interpartum period suggest that Savi's pine vole is less an r-strategist than other *Microtus* species (i.e. *M. arvalis*).[29] This might suggest that this species could be more manageable than other species of voles characterised by population outbreaks.

In reviewing the work published to date on this species, and trying to provide useful information for a more effective management, a gap in the current knowledge of Savi's pine vole emerged. This gap regards the behaviour of the species. Such knowledge may be of importance for planning monitoring and

Table 2. Mating systems of European fossorial voles

Species	Activity	Mating system
Microtus cabrerae	Semi-fossorial	Monogamy[80]
Microtus duodecimcostatus	Fossorial	Monogamy[81]
Microtus lusitanicus	Semi-fossorial	Monogamy[82]
Microtus multiplex	Fossorial	Monogamy[83]
Microtus oeconomus	?	Polygamy[84]
Microtus subterraneus	Fossorial	Polygamy[28]
Microtus tatricus	?	Polygamy[85]

control programmes, as the most appropriate control programmes imply integrated strategies rather than a single technique.[67]

Adopting the behavioural approach is not easy, especially in cases of fossorial organisms that cannot be observed directly in the field. However, a wider knowledge of Savi's pine vole behaviour may prove essential in order to gain a better understanding of its biology and perform effective control actions.

Savi's pine voles live in groups,[28] but group composition may vary between populations or depending on season. Knowing the group composition would make it possible to estimate the number of animals present in an area, based on the number of tunnels and holes, using for example an active burrow index.[68] This could help to understand whether interventions are needed. Furthermore, the Savi's pine vole's mating system is still unknown. Comparison with other European fossorial species of the genus *Microtus* does not help to make predictions because the majority are monogamous, but there are exceptions (Table 2). Mating systems influence effective population size (N_e): in the case of a promiscuous species, members of the more abundant sex might have a greater opportunity to breed and this would lead to a larger N_e than at monogamy (used here as a basis for comparison). In the case of polygyny or polyandry, instead, N_e declines because fewer males (polygyny) or females (polyandry) contribute genetically to the next generation.[69] Given the species' status as a recognised pest, ascertaining its reproductive strategies would be important and could help to make predictions about population fluctuations.

Models show that the removal of certain age/sex classes from a population may affect population growth rates.[69] Thus, in those species that exhibit infanticide, the removal of males results in a reduction in population size, because immigrating males kill the offspring of deceased or ousted males.[69] Infanticide occurs in some microtine species,[70] but there are no data for Savi's pine vole. Acquiring this information may allow the control of whole populations, targeting only specific demographic classes.[71]

Overall, studies aimed specifically at understanding the behavioural perspective would integrate the purely ecological approach, which is usually adopted in the study of the pests, and may be advantageous to understanding how the target species reacts to habitat manipulations.[72,73]

REFERENCES

1 Capizzi D, Bertolino S and Mortelliti A, Rating the rat: global patterns and research priorities in impacts and management of rodent pests. *Mammal Rev* **44**(2):148–162 (2014).

2 Elton CS, *Voles, Mice and Lemmings: Problems in Population Dynamics*. Clarendon Press, Oxford, UK (1942).

3 Contreras LC and McNab BK, Thermoregulation and energetics in subterranean mammals. *Prog Clin Biol Res* **335**:231–250 (1990).

4 Abt KF and Bock WF, Seasonal variations of diet composition in farmland field mice (*Apodemus* spp.) and bank voles (*Clethrionomys glareolus*). *Acta Theriol* **43**:379–389 (1998).

5 Jacob J and Tkadlec E, Rodent outbreaks in Europe: dynamics and damage, in *Rodent Outbreaks – Ecology and Impacts*, ed. by Singleton GR, Belmain S, Brown PR and Hardy B. International Rice Research Institute, Manila, the Philippines, pp. 217–233 (2010).

6 Jacob J, Manson P, Barfknecht R and Fredricks T, Common vole (*Microtus arvalis*) ecology and management: implications for risk assessment of plant protection products. *Pest Manag Sci* **70**(6):869–878 (2014).

7 Caltran S, I roditori dannosi alle colture erbacee ed arboree si combattono durante l'inverno. *Vita in Campagna* **11**:29–32 (2002).

8 Contoli L, Caratteri generali dei *Microtus* (*Terricola*) del 'gruppo savii', in *Fauna d'Italia. Mammalia II. Erinaceomorpha, Soricomorpha, Lagomorpha, Rodentia, Vol. XLIV*, ed. by Amori G, Contoli L and Nappi A. Edizioni Calderini, Milan, Italy, pp. 525–535 (2008).

9 Contoli L, Microtus savii, *in* The Atlas of European Mammals, ed. by Mitchell-Jones AJ, Amori G, Bogdanowicz W, Kryštufek B, Reijnders PJH, Spitzenberger F *et al.* Academic Press, London, UK (1999).

10 Contoli L, On subspecific taxonomy of *Microtus savii* (Rodentia, Arvicolidae). *Hystrix* **14**:1–2 (2003).

11 Le Louarn H and Quéré JP, *Les Rongeurs de France*. INRA Editions, Paris, France, pp. 171–173 (2003).

12 Castiglia R, Annesi F, Aloise G and Amori G, Systematics of the *Microtus savii* complex (Rodentia, Cricetidae) via mitochondrial DNA analyses: paraphyly and pattern of sex chromosome evolution. *Mol Phylogenet Evol* **46**(3):1157–1164 (2008).

13 Jaarola M, Martínková N, Gündüz İ, Brunhoff C, Zima J, Nadachowski A *et al.*, Molecular phylogeny of the speciose vole genus *Microtus* (Arvicolinae, Rodentia) inferred from mitochondrial DNA sequences. *Mol Phylogenet Evol* **33**(3):647–663 (2004).

14 Acosta MJ, Marchal JA, Fernández-Espartero C, Romero-Fernández I, Rovatsos MT, Giagia-Athanasopoulou EB *et al.*, Characterization of the satellite DNA Msat-160 from species of *Terricola* (*Microtus*) and *Arvicola* (Rodentia, Arvicolinae). *Genetica* **138**(9–10):1085–1098 (2010).

15 Gornung E, Bezerra A and Castiglia R, Comparative chromosome mapping of the rRNA genes and telomeric repeats in three Italian pine voles of the *Microtus savii* sl complex (Rodentia, Cricetidae). *Comp Cytogenet* **5**(3):247–257 (2011).

16 Galleni L, Tellini A, Stanyon R, Cicalò A and Santini L, Taxonomy of *Microtus savii* (Rodentia, Arvicolidae) in Italy: cytogenetic and hybridization data. *J Mammal* **75**(4):1040–1044 (1994).

17 Galleni L, Stanyon R, Contadini L and Tellini A, Biogeographical and karyological data of the *Microtus savii* group (Rodentia, Arvicolidae) in Italy. *Bonn Zool Beitr* **47**:277–282 (1998).

18 Nappi A, Brunet-Lecomte P and Montuire S, Dental morphology of *Microtus* (*Terricola*) voles from Calabria (Southern Italy) and relationships with *M. (T.) savii* (Rodentia, Arvicolidae). *Hystrix* **16**(1):75–85 (2005).

19 Nappi A, Brunet-Lecomte P and Montuire S, Intraspecific morphological tooth variability and geographical distribution: application to the Savi's vole, *Microtus (Terricola) savii* (Rodentia, Arvicolinae). *J Nat Hist* **40**(5–6):345–358 (2006).

20 Salvioni M, *Pitymys savii* (de Selys-Longchamps, 1838), in *Mammiferi della Svizzera*, ed. by Hauser J. Commissione delle Memorie dell'Accademia Svizzera di Scienze Naturali, Birkhäuser Verlag, Basel, Switzerland, pp. 314–318 (1995).

21 Santini L, *I Roditori italiani: di interesse agrario e forestale*. Consiglio Nazionale delle Ricerche, Rome, Italy (1983).

22 Capizzi D and Santini L, *I Roditori Italiani: Ecologia, Impatto sulle Attività Umane e Sugli Ecosistemi, Gestione delle Popolazioni*. Antonio Delfino Editore, Rome, Italy (2007).

23 Cagnin M and Grasso R, The communities of terrestrial small mammals (Insectivora, Rodentia) of the Nebrodi Mountains (north-eastern Sicily). *Ital J Zool* **66**(4):369–372 (1999).

24 Osella G and Montolli A, The small mammals of an upper piedmontese Po plain site (Leinì, Turin prov.)/La micromammalofauna di una stazione planiziaria piemontese. *Hystrix* **1**(2):119–136 (1986).

25 Canova L, Distribution and habitat preference of small mammals in a biotope of the north Italian plain. *B Zool* **59**(4):417–420 (1992).

26 Sarà M, *I Mammiferi delle Isole del Mediterraneo.* L'Epos, Palermo, Italy, pp. 1–166 (1998).

27 Cagnin M, Moreno S, Aloise G, Garofalo G, Villafuerte R, Gaona P *et al.*, Comparative study of Spanish and Italian terrestrial small mammal

coenoses from different biotopes in Mediterranean peninsular tip regions. *J Biogeogr* **25**(6):1105–1113 (1998).
28 Salvioni M, Home range and social behavior of three species of European *Pitymys* (Mammalia, Rodentia). *Behav Ecol Sociobiol* **22**(3):203–210 (1988).
29 Caroli L, Capizzi D and Luiselli L, Reproductive strategies and life-history traits of the Savi's pine vole, *Microtus savii*. *Zool Sci* **17**:209–216 (2000).
30 Caroli L and Santini L, The postnatal development of the Savi's pine vole, *Microtus savii* De Sel. L. (Rodentia, Arvicolidae). *Proc 1st Eur Congr Mammalogy*, Lisbon, Portugal, pp. 299–308 (1996).
31 Cornulier T, Yoccoz NG, Bretagnolle V, Brommer JE, Butet A, Ecke F *et al.*, Europe-wide dampening of population cycles in keystone herbivores. *Science* **340**(6128):63–66 (2013).
32 Zaccaroni M, Bertolino S, Capizzi D, Dell'Agnello F, Martini M, Mazza V *et al.*, Savi's pine vole population dynamics in agro-ecosystems. *10th Eur Vertebrate Pest Management Conf*, Seville, Spain (2015).
33 Contoli L, Micro-mammals and environment in central Italy: data from *Tyto alba* (Scop.) pellets. *Ital J Zool* **42**(2–3):223–229 (1975).
34 Contoli L and Sammuri G, Predation on small mammals by tawny owl and comparison with barn owl in the Farma valley (central Italy). *Ital J Zool* **45**(4):323–335 (1978).
35 Pezzo F and Morimando F, Food habits of the barn owl, *Tyto alba*, in a Mediterranean rural area: comparison with the diet of two sympatric carnivores. *Ital J Zool* **62**(4):369–373 (1995).
36 Varuzza P, Capizzi D, Santini L and Apollonio M, Barn owl *Tyto alba* predation on small mammals in relation to the Mediterranean environment (Pisa Province, Italy). *Acta Ornithol* **36**(2):153–160 (2001).
37 Luiselli L and Capizzi D, Composition of a small mammal community studied by three comparative methods. *Acta Theriol* **41**:425–432 (1996).
38 Casagrande S, Nieder L, Di Minin E, La Fata I and Csermely D, Habitat utilization and prey selection of the kestrel *Falco tinnunculus* in relation to small mammal abundance. *Ital J Zool* **75**(4):401–409 (2008).
39 Massa B and Lo Verde G, The vole of Savi, *Microtus savii* (De Selys Longchamps), in Sicilian vineyards and citrus groves. *Inf Fitopatol* **57**:23–26 (2007).
40 Amori G, Corsetti L and Esposito C, Mammiferi dei Monti Lepini. *Quad Cons Nat* **11**:108–110 (2002).
41 Fais I, Costanzo M and Massa B, First data on the feeding habits of the red fox (*Vulpes vulpes* L.) in Sicily/Primi dati sulla posizione trofica della Volpe (*Vulpes vulpes* L.) in Sicilia. *Hystrix* **3**(1):105–112 (1991).
42 Capula M and Luiselli L, Contributo allo studio della microteriofauna di un'area dell'Italia centrale (Monti della Tolfa, Lazio) mediante analisi del contenuto stomacale di Vipera (*Vipera aspis*). *Hystrix* **2**:101–108 (1990).
43 Santini L, European field voles of the genus *Pitymys* McMurtrie and their damage in agriculture, horticulture and forestry. *EPPO Bull* **7**(2):243–253 (1977).
44 Caroli L, *Nuove problematiche da parassiti animali in impianti arborei inerbiti. PhD dissertation*, Università di Pisa, Pisa, Italy (1992).
45 Rapisarda C, Santini L, Lo Giudice V and Schilirò E, *Atti del Convegno su Le Arvicole. Una Crescente Minaccia per gli Agrumeti. Biologia, Danni e Strategie di Controllo*, Regione Siciliana, Assessorato Agricoltura e Foreste, Servizi allo Sviluppo (1998).
46 Santini L, Criteri per una lotta integrata alle arvicole dei frutteti. *Atti SITE* **8**:161–171 (1989).
47 Galliano A, Vittone F and Santini L, Esperienze di lotta all'arvicola del Savi. *Inf Agrario* **47**:71–73 (1995).
48 Santini L, The problem of *Pitymys* voles in orchards in central and southern Italy. *EPPO Bull* **18**(3):463–468 (1988).
49 D'Errico FP, Nicotina M and Russo LF, Danni da *Pitymys savii* de Selys Longchamp a diverse colture in Campania (Italia) e prove di lotta. *Inf Fitopatol* **31**(3):27–30 (1981).
50 Bertolino S, Asteggiano L, Saladini MA, Giordani L, Vittone G and Alma A, Environmental factors and agronomic practices associated with Savi's pine vole abundance in Italian apple orchards. *J Pest Sci* **88**:135–142 (2015).
51 Delattre P, Clarac R, Melis JP, Pleydell DRJ and Giraudoux P, How moles contribute to colonization success of water voles in grassland: implications for control. *J Appl Ecol* **43**(2):353–359 (2006).
52 Lindgren PM, Sullivan TP and Crump DR, *Review of synthetic predator odor semiochemicals as repellents for wildlife management in the Pacific Northwest*. National Wildlife Research Center Repellents Conf, Lincoln, NE (1995).
53 Curtis PD, Rowland ED and Good GL, Developing a plant-based vole repellent: screening of ten candidate species. *Crop Prot* **21**(4):299–306 (2002).
54 Figueroa JA, Kimball BA and Perry KR, Lagomorph and rodent responses to two protein hydrolysates. *Crop Prot* **27**(3):851–854 (2008).
55 Wager-Pagé SA, Epple G and Mason JR, Variation in avoidance of Siberian pine needle oil by rodent and avian species. *J Wildl Manag* **61**(1):235–241 (1997).
56 Hodge SJ and Pepper HW, *The Prevention of Mammal Damage to Trees in Woodland*. Forestry Commission, Edinburgh, UK (1998).
57 Haim A, Shanas U, Brandes O and Gilboa A, Suggesting the use of integrated methods for vole population management in alfalfa fields. *Integr Zool* **2**(3):184–190 (2007).
58 Sullivan TP and Sullivan DS, Influence of a granivorous diversionary food on population dynamics of montane voles (*Microtus montanus*), deer mice (*Peromyscus maniculatus*), and western harvest mice (*Reithrodontomys megalotis*). *Crop Prot* **23**(3):191–200 (2004).
59 Sullivan TP and Sullivan DS, Vole-feeding damage and forest plantation protection: large-scale application of diversionary food to reduce damage to newly planted trees. *Crop Prot* **27**(3):775–784 (2008).
60 Zhang Z, Chen A, Ning Z and Huang X, Rodent pest management in agricultural ecosystems in China, in *Ecologically-based Management of Rodent Pests*. Australian Centre for International Agricultural Research (ACIAR), Canberra, Australia, pp. 261–284 (1999).
61 Saucy F, Manipulating dispersal as a tool in the biological control of small mammals, in *Advances in Vertebrate Pest Management III*, ed. by Feare CJ and Cowan DP. Filander Verlag, Fürth, Germany (2004).
62 Sage M, Coeurdassier M, Defaut R, Lucot É, Barbier B, Rieffel D *et al.*, How environment and vole behaviour may impact rodenticide bromadiolone persistence in wheat baits after field controls of *Arvicola terrestris*. *Environ Pollut* **148**(1):372–379 (2007).
63 Merwin IA, Ray JA and Curtis PD, Orchard groundcover management systems affect meadow vole populations and damage to apple trees. *Hort Sci* **34**(2):271–274 (1999).
64 Niemeyer H, Field tests on rodenticide-free control of voles in forestry. *Anz Schädlingskde Pflzschutz Umweltschutz* **70**(2):25–29 (1997).
65 Kan I, Motro Y, Horvitz N, Kimhi A, Leshem Y, Yom-Tov Y and Nathan R, Agricultural rodent control using barn owls: is it profitable? *Am J Agric Econ* **96**(3):733–752 (2014).
66 Rondinini C, Battistoni A, Peronace V and Teofili C, *Lista Rossa IUCN dei Vertebrati Italiani.* Comitati Italiano IUCN e Ministero dell'Ambiente e della Tutela del Territorio e del Mare, Rome, Italy (2013).
67 Singleton GR, Hinds LA, Leirs H and Zhang ZB, *Ecologically-based Management of Rodent Pests – Re-evaluating our Approach to an Old Problem*. Australian Centre for International Agricultural Research (ACIAR), Canberra, Australia, pp. 17–29 (1999).
68 Tkadlec E and Stenseth NC, A new geographical gradient in vole population dynamics. *Proc R Soc Lond* **268**:1547–1552 (2001).
69 Caro T, Behavior and conservation: a bridge too far? *Trends Ecol Evol* **22**(8):394–400 (2007).
70 Webster AB, Gartshore RG and Brooks RJ, Infanticide in the meadow vole, *Microtus pennsylvanicus*: significance in relation to social system and population cycling. *Behav Neur Biol* **31**:342–347 (1981).
71 Boonstra R, Infanticide in microtines: importance in natural populations. *Oecologia* **46**(2):262–265 (1980).
72 Jacob J, Response of small rodents to manipulation vegetation height in agro-ecosystems. *Integr Zool* **3**:3–10 (2008).
73 Bertolino S, Colangelo P, Mori E and Capizzi D, Good for management, not for conservation: an overview of research, conservation and management of Italian small mammals. *Hystrix* **26**:25–35 (2015).
74 Schadler MH, Reproductive patterns in the pine vole. *2nd Eastern Pine and Meadow Vole Symp*, Beltsville, MD, pp. 82–87 (1978).
75 Oksanen TA, Jonsson P, Koskela E and Mappes T, Optimal allocation of reproductive effort: manipulation of offspring number and size in the bank vole. *Proc R Soc Lond B Biol* **268**(1467):661–666 (2001).
76 Grocock CA and Clarke JR, Duration of spermatogenesis in the vole (*Microtus agrestis*) and bank vole (*Clethrionomys glareolus*). *J Reprod Fertil* **47**(1):133–135 (1976).
77 Cudworth NL and Koprowski JL, *Microtus californicus* (Rodentia: Cricetidae). *Mammal Spec* **42**(1):230–243 (2010).
78 Guédon G, Pascal M and Mazouin F, Le campagnol provençal en captivité (*Pitymys duodecimcostatus* de Sélys-Longchamps, 1839) (Rongeurs, Microtidés). II) La croissance. *Mammalia* **55**(3):397–406 (1991).

79 Pinter AJ, Effects of diet and light on growth, maturation, and adrenal size of *Microtus montanus*. *Am J Phys* **215**(2):461–466 (1968).
80 Ventura J, López-Fuster MJ and Cabrera-Millet M, The Cabrera vole, *Microtus cabrerae*, in Spain: a biological and a morphometric approach. *Neth J Zool* **48**(1):83–100 (1997).
81 Paradis E and Guédon G, Demography of a Mediterranean microtine: the Mediterranean pine vole, *Microtus duodecimcostatus*. *Oecologia* **95**(1):47–53 (1993).
82 Ventura J, Jiménez L and Gisbert J, Breeding characteristics of the Lusitanian pine vole, *Microtus lusitanicus*. *Anim Biol* **60**(1):1–14 (2010).
83 Fink S, Excoffier L and Heckel G, Mammalian monogamy is not controlled by a single gene. *Proc Natl Acad Sci USA* **103**(29):10 956–10 960 (2006).
84 Heske EJ and Ostfeld RS, Sexual dimorphism in size, relative size of testes, and mating systems in North American voles. *J Mammal* **71**(4):510–519 (1990).
85 Rudá M, Kocian LU, Martínková N and Žiak D, Population dynamics and spatial behaviour of *Microtus tatricus* (Arvicolinae, Rodentia). *Acta Theriol* **55**(1):81–88 (2010).

