Common vole, *Microtus arvalis*
Bank vole, *Myodes glareolus*
Yellow-necked mouse, *Apodemus flavicollis*
Wood mouse, *Apodemus sylvaticus*
Water vole, *Arvicola amphibius*
Southern water vole, *Arvicola sapidus*

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Brief description of the species/group of species: basic ecology and its relevance from an epidemiological perspective

The above mentioned species have been grouped according to the broad similarities in methods used to estimate density, determine abundance indices or simple presence/ absence indicators. They occupy a wide variety of habitats, display different population dynamics and are reservoir hosts for multiple pathogens. Although this group incorporates species from two different families (Cricetidae and Muridae; Wilson and Reeder, 2005), the methods to determine population density are nevertheless comparable. Species specific suggestions and pitfalls of abundance estimation can be found under points 3.2 and 3.3. Various pathogens have been identified previously using pathogen-specific methods (for reviews see Meerburg et al., 2009; Ulrich et al., 2009), but recently also using broad-spectrum nucleic acid amplification methods (see Drexler et al., 2012) and next-generation sequencing (Phan et al., 2011). Some rodent species carry also non-zoonotic pathogens, such as herpesviruses (Ehlers et al., 2007), adenoviruses (Klempa et al., 2009) and papillomaviruses (Schulz et al., 2012). Here for each species only the pathogens with zoonotic potential are summarized. Brief ecological descriptions and epidemiological relevance are as follows:

***Microtus arvalis* (Family: Cricetidae)**

The common vole *M. arvalis* (Pallas, 1778) is the most abundant mammal in Europe. It inhabits an almost continuous range throughout the continental European area from the Atlantic coast of France to central Russia with isolated populations on the Iberian Peninsula where it can occur from sea level up to 3,000 m (Braun and Dieterlen, 2005; http://www.iucnredlist.org/europe). It is absent from the Mediterranean, most of Fennoscandia, northern Russia and the British Isles, except Orkney Islands, where it had been introduced prehistorically approximately 4,800±120 BP (Haynes et al., 2003). The eastern distribution is limited to Ukraine and Russia, from the Dniester River towards the north-east (Mitchell-Jones et al., 1999). Their main habitat is open grassland but also cultivated agricultural land and short meadows (for review see Jacob et al., 2014), where high densities of >3,000 individuals per ha have been reported (Bryja et al., 2001). Common voles show a polyphasic, short-termed activity rhythm of ca. 2 h. This rhythm seems to be dusk/dawn-locked (Daan and Slopsema, 1978).

The population density of *M. arvalis* can fluctuate on various temporal scales. Annually, densities generally increase from spring onwards reaching a peak in autumn, while on a multiannual level cyclic superabundant densities (outbreaks) can be observed roughly every 3-5 years, often followed by a rapid collapse of the population (Jacob & Tkadlec, 2010). The reasons for explosive dynamics seem to be two remarkable features: first, females can already mate at 2 weeks of age (Tkadlec and Zejda;

1995) and second, due to a highly flexible social behaviour, they form large groups or colonies of related individuals (Frank 1957). More recently, a Europe-wide dampening of these cyclic events has been described for several vole species suggesting large scale climate change as a prominent driver for this phenomenon (Cornulier et al., 2013).

M. arvalis is a well-known reservoir host for *Tula hantavirus* (TULV), tick-borne *Encephalitis virus* (TBEV), *cowpox* virus, *Borrelia* spp. *Cryptosporidium* spp., *Leptospira* spp., *Listeria monocytogenes*, *Francisella tularensis*, *Brucella microti*, *Babesia microti*, *Echinococcus multilocularis* and *Coxiella burnetii* (Ulrich et al., 2009; Meerburg et al., 2009; Schmidt-Chanasit et al., 2010; Achazi et al., 2011; Kinnunen et al., 2011; Kuiken et al., 1991; Scholz et al., 2008; Bajer, 2008; Hansen et al., 2004; Schmidt et al., 2014).

***Myodes glareolus* (Family: Cricetidae)**

The bank vole *M. glareolus* (Schreber, 1780), formerly *Clethrionomys glareolus*, is one of the most common rodents in Europe and is considered a pest in forests due to the occurrence of abundance peaks in association with damage to young forest trees (Hansson and Zejda, 1977). Bank voles are distributed from the British Isles (introduced to Ireland in 1964 (Smal, 1987)) to Lake Baikal and northern Asia (http://www.iucnredlist.org/europe). In the north of Europe they occur up to the northern limit of Norway spruce at the latitudes 68-69 N and in the south to the Balkans, Italian mountains and northern Spain. They are absent from the Mediterranean islands, but prevalent on most Baltic and Atlantic islands. Bank voles can be found from sea level to an altitude of 2,376 m (Spitzenberger, 2001). In the temperate zone, their multiannual fluctuations are closely associated with a tree seed production (masting) (Secher-Jensen, 1981, Jedrzejewski et al, 1991, Clement et al., 2010; Tersago et al., 2009) while in boreal northern Europe vole fluctuations are predator driven (Henttonen et al. 1987, Hanski et al. 1991, Hanski et al. 2001, Korpela et al 2014). This species prefers moist deciduous, mixed, conifer and montane forests, but is also observed in parks, gardens, hedgerows, clear-cuttings but rarely on plain grassland (Mitchell-Jones et al., 1999). Bank voles exhibit multi-phase activity pattern with peak activity reached at dusk and dawn (Braun and Dieterlen, 2005), though this pattern can vary seasonally (Wojcik & Wolk, 1985). Peak densities in bank voles are lower compared to open habitat vole species. Early work in southern Sweden reported peak densities of up to 200 individuals per hectare (Bergested, 1965). Similar values have been reported for the forest of Bialowieza in Poland (Stenseth et al.,2002).

M. glareolus is a well-known reservoir host for Puumala hantavirus, TBEV, cowpox virus, Ljungan virus, hepacivirus, *Borrelia* spp., *Leptospira* spp., *Francisella tularensis*, *Bartonella* spp., *Cryptosporidium* spp., *Capillaria hepatica* and *Babesia microti* (Ulrich et al., 2009; Meerburg et al., 2009; Schmidt et al., 1998; Telfer et al., 2011; Schmidt et al., 2014; Achazi et al., 2011; Kinnunen et al., 2011; Drexler et al., 2013; Hubalék, 2007).

***Arvicola amphibius; Arvicola sapidus* (Family: Cricetidae)**

There is some debate regarding the taxonomy of *Arvicola* at least for certain European regions (Gippoliti, S. 2012, Carleton & Musser, 2005) resulting in confusing use of species names. There are two distinct ecotypes within *Arvicola amphibius* (Linnaeus, 1758) that have only recently been treated as separate species with still debated nomenclature. The aquatic form inhabits wetland and riverine habitats with a preference for aquatic habitats and is referred to as *A. amphibius*. The terrestrial form inhabits grassland, orchards or horticulture and exhibits rather classic fossorial traits and is named *A. scherman*. This is reflected in the polymorphism within the species as size and fur colour vary substantially. *A. scherman* also exhibits far greater abundance amplitudes during outbreak scenarios with up to 600 ind/ha (Giraudoux et al., 1997) causing severe damage in horti- and agriculture, while *A. amphibius* rarely exceed 100 ind/ha (Jacob & Tkadlec, 2010). *A. amphibius* is a widespread Palaearctic species whose distribution ranges from Great Britain, where it is considered endangered, to Siberia in the East and from the Arctic circle in the north to northern Iran and the Near East in the south (http://www.iucnredlist.org/europe). *A. amphibius* is herbivorous, feeding mainly on the above-ground parts of plants as well as tree roots and bulbs. *Arvicola sapidus* (Miller, 1908) is restricted to Western Europe and the Iberian Peninsula (http://www.iucnredlist.org/europe), where it is strictly water-dependent (Mitchell-Jones et al., 1999) inhabiting sedge or reed vegetation (Pita et al., 2011) similar to the aquatic form of *A. amphibius*. *A. sapidus* depends on bank-side grass and other green vegetation as food source and probably does not exceed 5 individuals /100m river bank length (Mitchell-Jones et al., 1999).

French populations of the water vole were reported to host hantavirus, lymphocytic choriomeningitis virus as well as cowpox virus (Charbonnel et al., 2008). A more recent study confirmed molecularly Tula virus infections in *A. amphibius* from different regions of Germany and Switzerland, most likely representing spillover infections (Schlegel et al., 2012). For British populations pathogens include *Leptospira* spp., *Bartonella* spp., *Giardia* spp. and *Campylobacter* spp. (Gelling et al., 2011). Infections

of *Arvicola amphibius* with pathogens such as *Listeria monocytogenes*, *Francisella tularensis*, *Echinococcus multilocularis* were also reported (Meerburg et al., 2009; Mörner and Addison, 2001).

***Apodemus flavicollis; Apodemus sylvaticus* (Family: Muridae)**

In contrast to the other species in this review both the yellow-necked mouse *A. flavicollis* (Melchior 1834) and wood mouse *A. sylvaticus* (Linnaeus 1758) belong to the Muridae family and are sympatric over a large part of their distribution (http://www.iucnredlist.org/europe). They can be predominately found in deciduous woodland, , although *A. sylvaticus* is known to use open habitat as well (Tew et al., 2006). *Apodemus* spec. are mainly granivorous feeding on seeds but also eat berries, fungi or insects (Hansson, 1985). Population densities fluctuate but the peak densities are not comparable to the densities reached during vole outbreaks *A. flavicollis* can reach up to 58 ind/ha (Niethammer & Krapp, 1978) while for *A. sylvaticus* a value of 92 ind/ha was shown (Halle, 1993). High population densities have been associated with the mast of forest trees in the previous year. In combination with beneficial winter climate this can lead to rapid population growth in the following spring.

Apodemus sp. is a reservoir host for *Cryptosporidium parvum* (Bajer et al., 1997) and *Toxoplasma gondii* (Hejlicek & Literak, 1998). In many areas of southeastern Europe the Dobrava-Belgrade hantavirus (DOBV), genotype Dobrava, has been associated with *Apodemus flavicollis* (Klempa et al., 2013). In addition, *Apodemus* spp. was found to be infected by TBEV, cowpox virus, *Borrelia* spp., *Leptospira* spp., *Babesia microti*, *Bartonella* spp., *Escherichia coli* (STEC/VTEC), *Capillaria hepatica* and *Francisella tularensis* (Ulrich et al., 2009; Meerburg et al., 2009; Schmidt et al., 1998; Achazi et al., 2011; Kinnunen et al., 2011; Tadin et al., 2012; Schmidt et al., 2014).

Recommended method(s) for most accurate population estimation

The gold standard to estimate population densities species that are regularly active above ground is trapping with live traps (e.g., Ugglan or Sherman traps) and applying a capture-mark-recapture method (Seber, 1965). It was first used by C.G.J. Petersen in 1896 (Southwood and Henderson, 2000) and is successfully applied to many different study aims since (see Chapter 3.2.1). Population size can be estimated from four to five visits to the trapping site, but more visits can be made, especially if further information on survival or movement is desired. Animals are released and remain unharmed. Besides the possibility to monitor and identify a broad range of small mammal species accurately or to take additional sampling, e.g. blood and tissues, live trapping is a time consuming, expensive and work-intensive process (Sibbald et al., 2006). Handling of live animals (blood sampling, marking) does require country-specific permits (animal ethics), which have to be considered well in advance. For subterranean species, burrow counts are recommended.

Mini-review of methods applied in Europe

General reviews

A variety of methods have been used to estimate the abundance of small mammals (Schwarz & Seber 1999; Sibbald et al., 2006).

Capture-mark-recapture

A sound estimation of population density using capture-mark-recapture methods (CMR) is well established in population abundance estimation. The statistical models (see review in Seber, 1986) have been and are still undergoing constant evaluation to adjust for departures from the underlying assumptions (see review by Schwarz, 1999; Efford, 2004; Efford et al., 2009). Heterogeneity in model parameters, especially in secretive small mammals has been shown to occur from a variety of intrinsic or extrinsic sources. Observed variability in capture probability, due to different activity and home ranges of different functional groups in the populations, violating the underlying conventional estimation assumptions, are often being identified as a crucial pitfall in population density determination. Factors like species, age or gender can influence individual home ranges. In relation to the layout of the trapping-grid (i.e. edge effects) this is often leading to high degrees of capture heterogeneity among individuals (Pledger and Efford, 1998). A much overlooked determinant of precision in CMR-studies, especially for small mammals, is the trap setup. A web-grid with varying trap-spacing improves the estimation of movement pattern within the trapping area and allows for accurate estimation of the effective trapping area reducing edge effects (Parmenter, 2003). Additionally, estimates of home ranges of target species should be incorporated into calculating the trap layout and spacing. More recently, spatially explicit capture-recapture statistics have been proposed to reduce edge effects altogether (Efford & Fewster, 2012).

Snap-trapping

This method is well established in estimating rodent abundance (Lidicker, 1973; Village and Myhill, 1990), and has advantages especially in studies designed for pathogen monitoring. When country specific permits are obtained it allows for the analysis of various organs that might be of interest for

studying a particular pathogen. Although several parameters of population dynamics cannot be estimated by snap trapping (survival, movement) it is sufficient for most pathogen studies compared to the more labor intensive live-trapping method and traps designed to be inserted in tunnels can catch subterranean species. Results on estimated abundance seem to be well correlated to live-trapping estimates (Hanski et al., 1994). However, it has been discussed that removal trapping might introduce a bias towards trapping more transient, dispersing individuals when used frequently (>3 times per year) at the same site over a long period of time (Stenseth et al., 2002). This has to be taken into account when defining the method of choice for a particular study goal.

Active burrow index

A very important index for estimations of vole abundance in middle and Eastern Europe are counts of active burrow entrances in a defined area (Liro, 1974). Since 1970 the active burrow count replaced live trapping methods in agricultural monitoring, because in comparison to them the index of active burrow entrances is inexpensive and easier to measure (Lisicka et al., 2007). However, at low population densities the relative sampling error can reach 400%. In contrast at high population densities the error will be less than 10%. Lisicka and co-workers also proved that at high densities the population change will be overestimated due to a non-linear relation between the index and the population size (Lisicka et al., 2007). Based on field observations Heise and Wieland (1991) reported that each individual of German common vole population in Thuringia is capable of opening on average 2.5 burrow entrances per day. This can allow the conversion of an index to actual population density, though the impact of sex ratio and the social structure of a population on burrowing capacity in relation to abundance are still unknown.

Owl pellet analysis

The relative abundance can be estimated by analysing the diet of avian predators. As these birds cannot digest bones, claws, teeth and fur, they have to disgorge these components regularly. Therefore, large sample sizes of the prey can be easily identified to species level by examining jawbones, teeth or skulls from spit pellets (Love et al., 2000). In Europe the barn owl is mostly used for pellet analysis in small mammals as around 90% of its diet consists of rodents and shrews. The favoured roosting sites are in man-made constructions and pellets are therefore easier to find and decompose less rapidly compared to pellets from other owls (Glue, 1974). Further advantages of pellet analysis are low cost, the variety of prey species obtained including mainly subterranean species, detecting rare species and the recognition of annual and seasonal changes of pellet composition. Since barn owls are nocturnal and the habitat of small mammals may differ from owl territories, certain prey species may be under-represented (Sibbald et al., 2006). *Arvicola* spec. is a large prey for the barn owl to tackle and in the presence of alternative food sources might give misleading results in abundance estimation.

Field sign index

Various indices of population size for burrowing mammals exist (Hubbs et al., 2000) and are commonly used to assess population abundance in ecological studies, although all indices lack total confidence in accurate species identification. Wilkinson et al., (2004) reported that for lowland habitats the presence of surface runways is a good sign index for field vole (*Microtus agrestis*) activity. However, identifying specific vole species using this method could prove to be problematic. In contrast Lambin et al. (2000) found that for upland habitats fresh grass clippings were better indicators of vole activity than runways or fresh/old droppings. Although some species leave characteristic feeding signs, it can be difficult to distinguish between grass clippings of different vole species (Sibbald et al., 2006). Moreover, fresh and old droppings might not be suitable for vole identification to species level (Sargent and Morris, 2003).

An additional, simple and economical method for estimating relative abundance is footprint tracking by tracking-tunnels or track-plates (Carey et al., 1991). A cardboard with non-drying and sealed ink is deployed. Problems associated with tracking counts are overlaid footprints that disturb a proper identification (Brown et al., 1996) or in general to distinguish between prints of different rodent genera. Thus only trained experts may verify the genus or species (Hasler et al., 2004). Tracking-plates are rarely used in monitoring abundance of the relevant species because it is difficult to distinguish tracks of closely related sympatric species. In addition, stability of boards and tracks are higly dependent on weather conditions, which is a reason for applying tracking plates mainly indoors. Overall, the sign index could give misguided estimates of relative abundance if more than one species is responsible for the occurrence of field signs (Village and Myhill, 2009).

Exemptions to the nonspecific sign indices are hair traps. Baited tunnels with sticky tape allow for obtaining hair samples from multiple individuals. Where DNA extraction and PCR protocol are established (Ruibal et al., 2010) individuals can be identified and used for density estimation.

APHAEA protocol (for harmonization at large scale)

Abundance estimation by snap trapping according a standard protocol given.

References

Achazi K, Růžek D, Donoso-Mantke O, Schlegel, M, Ali HS, Wenk M, Schmidt-Chanasit J, Ohlmeyer L, Rühe F, Vor T, Kiffner C, Kallies R, Ulrich RG, Niedrig M. 2011. Rodents as sentinels for the prevalence of tick-borne *encephalitis virus*. *Vector-Borne and Zoonotic Diseases* 11:641-647.

Bajer A, Bednarska M, Sinski E.1997. Wildlife rodents from different habitats as a reservoir for *Cryptosporidium parvum*. *Acta Parasitologica* 42:192-194.

Bajer A. 2008. Between-year variation and spatial dynamics of *Cryptosporidium* spp. and Giardia spp. infections in naturally infected rodent populations. *Parasitology* 135(14):1629-1649.

Bergstedt BO. 1965. Distribution, reproduction, growth and dynamics of the rodent species *Clethrionomys glareolus* (Schreber), *Apodemus flavicollis* (Melchior) and *Apodemus sylvaticus* (Linne) in southern Sweden. *Oikos*, pp.132-160.

Braun M, Dieterlen F. 2005. *Die Säugetiere Baden-Württembergs*, Band 2. Ulmer. 1:297-311.

Brown KP, Moller H, Innes J, Alterio N. 1996. Calibration of tunnel tracking rates to estimate relative abundance of ship rats (*Rattus rattus*) and mice (*Mus musculus*) in a New Zea-land forest. *N. Z. J. Ecol.* 20:271-275.

Bryja J, Tkadlec E, Nesvadbová J, Gaisler J, Zejda J. 2001. Comparison of enumeration and Jolly-Seber estimation of population size in the common vole *Microtus arvalis*. *Acta Theriologica* 46:279-285.

Carey AB, Biswell BL, Witt JW. 1991. Methods for measuring the abundance of arbo-real rodents. USDA Forest Service, technical report, Oregon.

Carleton MD, Musser GG. 2005. Order Rodentia. In: Wilson DE, Reeder DAM. (Eds.). *Mammal species of the World: a taxonomic and geographic reference*. 3rd Ed. Vol. II. John Hopkins University Press, Baltimore, pp. 745–752.

Charbonnel N, Deter J, Chaval Y, Laakkonen J, Henttonnen H, Voutilainen L, Vapalahti O, Vaheri A, Morand S, Cosson JF. 2008. Serological evidence of viruses naturally associated with the montane Water vole (*Arvicola scherman*) in Eastern France. *Vector-Borne and Zoonotic Diseases* 8:763-767.

Clement J, Maes P, van Ypersele de Strihou C, van der Groen G, Barrios JM, Verstraeten WW, van Ranst M. 2010. Beechnuts and outbreaks of *Nephropathia epidemica* NE: of mast, mice and men. *Nephrol Dial Transplant.* 25(6):1740-1746.

Cornulier T, Yoccoz NG, Bretagnolle V, Brommer JE, Butet A, Ecke F, Elston DA, Framstad E, Henttonen H, Hörnfeldt B, Huitu O, Imholt C, Ims RA, Jacob J, Jedrzejeaska B, Millon A, Petty S, Pietiäinen H, Tkadlec E, Zub K, Lambin X. 2013. Europe-wide dampening of population cycles in keystone herbivores. *Science* 340:63-66.

Daan S, Slopsema S. 1978. Short-Term Rhythms in Foraging Behaviour of the Common Vole, *Microtus arvalis*. *J. Comp. Neurol.* 127:215-27.

Drexler JF, Corman VM, Müller MA, Maganga GD, Vallo P, Binger T, Gloza-Rausch F, Rasche A, Yordanov S, Seebens A, Oppong S, Sarkodie YA, Pongombo C, Lukashev AN, Schmidt-Chanasit J, Stöcker A, Carneiro AJB, Erbar S, Maisner A, Fronhoffs F, Buettner R, Kalko EKV, Kruppa T, Franke CR, Kallies R, Yandoko ERN, Herrler G, Reusken C, Hassanin A, Krüger DH, Matthee S, Ulrich RG, Leroy EM, Drosten C. 2012. Bats host major mammalian paramyxoviruses. *Nature Comm.* 3:796.

Drexler JF, Corman VM, Müller MA, Lukashev AN, Gmyl A, Coutard B, Adam A, Ritz D, Leijten LM, van Riel D, Kallies R, Klose SM, Gloza-Rausch F, Binger T, Annan A, Adu-Sarkodie Y, Oppong S, Bourgarel M, Rupp D, Hoffmann B, Schlegel M, Kümmerer BM, Krüger DH, Schmidt-Chanasit J, Setién AA, Cottontail V, Hemachudha, T, Wacharapluesadee S, Osterrieder K, Bartenschlager R, Matthee S, Beer M, Kuiken T, Reusken C, Leroy EM, Ulrich RG, Drosten C. 2013. Evidence for novel hepaciviruses in rodents. *PLoS Pathog.* **9(6)**:e1003438.

Efford M. 2004. Density estimation in live-trapping studies. *Oikos* 106:598-610.

Efford MG, Borchers DL, Byrom AE. 2009. Density estimation by spatially explicit capture-recapture:likelihood-based methods, in: Cooch EG, Hompson DL, Onroy MJ, editors. Modelling demographic processes in marked populations. *Springer, New York,* pp. 255-69.

Efford MG, Fewster RM, 2012. Estimating population size by spatially explicit capture-recapture. *Oikos* DOI: 10.1111/j.1600-0706.2012.20440.x

Ehlers B, Küchler J, Yasmum N, Dural G, Voigt S, Schmidt-Chanasit J, Jäkel T, Matuschka FR, Richter D, Essbauer S, Hughes DJ, Summers C, Bennett M, Stewart JP, Ulrich RG. 2007. Identification of novel rodent herpesviruses, including the first *Gammaherpesvirus* of *Mus musculus*. *J Virol.* 81(15): 8091-100.

Frank F. 1957. The causality of microtine cycles in Germany. *J. Wildl. Manag.* 21:113-121.

Gelling M, Macdonald DW, Telfer S, Jones T, Brown K, Birtles R, Mathews F. 2011. Parasites and

pathogens in wild populations of water voles (*Arvicola amphibius*) in the UK. *Eur. J. Wildl. Res.* 58:615-619.

Gippoliti S. 2012. The name of the Italian water vole *Arvicola* cf. *amphibius* (Linnaeus, 1758). *Hystrix, the Italian J. Mammal.* 23:1-3.

Giraudoux P, Delattre P, Habert M, Quéré JP, Deblay S, Defaut R, Duhamel R, Moissenet MF, Salvi D, Truchetet D. 1997. Population dynamics of fossorial water vole (*Arvicola terrestris scherman*): a land use and landscape perspective. *Agriculture, Ecosystems and Environment* 66:47-60.

Glue DE. 1974. Food of the Barn owl in Britain and Ireland. Bird Study. 21:200-213.

Halle S. 1993. Wood mice (*Apodemus sylvaticus* L.) as pioneers of recolonization in a reclaimed area. *Oecologica* 94:120-127.

Hansen F, Jeltsch F, Tackmann K, Staubach C, Thulke HH. 2004. Processes leading to a spatial aggregation of *Echinococcus multilocularis* in its natural intermediate host Microtus arvalis. *Int J Parasitol* 34:37-44.

Hanski I, Hansson L, Henttonen, H**.** 1991. Specialist predators, generalist predators, and the microtine rodent cycle. *J. Anim. Ecol.* 69, 353-367. Hanski I, Henttonen H, Hansson L. 1994. Temporal variability of population density in microtine rodents: a reply to Xia and Boonstra. *American Naturalist* 144:329-342. Hanski I, Henttonen H, Korpimäki E, Oksanen L, Turchin P. 2001. Small rodent dynamics and predation. *Ecology* 82:1505-1520.

Hansson L, Zejda J. 1977. Plant Damage by Bank Voles (*Clethrionomys glareolus* [Schreber]) and Related Species in Europe. EPPO Bulletin. 7:223–242.

Hansson, L. 1985. The food of bank voles, wood mice and yellow-necked mice. *Symp. zool. Soc. Lond*. 55:141-168.

Hasler N, Klette R, Rosenhahn B, Agnew W. 2004. Footprint recognition of rodents and insects. In: Image and Vision Computing 2004 (Ed. by D. Pariman, H. North and S. McNeill). pp.167-172. Landcare Research Ltd. Akaroa, New Zealand.

Haynes S, Jaarola M, Searle JB. 2003. Phylogeography of the common vole (*Microtus arvalis*) with particular emphasis on the colonization of the Orkney archipelago. *Molecular Ecology* 12: 951-956.

Heise S, Wieland H. 1993. Zu den Methoden der Abundanzbestimmung bei Feldmauspopulationen als Grundlage eines umweltgerechten Pflanzenschutzes. *Nachrichtenbl*. *Deutsch. Pflanzenschutzdienst* 43:30-33.

Hejlicek K, Literak I. 1998. Long-term study of *Toxoplasma gondii* prevalence in small mammals (Insectivora and Rodentia). *Folia Zool.* 47:93-102. Henttonen H, Oksanen T, Jortikka A, Haukisalmi V. 1987. How much do weasels shape microtine cycles in the northern Fennoscandian taiga? *Oikos* 50:353-365. Hubálek Z, Scholz HC, Sedláček I, Melzer F, Sanogo YO, Nesvadbová J. 2007. Brucellosis of the Common Vole (*Microtus arvalis*). *Vector-borne and Zoonotic Diseases* 7(4): 679-688.

Hubbs AH, Karels T, Boonstra R. 2000. Indices of population size for burrowing mammals. *J. Wildl. Manage.* 64:296-301.

Jacob J, Hempel N. 2003. Effects of farming practices on spatial behaviour of common voles. *Journal of Ethology* 21:45-50.

Jacob J. 2008. The response of small rodents to manipulations of vegetation height in agro-ecosystems. *Journal of Integrated Zoology* 3:3–10.

Jacob J, Tkadlec E. 2010. Rodent outbreaks in Europe: dynamics and damage. In 'Rodent Outbreaks – Ecology and Impacts'. (Eds G. R. Singleton, S. Belmain, P. R. Brown and B. Hardy.) pp. 207–223. (International Rice Research Institute: Los Baños, Philippines.).

Jacob J, Manson P, Barfknecht R, Fredricks T. 2014. Common vole (Microtus arvalis) ecology and management: implications for risk assessment of plant protection products. *Pest management science* 70:769-878.

Kinnunen PM, Henttonen H, Hoffmann B, Kallio ER, Korthase C, Laakkonen J, Niemimaa J, Palva A, Schlegel M, Ali HS, Suominen P, Ulrich RG, Vaheri A. Vapalahti O. 2011. Orthopox virus infections in Eurasian wild rodents. *Vector-Borne and Zoonotic Diseases* 11:1133-1140.

Klempa B, Krüger DH, Auste B, Stanko M, Krawczyk A, Nickel, KF, Uberla K, Stang A. 2009. A novel *cardiotropic murine adenovirus* representing a distinct species of *mastadenoviruses*. *J Virol.* 83(11):5749-59.

Klempa B, Avsic-Zupanc T, Clement J, Dzagurova TK, Henttonen H, Heyman P, Jakab F, Kruger, DH, Maes P, Papa A, Tkachenko, EA, Ulrich RG, Vapalahti O, Vaheri A. 2013. Complex evolution and epidemiology of Dobrava-Belgrade hantavirus: definition of genotypes and their characteristics. *Arch Virol.* 158(3):521-529.

Korpela K, Helle P, Henttonen H, Korpimäki E, Koskela E, Ovaskainen O, Pietiäinen H, Sundell J, Valkama J, Huitu O. 2014. Predator-vole interactions in boreal Europe: the role of small mustelids revised. Proc. R. Soc. B 281. 20142119. http://dx.doi.org/10.1098/rspb.2014.2119

Kuiken T, van Dijk JE, Terpstra WJ, Bokhout BA. 1991. The role of the common vole (*Microtus arvalis*)

in the epidemiology of bovine infection with *Leptospira interrogans* serovar hardjo. *Vet Microbiol.* 28(4):353-361.

Lambin X, Petty SJ, Mackinnon JL. 2000. Cyclic dynamics in field vole populations and generalist predation. *J. Anim. Ecol.* 69:106-118.

Lidicker Jr, WZ. 1973. Regulation of numbers in an island population of the California vole, a problem in community dynamics. *Ecological Monographs* 73:271-302.

Liro A. 1974. Renewal of burrows by the common vole as the indicator of its numbers. Acta *Theriologica* 19:259-272.

Lisicka L, Losik J, Zeijd J, Heroldov M, Nesvadbov J, Tkadlec E. 2007. Measurement error in a burrow index to monitor relative population size in the common vole. *Folia Zoologica* 56:169-176.

Love RA, Webbon CC, Glue DE, Harris S. 2000. Changes in the food of British Barn Owls (*Tyto alba*) between 1974 and 1997. *Mammal Review* 30:107-129.

Meerburg BG, Singleton GR, Kijlstra A. 2009. Rodent-borne diseases and their risks for public health. *Crit Rev Microbiol.* 35(3):221-270.

Michaux JR, Libois R, Filippucci M-G. 2005. So close and so different: comparative phylogeography of two small mammal species, the Yellow-necked fieldmouse (*Apodemus flavicollis*) and the Woodmouse (*Apodemus sylvaticus*) in the Western Palaearctic region. *Heredity* 94:52-63.

Mitchell-Jones AJ, Amori G, Bogdanowicz W, Kryštufek B, Reijnder PJH, Spitzenberger F, Stubbe, M, Thissen JBM, Vohraík V, Zima J. 1999. The Atlas of European Mammals. T & AD Poyser LTD London.

Mörner T, Addison E, 2001. Tularemia. In: Williams ES, Barker IK.: Infectious diseases of wild mammals, 3rd Ed. Iowa State University Press, Ames, Iowa, pp. 303-312.

Niethammer J, & Krapp F. 1978. Handbuch der Säugetiere Europas. Bd. 1: Nagetiere I. – 476 S.; Wiesbaden (Akademische Verlagsgesellschaft).

Parmenter RR, Yates TL, Anderson DR, Burnham KP, Dunnum JL, Franklin AB, Friggens MT, Lubow BC, Miller M, Olson GS, Parmenter CA, Pollard J, Rexstad E, Shenk TM, Stanley TR, White GC. 2003. Small-mammal density estimation: a field comparison of grid-based vs. web-based density estimations. Ecological Monographs, 73(1):1-26.

Phan TG, Kapusinszky B, Wang C, Rose RK, Lipton HL, Delwart EL. 2011. The Fecal Viral Flora of Wild Rodents. *PLoS Pathog* 7(9), e1002218.

Pita R, Mira A, Beja P. 2011. Assessing habitat differentiation between coexisting species: The role of spatial scale. *Acta Oecologica* 37:124-132.

Pledger S, Efford M. 1998. Correction of bias due to heterogeneous capture probability in capture-recapture studies of open populations. *Biometrics* 54:888-898.

Proulx G. 1997. A preliminary evaluation of four types of traps to capture northern pocket gophers, Thomomys talpoides. *Canadian Field-Naturalist* 111:640-643.

Radda A, Pretzmann G, Steiner HM. 1969. Bionomische und ökologische Studien an österreichischen Populationen der Gelbhalsmaus (*Apodemus flavicollis*, Melchior, 1834) durch Markierungsfang. *Oecologica* 3:351-373.

Redpath CJ, Thirgood SJ, Redpath SM. 1995. Evaluation of methods to estimate field vole abundance in the uplands. *Journal of Zoology* 237:49-57.

Rigaux P, Vaslin M, Noblet JF, Amori G, Palomo LJ. 2008. *Arvicola sapidus*. In: IUCN 2012. IUCN Red List of Threatened Species.

Ruibal M, Peakall R, Claridge A, Murray A, Firestone K. 2010. Advancement to hair-sampling surveys of a medium-sized mammal: DNA-based individual identification and population estimation of a rare Australian marsupial, the spotted-tailed quoll (*Dasyurus maculatus*). *Wildlife Research* 37:27-38.

Sargent G, Morris P. 2003. How to Find and Identify Mammals. The Mammal Society, London.

Schlegel, M., Kindler, E. Essbauer, S.S., Wolf, R., Thiel, J., Groschup, M.H., Heckel, G., Oehme, R.M., Ulrich RG. 2012. Tula virus infections in the Eurasian water vole in Central Europe. *Vector Borne Zoonotic Dis.* 12(6):503-513.

Schmidt-Chanasit J, Essbauer S, Petraityte R, Yoshimatsu K, Tackmann K, Conraths FJ, Sasnauskas K, Arikawa J, Thomas A, Pfeffer M, Scharninghausen JJ, Splettstoesser W, Wenk M, Heckel G, Ulrich RG. 2010. Extensive host sharing of Central European Tula virus. *Journal of Virology* 84: 459-474.

Schmidt S, Haupt W, Ribbeck R. 1998. Capillaria hepatica - ein seltener Zoonose-Erreger. Vorkommen bei Mäusen. Tropenmed. *Parasitol.* 20:131 - 136.

Schmidt S, Essbauer SS, Mayer-Scholl A, Poppert S, Schmidt-Chanasit J, Klempa B, Henning K, Schares G, Groschup MH, Spitzenberger F, Richter D, Heckel G, Ulrich RG. 2014. Multiple infections of rodents with zoonotic pathogens in Austria. *Vector Borne Zoonotic Dis.* 14:467-475.

Scholz HC, Hubalek Z, Sedlácek I, Vergnaud G, Tomaso H, Al Dahouk S, Melzer F, Kämpfer P, Neubauer H, Cloeckaert A, Maquart M, Zygmunt MS, Whatmore AM, Falsen E, Bahn P, Göllner C, Pfeffer M, Huber B, Busse HJ, Nöckler K. 2008. *Int J Syst Evol Microbiol.* 58(2):375-382.

Schulz E, Gottschling M, Ulrich RG, Richter D, Stockfleth E, Nindl I. 2012. Isolation of three novel rat and mouse papillomaviruses and their genomic characterization. *PLoS One* 7 (10), e47164.
Schwarz CJ, Seber GAF. 1999. Estimating animal abundance: review III. Statistical Science, 14:427-456.
Seber GAF. 1965. A note on the multiple-recapture census. *Biometrica* 52:249-259.
Seber GAF. 1986. A Review of Estimating Animal Abundance. *Biometrics* 42:267-92.
Sibbald S, Carter P, Poulton S. 2006. Proposal for a National Monitoring Scheme for Small Mammals in the United Kingdom and the Republic of Eire. The Mammal Society Research Report No. 6.
Smal CM, 1987. The diet of the Barn Owl *Tyto alba* in southern Ireland, with reference to a recently introduced prey species the Bank Vole *Clethrionomys glareolus*. Bird Study, 34(2):113-125.
Southwood TRE, Henderson P. 2000. Ecological Methods. Blackwell Science 3rd Ed. Oxford.
Spitzenberger F. 2001. Die Säugetierefauna Österreichs, 13th Ed. Gratz: Bundesministerium für Land- und Forstwirtschaft Umwelt und Wasserwirtschaft.
Stenseth NC, et al. 2002. Population dynamics of *Clethrionomys glareolus* and *Apodemus flavicollis*: seasonal components of density dependence and density independence." *Acta Theriologica* 47.1: 39-67.
Tadin A, Turk N, Korva M, Margaletić J, Beck R, Vucelja M, Habuš J, Svoboda P, Zupanc A, Henttonen H, Markotić A. 2012. Multiple co-infections of rodents with hantaviruses, Leptospira, and Babesia in Croatia. *Vector Borne Zoonotic Dis.* 12(5):388-392.
Tersago K, Verhagen R, Servais A, Heyman P, Ducoffre G, Leirs H. 2009. Hantavirus disease (nephropathia epidemica) in Belgium: effects of tree seed production and climate. *Epidemiol Infect.* 137(2):250-256.
Tew TE, Todd IA, Macdonald DW. 2000. Arable habitat use by wood mice (Apodemus sylvaticus). 2. Microhabitat. *Journal of Zoology* 250(3):305-311.
Tkadlec E, Zejda J. 1995. Precocious breeding in female common voles and its relevance to rodent fluctuations. *Oikos* 73:231-236.
Ulrich RG, Heckel G, Pelz HJ, Wieler LH, Nordhoff M, Dobler G, Freise J, Matuschka FR, Jaco, J, Schmidt-Chanasit J, Gerstengarbe FW, Jäkel T, Süss J, Ehlers B, Nitsche A, Kallies R, Johne R, Günther S, Henning K, Grunow R, Wenk M, Maul LC, Hunfeld KP, Wölfel R, Schares G, Scholz HC, Brockmann SO, Pfeffer M, Essbauer SS. 2009. [Rodents and rodent associated disease vectors: the network of "rodent carrying pathogens" introduces itself]. *Bundesgesundheitsblatt Gesundheitsforschung Gesundheitsschutz* 52(3):352-69.
Village A, Myhill D. 1990. Estimating small mammal abundance for predator studies - snap trapping versus sign indexes. *Journal of Zoology* 222:681-689.
Wilkinson SAJ, Craze PG, Harris S. 2004. Monitoring field vole (*Microtus agrestis*) in lowland Britain. In: Society, T.M. (Ed.), The Mammal Society research report No.4, London.
Wilson DE, Reeder DAM. (Eds.). 2005. Mammal species of the World: a taxonomic and geographic reference. 3rd Ed. Vol. II. Johns Hopkins University Press, 2:142 pp.
Wójcik JM, Wołk K. 1985. “The daily activity rhythm of two competitive rodents: Clethrionomys glareolus and Apodemus flavicollis." *Acta Theriologica* 30.9-20:241-258.

Tables

See next page.

Table 1. Peculiarities of the species that modulate the methods to be used.

Characteristic	Observations
Distribution	All species have wide distributional ranges (see descriptions under point 1). Special care has to be taken when considering populations of *A. sylvaticus* and *A. flavicollis*. Both have overlapping distribution and share many morphological characteristics (Michaux et al., 2005). For example, a gradient in the visibility of the characteristic yellow collar of *A. flavicollis* is known from north to south (Niethammer & Krapp, 1978). In regions with close resemblance, species determination in the field solely based on fur colour could be misleading. *Arvicola sapidus* and *Arvicola amphibius* only have regionally overlapping ranges and can be distinguished morphologically.
Population trends	Care should be taken when populations are locally endangered. In such cases live trapping or sign indices need to have priority. Although most species in this group are not threatened, local habitat modification can lead to increased fragmentation of isolated subpopulations, threatening populations in the long term. This holds especially true for *A. sapidus* and the aquatic ecotype of *A. amphibius* in Great Britain. The decline of wetland habitat in its distributional range has led to a marked reduction in total abundance and *A. sapidus* populations are consequently classified as vulnerable under IUCN (Rigaux et al., 2008).
Density range	Populations of all species in this review fluctuate considerably temporally as well as spatially. During high abundances, species can spread from refuges to a variety of adjacent areas where food and habitat can be found (*A. amphibius* in crops, orchards; *M. arvalis* in annual crops). *M. arvalis* typically invades annual crop fields from nearby refuges during outbreaks. Generally, during low abundance sign indices are an easy way to identify potential refuges where then more sophisticated methods can be applied. All suggested methods in section 3 are highly dependent on target species density (Parmenter, 2003; Lisicka et al., 2007). Especially, density estimates from live trapping are often precluded or produces misleading results when few individuals are captured and recaptured. Species of generally low abundance (*A. sapidus* or the amphibious ecotype of *A. amphibius*) are consequently susceptible to density estimation errors.
Main habitat	Predominantly woodland species (*M. glareolus, A. sylvaticus, A., flavicollis*) often preclude the use of sign indices (activity, grass clipping, droppings etc.) due the irregular composition of the forest floor often depending on soil type and dominant tree species.
Introduction-Releases	No releases affecting abundance estimation are known.
Activity rhythms	Most species in this group show polyphasic, short-termed activity patterns of several hours. These rhythms seem to be dusk/dawn-locked (Daan and Slopsema, 1978).
Detectability	Detectability is dependent on multiple extrinsic and intrinsic factors. For all species a rough estimate of general home range sizes has to form the basis for calculating the optimal trapping area and trap spacing. These can vary substantially, ranging from <100m^2 for *M. arvalis* (Jacob & Hempel 2003) to up to 22,000m^2 for *A. flavicollis* (Radda et al., 1969). For grassland species (e.g. *M. arvalis*) vegetation height is critical as short vegetation has been shown to reduce activity (Jacob, 2008). *Arvicola* generally requires larger traps compared to smaller species as small traps would preclude entrance. In live-trapping studies *Arvicola* spec. might be reluctant to enter above-ground traps due to the strict fossorial lifestyle. To increase trapping success live traps can be inserted into excavated burrow systems (see review by T Prolux (1997). This is however labour intensive, only suitable for small scale studies and needs to be considered carefully.

Table 2. Classification of the different methods (all cited in this species' review, incl. the recommended method(s) for most accurate results) based on desirable characteristics for monitoring populations from an epidemiological perspective (1- very low, 5-very high). ***Superscript numbers associated with method describe the suitability of that particular method for the corresponding species (*[1]*=Microtus arvalis;* [2]*=Myodes glareolus;* [3]*=Apodemus* **spp.***;* [4]*=Arvicola* **spp.).**

Method	**Gold standard**[1,2,3,4]	**Snap-trapping**[1,2,3,4]	**Active burrow counts**[1,4]	**Owl pellet analysis**[1,2,3]	**Field signs**[1,4]
Abundance / **D**ensity	A/D	A/D	A/D	A	A
Temporal / **S**patial trends	T/S	T/S	T/S	T	T/S
Info on population structure (**Y**/**N**)	4	4	3	?	?
Precision	4	3	2	2	2
Seasonal independence	4	3	2	2	2
Visibility independence	5	5	5	5	5
Effort effectiveness	2	3	4	3	4
Budget effectiveness					
Ease of learning	2	4	5	3	5
Applicable at large scales	2	3	5	4	
Useful at very low density	3	4	3	?	?
Useful at very high density	4	4	4	?	?