

Recovery of small rodent populations after population collapse

S. Hein^{A,B,C} and J. Jacob^A

^AJulius Kühn Institute, Federal Research Centre for Cultivated Plants, Institute for Plant Protection in Horticulture and Forests, Toppeheideweg 88, 48161 Muenster, Germany.

^BWestphalian Wilhelms University, Institute for Landscape Ecology, Heisenbergstraße 2, 48149 Muenster, Germany.

^CCorresponding author. Email: susanne.hein@jki.bund.de

Abstract In this review we summarise published knowledge regarding small mammal population recovery following sudden population collapse, regardless as to whether the collapse is caused by natural or man-made events. We determine recovery mechanisms, recovery time and recovery rate, and suggest how to adapt and optimise current methods to regulate small mammal population size, for pest management and/or conservation. It is vital that the principles underlying the recovery mechanisms are known for both pest control and conservation to align management methods to either maintain animal numbers at a permanent minimum level or increase population size. Collapses can be caused naturally, as in the declining phase of multi-annual fluctuations and after natural disasters, or by man-made events, such as pesticide application. In general, there are three ways population recovery can occur: (1) *in situ* survival and multiplication of a small remaining fraction of the population; (2) immigration; or (3) a combination of the two. The recovery mechanism strongly depends on life history strategy, social behaviour and density-dependent processes in population dynamics of the species in question. In addition, the kind of disturbance, its intensity and spatial scale, as well as environmental circumstances (e.g. the presence and distance of refuge areas) have to be taken into account. Recovery time can vary from a couple of days to several years depending on the reproductive potential of the species and the type of disturbances, regardless of whether the collapse is man made or natural. Ultimately, most populations rebound to levels equal to numbers before the collapse. Based on current knowledge, case-by-case decisions seem appropriate for small-scale conservation. For pest control, a large-scale approach seems necessary. Further investigations are required to make sound, species-specific recommendations.

Additional keywords: conservation, migration, pest control, pest management, re-colonisation, rodenticides.

Received 14 August 2014, accepted 30 January 2015, published online 20 March 2015

Introduction

Small mammal communities are vital components of ecosystems worldwide (Zhang *et al.* 1998; Singleton *et al.* 2003; Jacob *et al.* 2014). They play an important role in food webs (Halle 1993b) and in the ecosystem per se, such as providing shelter for other animals that use old and abandoned burrow systems (Martin 2003). Sometimes, small rodent populations are classified as pests because they destroy agricultural crops (Jacob and Tkadlec 2010) and transfer diseases to humans and livestock (Pikula *et al.* 2002; Sinski *et al.* 2006; Jacob *et al.* 2008; Gassner *et al.* 2013). In addition, they can cause damage to infrastructure, such as gnawing on cables or digging burrow systems (Jacob and Tkadlec 2010), leading to further costs. Thus, it is sometimes challenging to keep the population density of the pest species down for human interests while sustaining the function of the pest species in the ecosystem (Aplin and Singleton 2003).

Relevance of population recovery for pest control and conservation

Population recovery is of interest for both sustainable pest control and conservation. In ecologically based rodent management

(EBRM) and other integrated pest management (IPM) systems, it is important to base pest control methods on sound ecological knowledge (Singleton *et al.* 2007) to ensure a reasonable balance between fighting pest species and adverse effects on ecosystems. To this end, information about population recovery is vital to develop an appropriate and practical approach for both pest control and conservation.

The abundance of small mammal populations fluctuates among seasons and, for several species living in temperate climatic regions, follows multi-annual cycles (Elton 1924; Lambin *et al.* 2006). There are many examples of cyclic mammal populations, including snowshoe hares (*Lepus americanus*; Ims *et al.* 2008), voles (Korpimäki *et al.* 2003) and shrews (Zub *et al.* 2012).

There can be many reasons for population collapse (sudden declines to minimal population abundance). Natural collapses include the decline phase of multi-annual population cycles (Korpimäki *et al.* 2004). Moreover, natural disasters, such as floods (Jacob 2003a; Zhang *et al.* 2007), severe droughts (Bradley *et al.* 2006), earthquakes (Zhang *et al.* 2011), wildfires (Lindenmayer *et al.* 2005; Banks *et al.* 2011) and volcanic eruptions (MacMahon *et al.* 1989), can cause rapid population

declines. Finally, human actions, including pest control, can markedly reduce population size in a short time.

Population decline for pest control

Rodent pest species can cause tremendous crop losses, with substantial monetary losses, worldwide. In Australia, the house mouse (*Mus domesticus*) is known to be the main rodent pest species causing monetary losses of up to AU\$60 million during outbreaks (Brown and Singleton 2000). In addition, African farmers have to deal with crop losses caused by several species, including the multimammate mouse (*Mastomys natalensis*; Stenseth *et al.* 2003). In Asia, rice field rats (*Rattus argentiventer*) have been reported as one of the most important pest species (Stenseth *et al.* 2003; Brown *et al.* 2006; Jacob *et al.* 2010). Crop losses of only 6% in South-east Asia amount to several million tonnes of food, which is enough to feed the entire population of Indonesia for 1 year (Singleton 2003). South American farmers are battling leaf-eared mice (*Phyllotis darwini*) in particular, whereas in North America they strive to control pocket gophers (*Thomomys talpoides*), especially in orchards (Engeman and Campbell 1999; Sullivan *et al.* 2001). In Europe, the common vole (*Microtus arvalis*) is one of the most important agricultural vertebrate pest species (Jacob 2013) and can cause tremendous crop losses during multi-annual outbreaks. The latest outbreak in 2012 affected approximately 500 000 ha, resulting in crop losses in excess of €100 million (Barten and Lauenstein 2013).

There are a few substances that are authorised for use as rodenticides to protect plants in the European Union, including aluminium phosphide, bromadiolone, calcium phosphide, carbon dioxide, difenacoum, magnesium phosphide and zinc phosphide (see http://ec.europa.eu/sanco_pesticides/public/?event=activesubstance.selection, accessed 18 February 2015). In Germany, zinc phosphide (Zn_2P_3) is the only acute poison authorised for use as a rodenticide for outdoor plant protection. Its use is limited to one application per crop per year and is associated with other restrictions, such as burrow baiting to minimise bait uptake by non-target species. Application usually occurs before the start of the reproduction period for the small mammals to minimise the founder population. Although the use of rodenticides is generally allowed, restrictions can make it costly and difficult to use them at an appropriately large scale, despite important management targets, such as the protection of crops, public health and infrastructure.

The underlying goal for agricultural pest management is not to extirpate a species, but to control its numbers to a level where crop damage is acceptable. This requires a sound ecological knowledge of population dynamics, development and demographics to develop an appropriate approach. Naturally, this should include the aspect of recovery from population collapse. However, the issue of population recovery is rarely considered in great detail in pest rodent control (Jacob *et al.* 2014). This is in contrast with population collapses of bird and fish species after human-driven population declines, which have been studied in considerable detail (Myers *et al.* 1997; Fabrizio *et al.* 2001; Esler *et al.* 2002).

Population decline for conservation

As part of globalisation, the introduction of invasive species can lead to the replacement of native species in many places, flora

as well as fauna. Some species became endangered due to landscape modification and fragmentation, habitat destruction and general pollution of their ecosystems (Nakagiri *et al.* 2001; Ceballos and Ehrlich 2002; Woinarski *et al.* 2011; Pita *et al.* 2014). In this regard, knowledge of the recovery mechanisms of threatened populations can be used to understand and support their recovery, and to help preserve wildlife and habitat permanently, because it is sometimes necessary to promote recovery following unwanted population collapse. Only a few studies have specifically dealt with population recovery for conservation reasons. Some of these studies focused on ecological research, which was then used to support species recovery (e.g. by providing suitable habitat (Smith *et al.* 2014) or eradicating non-native predator species (Witmer *et al.* 2007b)). The eradication of non-native predator species includes the use of rodenticides for conservation reasons (Witmer *et al.* 2007a).

Knowledge of the mechanisms of population recovery of endangered species helps identify possible factors that can prevent the recovery of a population, such as predator pressure (Sinclair *et al.* 1998), invasive species (Witmer *et al.* 2007b), loss of habitat or shelter (Fahrig 2001) and landscape fragmentation (Diffendorfer *et al.* 1995; Smith *et al.* 2014). Extensive studies have evaluated the recovery of bird and fish species after population declines in response to man-made disasters, such as after the Exxon Valdez oil spill in 1989 and after the explosion of the oil platform Deepwater Horizon in 2010, which polluted the Atlantic ocean (Esler *et al.* 2002; Bradley *et al.* 2006). In addition, several studies have investigated the regeneration of fish species after overfishing (Myers *et al.* 1997; Fabrizio *et al.* 2001; Fu *et al.* 2001). In contrast, studies on the population recovery of small rodents after the application of rodenticide are rare and have not been reviewed, apart from that of Shilova and Tchabovsky (2009) for Russia and the former USSR.

However, from a pest control point of view and for population conservation, the population recovery of rodent species is highly relevant. Therefore, it seems sensible to collate what has been published so far about the process of recovery, including recovery time and the rate of recovery of small mammal populations, to derive the principle mechanisms of recovery for small mammals in general (Engeman and Campbell 1999; Sullivan *et al.* 2001). This knowledge may help us adapt management strategies for both rodent control and conservation, to maintain an appropriate population size.

Types of collapses

Natural collapses do occur, such as crashes in rodent populations after multi-annual outbreaks (Krebs *et al.* 1973; Lambin *et al.* 2000; Klemola *et al.* 2002; Table 1). Although those population cycles were described scientifically almost a century ago (Elton 1924), their fundamental principles remain contentious (Boonstra *et al.* 1998; Oli 2003; Korpimäki *et al.* 2004; Lambin *et al.* 2006). The two most popular theories claim that multi-annual population cycles rely on predator–prey relationships and density-dependent population dynamics (Stenseth *et al.* 1996; Butet and Spitz 2001; Andreassen *et al.* 2013).

Other natural population collapses are caused by natural disasters resulting in a marked sudden decline in wildlife. These natural disasters include flooding, bush fire, volcanic

Table 1. Type of population collapses

Summary of different types of sudden population collapses of vertebrates included in this review. Causes for the collapses are divided into the two main categories: man-made and natural causes

Population collapse	References
Man-made	
Intended (pest control)	Emlen <i>et al.</i> (1948), Hamar and Tuta (1971), Knowles (1986), Kamarudin <i>et al.</i> (1991), Engeman and Campbell (1999), Zhang <i>et al.</i> (2004), Brakes and Smith (2005), Brown <i>et al.</i> (2002); Shilova and Tchabovsky (2009)
Unintended (oil spill)	Esler <i>et al.</i> (2002), Parker and Wiens (2005)
Natural	
Regular (multi-annual fluctuations and/or natural decline)	Boonstra (1994), Krebs <i>et al.</i> (1976), Cornulier <i>et al.</i> (2013), Westemeier <i>et al.</i> (1998)
Irregular	
Fire	Vacanti and Geluso (1985), Friend (1993), Sutherland and Dickman (1999), Letnic <i>et al.</i> (2004), Banks <i>et al.</i> (2011)
Drought	Bradley <i>et al.</i> (2006)
Flood	Jacob (2003a), Zhang <i>et al.</i> (2007), Golet <i>et al.</i> (2013)
Volcanic eruption	MacMahon <i>et al.</i> (1989)

eruptions and (with a longer lead time) severe drought (Table 1). Diseases can also cause sudden population collapses. Well-known examples of such crashes are the decline in the honey bee (*Apis mellifera*) population caused by varroa mites (*Varroa destructor*; Le Conte *et al.* 2010; Borsuk *et al.* 2012), the decline in amphibians caused by fungi (Mutschmann *et al.* 2000) and the effect of the plague bacterium (*Yersinia pestis*) on the human population (Butler 2013). Collapses in the rodent population due to disease have been reported for Norwegian rats (*Rattus norvegicus*) following infection with plague-transferring rat fleas (*Xenopsylla cheopis*; Perry and Fetherston 1997); this also occurs in great gerbils (*Rhombomys opimus*) as a major reservoir host species (Samia *et al.* 2011) in Asia, *Rattus rattus* in Madagascar (Andrianaivoarimanana *et al.* 2013) and black-tailed prairie dogs in the USA (George *et al.* 2013). Usually, the rodent hosts die, leading to delayed population collapses (St. Romain *et al.* 2013). Nevertheless, diseases are not frequently reported as a cause of major sudden population collapse and so are not further considered in this review.

Human activity can also cause populations to collapse (Table 1). This activity can include intentional management actions (e.g. culling for pest control) or unintended events. With regard to pest control, it is also important to identify the pest control strategy used (e.g. fertility or lethal control, long- or short-term actions), because this will influence recovery and, in particular, recovery time in different ways (Zhang 2000; Liu *et al.* 2012). Successful culling can result in population reductions of >95% (Singleton *et al.* 2007). In many cases it is not the magnitude of the reduction in population size that matters for pest control, but rather maintaining population numbers below a certain damage threshold (Singleton *et al.* 2007).

Accidents may lead to large-scale pollution of ecosystems, such as the *Exxon Valdez* oil spill in 1989, which resulted in a 2000-km² coastal area polluted with oil. Such disasters can be associated with major declines in vertebrate populations. For example, 13 years after the *Exxon Valdez* disaster, some bird species were still in the process of recovery (Esler *et al.* 2002). Studies on mammals are limited to large species of marine ecosystems, such as seals and otters (Garrott *et al.* 1993; Frost *et al.* 1999; Peterson *et al.* 2003). There is little information

regarding the recovery of small rodent species after man-made accidents, although some studies have considered population declines caused by a combination of anthropogenic and natural effects (LoGiudice 2006; Smyser *et al.* 2012). However, these studies concluded that further research on synergistic effects is needed (LoGiudice 2006), and that site-specific management actions need to be taken into account when identifying reasons for population decline (Smyser *et al.* 2012).

Recovery mechanisms

In general, there are two basic mechanisms by which small mammal population recovery can occur after population collapse: (1) *in situ* survival followed by reproduction; and/or (2) immigration from adjacent untreated or unaffected areas into depopulated regions (Knowles 1986; Lindenmayer *et al.* 2005; Banks *et al.* 2011). A few studies have suggested that recovery also strongly depends on the species and particular life history strategy, as well as social behaviour (Gardmark *et al.* 2003; Shilova and Tchabovsky 2009).

Life history strategies affect population dynamics (Reznick *et al.* 2002) and are also likely to impact on population recovery after collapse. The two main life history strategies, namely r-selection and K-selection (MacArthur 1962; MacArthur and Wilson 1967; Pianka 1974; Fleming 1979), differ with regard to reproductive patterns and longevity. Those animals using r-selection reproduce rapidly, produce many offspring and colonise fast. They do not provide extensive parental care and their population density can undergo pronounced fluctuations (Fleming 1979; Reznick *et al.* 2002). In contrast, animals that use K-selection are characterised by small numbers of offspring, slow reproduction and high life expectancy. The population densities of animals using K-selection often correlate with habitat size, and their population density is mostly stable (Reznick *et al.* 2002).

With regard to these two life history strategies, it is assumed that there are also two different ways of recovery. Typical r-selection strategists would be expected to re-establish populations rather rapidly due to high reproduction rates of either survivors or immigrants from adjacent areas; K-selection strategists

would be expected to repopulate vacant habitat more slowly than r-selection strategists.

Interestingly, this does not seem to be the case. Instead, the results of empirical studies strongly suggest that social behaviour and density-dependent population response play an important role in the recovery mechanism (Shilova and Tchabovsky 2009). Species that use r-selection start forming social breeding units after a collapse in the population density. In case of sudden population collapses, this would imply that r-selection strategists would recover even faster if they immigrate into depopulated areas and form new breeding units, leading to high numbers of offspring in a short period of time (this is assuming that the depopulated area is inhabited by individuals of the same species that are willing to form breeding units; Getz *et al.* 1993, 2005).

Dispersal behaviour differs among small mammal species (Gaines and McClenaghan 1980; Greenwood 1980). Wood mice (*Apodemus sylvaticus*) show low territoriality and flexible home ranges (Tew and Macdonald 1994). In contrast, adult common voles are highly territorial and usually tend to stay in their home range (Jacob and Hempel 2003). Hence, the possibility of immigration after population collapse is higher for adult wood mice than for common voles because wood mice cover greater distances than common voles. Therefore, *A. sylvaticus* would be more likely to discover distant undisturbed areas to recolonise and recover than *M. arvalis* (Halle 1993a). However, common voles, despite being a territorial species, readily claim available space (Reichstein 1960) and it is believed that recovery in this species takes place via dispersing animals (Hamar and Tuta 1971). Thus, spatial scale and the availability of suitable habitat within reach also play an important role in population recovery.

It is challenging to predict a general mechanism for the recovery of rodent populations after a collapse because life history strategy, social behaviour and territoriality jointly affect recovery via the survival of residents or immigration. Additional factors, such as climate, food supply and species-specific population cycles, may also impact on the recovery mechanism.

Examples of recovery mechanisms

It was claimed that the mechanism of recovery after population control with rodenticides strongly depends on life history strategy and the social behaviour of the particular species (Shilova and Tchabovsky 2009). For example, the population responses of Mongolian gerbils (*Meriones unguiculatus*) and Midday gerbils

(*M. meridianus*) to pest control with rodenticides differs markedly even though these two species belong to the same genus (Shilova and Tchabovsky 2009; Table 2). The highly social group-living Mongolian gerbils form new breeding units after a population collapse, leading to rapid recolonisation due to intense reproduction and recruitment of young. However, the solitary Midday gerbils form new founder populations that consist primarily of dispersed young individuals. Populations of Midday gerbils start recovering from rodenticide treatment after 2 months and need 4–8 months until full recovery (Shilova and Tchabovsky 2009). The different mechanisms of recovery seem to result in differences in recovery time. Mongolian gerbils have been reported to recover within several weeks, although post-collapse density levels reached only 39% of the original population (Shilova and Tchabovsky 2009; Table 2).

Similar findings were reported in a study of a large depopulated area of approximately 3500 km² of burned habitat for two mammal species, namely the Australian bush rat (*Rattus fuscipes*) and the marsupial agile antechinus (*Antechinus agilis*; Banks *et al.* 2011). Both species recovered *in situ* rather than through recolonisation. These findings were supported by Lindenmayer *et al.* (2005), who found that *in situ* survival and recolonisation by remaining residents and their offspring of the r-selection strategists *Rattus fuscipes* were aided by their life history attributes, which ‘underpin rapid population recovery’ (Lindenmayer *et al.* 2005).

Species that have been associated with recovery via immigration include black-tailed prairie dogs (*Cynomys ludovicianus*; Knowles 1986) and grey squirrels (*Sciurus carolinensis*; Lawton and Rochford 2007), as well as several vole species, including meadow voles (*Microtus pennsylvanicus*; Basquill and Bondrup-Nielsen 1999), field voles (*M. agrestis*; Dalkvist *et al.* 2013) and common voles (Hamar and Tuta 1971).

A study conducted on recolonisation of open-forest landscape in Australia after disturbance by sand mining (Fox and Fox 1984) concluded that recovery of the observed species takes place via immigration. After sand mining and fire, house mice (*Mus musculus*) and New Holland mice (*Pseudomys novaehollandiae*) recolonised vacant habitat by dispersing individual sub-adult males and adult females, but not complete breeding units (Fox and Fox 1984). House mice were replaced by *P. novaehollandiae* after disturbance by fire, suggesting that the latter were simply faster to migrate (Fox and Fox 1984). However, it was pointed out that house mouse populations may have been in the decline phase of their multi-annual

Table 2. Examples of recovery strategies and recovery time after population collapse in small rodents

Species	Strategy	Recovery time	References
<i>Meriones unguiculatus</i>	<i>In situ</i> survival	Several weeks	Shilova and Tchabovsky (2009)
<i>Meriones meridianus</i>	Immigration	4–8 months	Shilova and Tchabovsky (2009)
<i>Rattus fuscipes</i>	<i>In situ</i> survival	2–3 years	Lindenmayer <i>et al.</i> (2005), Banks <i>et al.</i> (2011)
<i>Cynomys ludovicianus</i>	Immigration	5 years	Knowles (1986)
<i>Thomomys talpoides</i>	Immigration	6–12 months	Engeman and Campbell (1999), Sullivan <i>et al.</i> (2001)
<i>Sciurus carolinensis</i>	Immigration	10 weeks	Lawton and Rochford (2007)
<i>Microtus arvalis</i>	Immigration	10–15 days	Hamar and Tuta (1971)
<i>Microtus arvalis</i>	Immigration	2–3 years	Jacob (2003a)

population cycle while the New Holland mouse population was increasing. Nevertheless, the findings of the study suggested population recovery of *M. musculus* via immigration, which is consistent with their life history strategy and social behaviour (Fox and Fox 1984).

Norwegian rats (*R. norvegicus*) are r-selection strategists that experience density-dependent breakdown of social population structures (Telle 1966). Due to fast reproduction of survivors and immigrants *R. norvegicus* should recover rapidly as it was also shown for other *Rattus* species, such as Malayan field rats (*R. tiomanicus*) and buff-breasted rats (*R. flavipectus*; Kamarudin *et al.* 1991; Zhang *et al.* 2007). However, it has been suggested that another *Rattus* species, *R. fuscipes*, recover via immigration into adjacent depopulated areas (Lindenmayer *et al.* 2005).

Despite being the most important mammalian pest species in European agriculture (Jacob *et al.* 2014) and the frequent use of rodenticides to reduce population sizes to protect plants (Jacob *et al.* 2014), there is surprisingly little known about the recovery mechanisms of common vole populations after population collapse. In the only published study investigating this issue, it was assumed that common vole recovery takes place via immigration on the basis of the ratio of marked and unmarked dead animals in toxaphene-treated plots and untreated control sites (Hamar and Tuta 1971).

Adult common voles rarely leave or change their home range. Even agricultural activities, such as harvesting, mowing and ploughing (Jacob 2003b), and flooding (Stein 1958; Jacob 2003a) do not seem to force common voles away. In addition, common voles in suitable habitat can tolerate a high population density of at least 1300 individuals per hectare (Briner *et al.* 2005; Leukers *et al.* 2012). However, a lack of food due to extreme drought can lead to emigration of whole colonies into adjacent habitats (Stein 1958). Sub-adult common voles readily claim available habitat (Stein 1958; Reichstein 1960). These movements suggest that common vole recovery most likely takes place via immigration (Leukers and Jacob 2010). At high population densities, common vole females form breeding units with communal parental care (Stein 1958). Such behaviour would suggest a combination of the survival of residents and recruitment of immigrated young to achieve population recovery, because it is also known that female common voles adopt alien pups (Stein 1958). Similar nursing behaviour has been described for Norwegian rats (Meaney and Stewart 1981; Butler and Whelan 1994) and house mice (Jo Manning *et al.* 1995), so that recovery would be expected to take place also via improved survival and recruitment of young (own offspring and 'stranger' offspring; Hayes 2000).

Contrasting results were reported for Norwegian rat and house mouse populations, which recovered primarily via immigration from adjacent areas (Fox and Fox 1984; Kamarudin *et al.* 1991; Zhang *et al.* 2007). The same immigration pattern was observed in a study on *R. fuscipes* (Banks *et al.* 2011), indicating that the recovery mechanisms may differ within a species depending on the intensity of the disturbance and the disposition of the survivors. Therefore, it needs to be noted that behaviour is an important, but not the only, factor influencing recovery mechanisms in small mammals (Turner *et al.* 1998; Franklin *et al.* 2000).

Recovery time and rate

The time required to recover from population collapse depends on inter- and intraspecific differences, the degree of decline, the time of the year, life history attributes, recovery mechanism and spatial scale (Gardmark *et al.* 2003; Shilova and Tchabovsky 2009).

It takes approximately 2 years for a population of *R. fuscipes* to recover to pre-disturbance levels (Lindenmayer *et al.* 2005), whereas *R. tiomanicus* populations recovered within 6–9 months (Kamarudin *et al.* 1991) and 12–18 months (Wood and Liao 1984) after a poisoning campaign with anticoagulants.

All species listed in Table 2 rebounded to pre-treatment levels or numbers similar to those in the control group (Engeman and Campbell 1999; Lawton and Rochford 2007). The population density of *R. fuscipes* recovered to pre-treatment densities according to the patch-carrying capacity of the particular habitat (Lindenmayer *et al.* 2005), suggesting that recovery primarily occurred as a result of suitable habitat in immediate reach. However, the spatial extent of population collapse in that study was low compared with the study of Banks *et al.* (2011), where a wildfire severely burned 3500 km² of woodland and where environmental circumstances were more threatening to the population.

Populations of the black-tailed prairie dog (*C. ludovicianus*) need up to 5 years to recover from Zn₂P₃ application to pre-treatment levels, and this time is strongly dependent on habitat and treatment (Knowles 1986). For example, populations in an only partially treated area recovered 1 year after treatment as a result of dispersal from the untreated centre of the colony (Knowles 1986). Three other colonies recovered 2 years after treatment. These findings were supported by Garrett (1982), who found that black-tailed prairie dogs tend to naturally disperse into peripheral structures, such as field edge strips, concluding that recovery takes place via immigration into neighbouring populations. In addition, it was expected that for those populations that were locally extinct, it would take at least an additional 1 year for the population to recover (Knowles 1986).

Pocket gopher populations (*T. talpoides*) in a reforestation unit needed between 6 months and 1 year to recover to population levels similar to pre-treatment densities after application of rodenticide baits (Engeman and Campbell 1999). A similar study of reinvasion dynamics showed that pocket gophers recovered mostly via immigration (Sullivan *et al.* 2001). In addition, immigrating adult pocket gophers would reproduce despite further removal of animals (Sullivan *et al.* 2001), leading to fast recovery.

Fast recovery within 10 weeks of removal trapping was observed for populations of grey squirrels (*S. carolinensis*) in woodlands of Ireland and Britain (Lawton and Rochford 2007). A similarly fast recovery time was noted for Mongolian gerbils (*M. unguiculatus*) after 1 month, although density levels reached only 39% of the original population (Shilova and Tchabovsky 2009). Meadow voles (*M. pennsylvanicus*) recovered within 12–16 months after controlled burning in a tall-grass prairie (Vacanti and Geluso 1985).

In contrast, *M. arvalis* populations need 1.5–2 years to recover from population decline due to flooding (Jacob 2003a). However, fast recovery was observed within days after small-scale

insecticidal treatment with toxaphene (Hamar and Tuta 1971). The authors of the latter study reasoned that common vole populations only need 10–15 days to recover from the lethal side effects of toxaphene treatments.

However, it is vital to always consider the size of the study area in each study because spatial scale is an essential parameter in population recovery. If the study area is large, it will be longer until population recovery is achieved via recolonisation and/or survival and reproduction. There are insufficient data available in the literature to correlate the size of the study area with recovery time.

The r-selection strategists usually have a lower bodyweight than K-selection strategists (Fleming 1979). This can be used to relate bodyweight to recovery time to check for a general pattern in the duration of recovery time regarding life history strategy. Comparisons of published data of average bodyweight and recovery time reveal a positive relationship between these parameters (Fig. 1), indicating that there may be a correlation between recovery time and life history strategy. Nevertheless, the number of available data points is insufficient to robustly reveal relationships.

Environmental effects on recovery

The recovery of small mammal populations after collapse is also influenced by environmental circumstances, including seasonal population dynamics, habitat fragmentation, possible availability of refuge areas and predation pressure. In addition, the intensity of collapse is an important variable for small mammal population recovery.

Refuge areas

Refuge areas play an important role in the population recovery of small mammals because they offer individuals the opportunity to survive and then recolonise the former territory (Lindenmayer *et al.* 2005). This was shown for deer mice (*Peromyscus* spp.) in flooded areas, where deer mice used trees as refuge areas (Golet *et al.* 2013). The same seems to be the case for wood mice

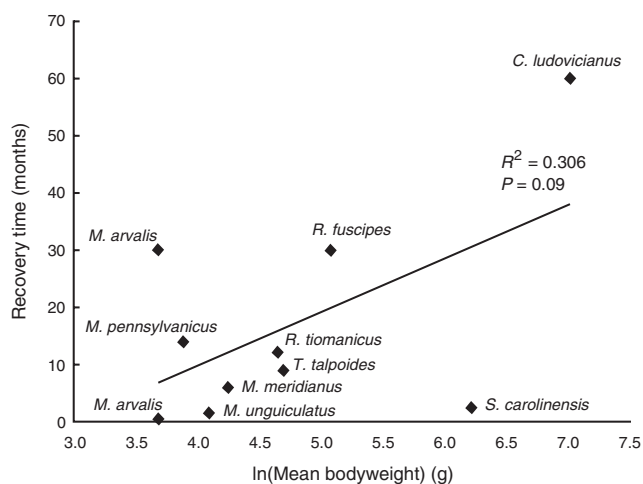


Fig. 1. Correlation between mean bodyweight and recovery time of nine small mammal species based on data presented in Table 2. Data points of mean bodyweight for each species have been log transformed.

(*A. sylvaticus*) and bank voles (*Myodes glareolus*) during flooding (Jacob 2003a; Golet *et al.* 2013). However, trees only provide refuge for species that are able to climb. Consequently, *Microtus montanus* (Andersen *et al.* 2000) and *M. arvalis* populations (Jacob 2003a) die off during flooding events, despite the presence of nearby trees.

Some refuges, such as wildflower strips, do not seem to be a source for recolonisation of crop fields by common voles (Briner *et al.* 2005). However, field edges or grassland areas below wind energy plants do provide common voles with the potential to reach high population densities and create dispersal pressure into arable land. Nevertheless, there are examples showing that this rarely happens, even at high densities of up to 1300 individuals per hectare (Leukers *et al.* 2012).

Intensity of disturbance

Another factor potentially influencing the way small mammal populations recover after population collapse is the intensity of the particular disturbance, meaning the degree of population decline. Less severe disturbances most likely evoke recovery via survival of residual individuals and their offspring. Severe disturbances most likely cause more complete collapse of a population so that immigration from adjacent areas seems to be the only option for recovery. However, even after extreme reduction of population size by a bush fire, recovery of *R. fuscipes* appeared to follow mechanisms that would be expected after a minor population decrease (Banks *et al.* 2011). This indicates that the relative intensity of a disturbance also influences which recovery mechanism is observed (Banks *et al.* 2011).

Population cycles

Populations of several small mammal species in temperate regions undergo multi-annual fluctuations, as well as less-pronounced seasonal fluctuations, during the year (Krebs and Myers 1974). The latter are usually caused by higher mortality during winter and reproduction in spring and summer (Korpimäki *et al.* 2004). The timing of the disturbance causing a population to collapse and the phase of the population cycle have considerable impact on recovery time. It seems likely that a population that is already decreasing in numbers needs a longer period of time to recover to predisturbance levels than a population that is already increasing. However, this also depends on the intensity of the disturbance. If populations are decreasing, it is possible that the few survivors are replaced by an invasive species, as has been proposed for *M. musculus* and *P. novaehollandiae* in an open-forest area after sand mining (Fox and Fox 1984).

Conclusions

There are two basic mechanisms for recovery to take place after population collapse: (1) survival of residents and recolonisation *in situ* through reproduction; and (2) immigration from adjacent refuges. Which mechanism acts depends on the species' life history strategy, as well as on social behaviour and density-dependent population responses. However, in some species a combination of the two strategies is observed, or one is followed by the other (Brown *et al.* 2002).

One key aspect in population recovery seems to be the intensity of the disturbance. There is no fundamental difference between the effects of man-made and natural disturbances on sudden population collapses across species or geographical regions. In fact, it was shown that house mouse populations in Australia react very similarly to populations of voles and lemmings of the Northern Hemisphere after natural population declines (Brown 2006). Most of the rodent species studied so far recover via immigration (Table 2), probably from nearby refuge areas. Nevertheless, this is not necessarily consistent with the species' life history strategy. For example, the r-selection strategist *R. norvegicus* would be expected to recover via survival of residents, but it recolonises depopulated areas from refuge zones (Zhang *et al.* 2007).

Predicting how small rodent populations will recover from population collapses needs to take several factors into account, including the species' life history strategy (Gardmark *et al.* 2003), social behaviour (Shilova and Tchabovsky 2009), current phase of the population cycle (Fox and Fox 1984) and environmental circumstances, such as the availability of nearby refuge areas (Golet *et al.* 2013), as well as the intensity of the disturbance (Banks *et al.* 2011).

Little is known about the recovery of small rodent populations after rodenticide application. In over 40 years, only five publications have explicitly dealt with that issue (e.g. Lawton and Rochford 2007; Shilova and Tchabovsky 2009). However, all studies have consistently demonstrated that recovery of r-selection strategists mostly occurs rather quickly via immigration from neighbouring areas, despite expected recovery via a combination of the survival of resident animals and recruitment of young immigrants. The K-selection strategist mammals, such as hares (*Lepus europaeus*) have low reproductive rates and the recovery of their populations generally takes several years (Reznick *et al.* 2002).

Given the many factors associated with recovery after population collapse, it is difficult to derive general assumptions as to how certain species in particular circumstances recover. Nonetheless, it is possible to use the information available to optimise species-specific pest control in distinct environmental scenarios, as has been reported for fertility control in Brandt's vole (*Microtus brandti*; Shi *et al.* 2002). In this scenario, fertility control needs to be applied the previous autumn (fall) or twice in early spring to match the effect of lethal control and additional management tools, such as fencing, are required to prevent quick recovery (Shi *et al.* 2002). However, fertility control is not used as a prime example in this review because it was predicted to be more effective in medium- or large-sized mammals (Zhang 2000) and it is also a rather slow process that causes a slow decline in small rodent populations (Jacob *et al.* 2008; Liu *et al.* 2012).

In Australia, *M. domesticus* and *R. norvegicus* can recover quickly if the reduction of population size by rodenticide use does not reach a certain threshold (Barnett and Bathard 1953; Brown *et al.* 2002). It was also suggested that house mouse control needs to consider that adjacent unbaited areas provide a source for reinvasion (Brown *et al.* 2002; Brown 2006). This is an issue of general relevance when regulations regarding the use of products for the protection of plants prevent the application of rodenticides in non-crop land, as is the case in Germany.

To accommodate immigration, a combination of short- and long-term reduction via different pest control methods can be considered (Brown *et al.* 2002). Which approaches can be taken differs between countries (e.g. aerial application in Australia vs burrow baiting in Europe), which makes it difficult to extrapolate general recommendations even if there is no difference between the recovery behaviour of species.

Spatial scale is another important parameter for population recovery. Over a large scale, it probably takes longer for an immigrating population to recover than in small areas simply because of the greater distances to be covered and large areas to be repopulated. Therefore, pest rodent abundance is more sustainably controlled by large-scale action (Stenseth *et al.* 2003). This applies particularly when recovery occurs by immigration from refuge zones (Leukers and Jacob 2010).

For the management of r-selection strategist pest rodents, it seems sensible to conduct management action across large areas, including potential refuges. Often, the use of rodenticidal products to protect plants is restricted to crop habitats. Exemptions that allow the application of rodenticides in non-crop refuges, as well as non-chemical techniques, may be useful to optimise management outcome, although this will require the action of registration authorities.

If refuge areas are far away from the depopulated area into which a (pest) species is about to immigrate, dispersal behaviour and migration disposition may influence the recovery time and rate of the particular species (Banks *et al.* 2011). In wood mice, for example, migrating young females only establish themselves in resident populations and reproduce when the number of mature resident females is low (Montgomery *et al.* 1997). Conversely, male wood mice only disperse into populations in which reproduction opportunities are high, regardless of the total number of active females present (Montgomery *et al.* 1997). Thus, preventing immigration may naturally keep population levels of *A. sylvaticus* low, although this process could take several years to affect population size. That way, it is not necessary to control the whole population, simply to prevent immigration and therefore reduce the number of reproductively active new females.

To develop appropriate management decisions for either pest control or conservation, it is essential to take the aforementioned environmental parameters and principles of recovery processes into account.

In particular, management methods for conservation reasons need to be developed on a case-by-case basis, taking the recovery ecology of the respective species into account. This leads to specific support measures, such as providing food, shelter, habitat, refuge areas or by minimising predator pressure (Blumstein *et al.* 2001; Fahrig 2001; Fletcher and Morris 2003; Ceballos *et al.* 2005; Angerbjörn *et al.* 2013; Smith *et al.* 2014). Because conservation usually occurs at a small scale and is often specifically designed for one target species at risk, it seems possible and beneficial to include knowledge of recovery mechanisms into management decisions.

Based on published information, it seems reasonable to manage r-selection strategist small rodents on a large spatial scale, including possible refuge areas, and to monitor the area for the presence of survivors after a couple of months. Conservation action to promote small mammal populations may require a

case-by-case approach because sufficient information is not available to develop general recommendations. Therefore, further research focusing on species-specific recovery mechanisms is strongly recommended.

References

- Andersen, D. C., Wilson, K. R., Miller, M. S., and Falck, M. (2000). Movement patterns of riparian small mammals during predictable floodplain inundation. *Journal of Mammalogy* **81**, 1087–1099. doi:10.1644/1545-1542(2000)081<1087:MPORSM>2.0.CO;2
- Andreassen, H. P., Glorvigen, P., Remy, A., and Ims, R. A. (2013). New views on how population-extrinsic and community-extrinsic processes interact during the vole population cycles. *Oikos* **122**, 507–515. doi:10.1111/j.1600-0706.2012.00238.x
- Andrianaivoarimanana, V., Kreppel, K., Elissa, N., Duplantier, J.-M., Carniel, E., Rajerison, M., and Jambou, R. (2013). Understanding the persistence of plague foci in Madagascar. *PLoS Neglected Tropical Diseases* **7**, e2382. doi:10.1371/journal.pntd.0002382
- Angerbjörn, A., Eide, N. E., Dalen, L., Elmhagen, B., Hellstrom, P., Ims, R. A., Killengreen, S., Landa, A., Meijer, T., Mela, M., Niemimaa, J., Noren, K., Tannerfeldt, M., Yoccoz, N. G., and Henttonen, H. (2013). Carnivore conservation in practice: replicated management actions on a large spatial scale. *Journal of Applied Ecology* **50**, 59–67. doi:10.1111/1365-2664.12033.
- Aplin, K. P., and Singleton, G. R. (2003). Balancing rodent management and small mammal conservation in agricultural landscapes: challenges for the present and the future. *ACIAR Monograph Series* **96**, 80–88.
- Banks, S. C., Dujardin, M., McBurney, L., Blair, D., Barker, M., and Lindenmayer, D. B. (2011). Starting points for small mammal population recovery after wildfire: recolonisation or residual populations? *Oikos* **120**, 26–37. doi:10.1111/j.1600-0706.2010.18765.x
- Barnett, S., and Bathard, A. (1953). Population dynamics of sewer rats. *The Journal of Hygiene* **51**(4), 483–491. doi:10.1017/S0022172400036767
- Barten R., Lauenstein G. (2013). 'Feldmäuse im Griff: Schäden erkennen, richtig vorbeugen.' (DLG-Verlag: Frankfurt am Main.)
- Basquill, S., and Bondrup-Nielsen, S. (1999). Meadow voles (*Microtus pennsylvanicus*) in farm landscapes, I. Population parameters in different habitats. *Annales Zoologici Fennici* **36**, 223–230.
- Blumstein, D. T., Daniel, J. C., and Bryant, A. A. (2001). Anti-predator behavior of Vancouver Island marmots: using congeners to evaluate abilities of a critically endangered mammal. *Ethology* **107**, 1–14. doi:10.1046/j.1439-0310.2001.00631.x
- Boonstra, R. (1994). Population cycles in microtines: the senescence hypothesis. *Evolutionary Ecology* **8**, 196–219. doi:10.1007/BF01238250
- Boonstra, R., Krebs, C. J., and Stenseth, N. C. (1998). Population cycles in small mammals: the problem of explaining the low phase. *Ecology* **79**, 1479–1488. doi:10.1890/0012-9658(1998)079[1479:PCISMT]2.0.CO;2
- Borsuk, G., Czerska, K., Olszewski, K., Strachecka, A., Paleolog, J., and Chobotow, J. (2012). Current state of knowledge of *Varroa destructor*. *Medycyna Weterynaryjna* **68**, 579–584.
- Bradley, R. D., Hanson, J. D., Amman, B. R., Baxter, B. D., Carroll, D. S., Durish, N. D., Haynie, M. L., Kageyama, M., Longhofer, L. K., Mendez-Harclerode, F. M., Reeder, S. A., Suchecki, J. R., Ruthven, D. C., Cajimat, M. N. B., Milazzo, C., Milazzo, M. L., and Fulhorst, C. F. (2006). Rapid recovery of rodent populations following severe drought. *The Southwestern Naturalist* **51**, 87–93. doi:10.1894/0038-4909(2006)51[87:RRORPF]2.0.CO;2
- Brakes, C. R., and Smith, R. H. (2005). Exposure of non-target small mammals to rodenticides: short-term effects, recovery and implications for secondary poisoning. *Journal of Applied Ecology* **42**, 118–128. doi:10.1111/j.1365-2664.2005.00997.x
- Briner, T., Nentwig, W., and Airoldi, J. P. (2005). Habitat quality of wildflower strips for common voles (*Microtus arvalis*) and its relevance for agriculture. *Agriculture, Ecosystems & Environment* **105**, 173–179. doi:10.1016/j.agee.2004.04.007
- Brown, P. R. (2006). Short- and long-term demographic changes in house mouse populations after control in dryland farming systems in Australia. *Wildlife Research* **33**, 457–466. doi:10.1071/WR06026
- Brown P. R. and Singleton G. R. (2000). Impacts of house mice on crops in Australia – costs and damage. In 'Human Conflicts with Wildlife: Economic Considerations. Proceedings of the Third NWRC Special Symposium.' 1–3 August 2000, Fort Collins, CO. (Ed. L. Clark) Paper 6, pp. 48–58. (National Wildlife Research Center: Fort Collins, CO). Available at <http://digitalcommons.unl.edu/nwrchumanconflicts/6> [verified 23 February 2015].
- Brown, P. R., Chambers, L. K., and Singleton, G. R. (2002). Pre-sowing control of house mice (*Mus domesticus*) using zinc phosphide: efficacy and potential non-target effects. *Wildlife Research* **29**, 27–37. doi:10.1071/WR01023
- Brown, P. R., Nguyen, P. T., Singleton, G. R., Phi Thi, T. H., Phung, T. H., Dao, T. H., Tran, Q. T., Nguyen, V. T., Jacob, J., and Muller, W. J. (2006). Ecologically based rodent management in the real world: applied to a mixed agroecosystem in Vietnam. *Ecological Applications* **16**, 2000–2010. doi:10.1890/1051-0761(2006)016[2000:EBMORI]2.0.CO;2
- Butet, A., and Spitz, F. (2001). Cyclic fluctuations of microtine populations: half a century of research. *Revue D Ecologie-La Terre et la Vie* **56**, 353–372. doi:10.1890/1051-0761(2006)016[2000:EBMORI]2.0.CO;2
- Butler, T. (2013). Review article: plague gives surprises in the first decade of the 21st century in the United States and worldwide. *The American Journal of Tropical Medicine and Hygiene* **89**, 788–793. doi:10.4269/ajtmh.13-0191
- Butler, F. T., and Whelan, J. (1994). Population structure and reproduction in brown rats (*Rattus norvegicus*) from pig farms, Co. Kildare, Ireland. *Journal of Zoology* **233**, 277–291. doi:10.1111/j.1469-7998.1994.tb08588.x
- Ceballos, G., and Ehrlich, P. R. (2002). Mammal population losses and the extinction crisis. *Science* **296**, 904–907. doi:10.1126/science.1069349
- Ceballos, G., Ehrlich, P. R., Soberón, J., Salazar, I., and Fay, J. P. (2005). Global mammal conservation: what must we manage? *Science* **309**, 603–607. doi:10.1126/science.1114015
- Cornulier, T., Yoccoz, N. G., Bretagnolle, V., Brommer, J. E., Butet, A., Ecke, F., Elston, D. A., Framstad, E., Henttonen, H., Hörnfeldt, B., Huitu, O., Imholt, C., Ims, R. A., Jacob, J., Jedrzejska, B., Millon, A., Petty, S. J., Pietiäinen, H., Tkadlec, E., Zub, K., and Lambin, X. (2013). Europe-wide dampening of population cycles in keystone herbivores. *Science* **340**, 63–66. doi:10.1126/science.1228992
- Dalkvist, T., Sibby, R. M., and Topping, C. J. (2013). Landscape structure mediates the effects of a stressor on field vole populations. *Landscape Ecology* **28**, 1961–1974. doi:10.1007/s10980-013-9932-7
- Diffendorfer, J. E., Gaines, M. S., and Holt, R. D. (1995). Habitat fragmentation and movements of three small mammals (*Sigmodon*, *Microtus*, and *Peromyscus*). *Ecology* **76**, 827–839. doi:10.2307/1939348
- Elton, C. S. (1924). Periodic fluctuations in the numbers of animals: their causes and effects. *British Journal of Experimental Biology* **2**, 119–163.
- Emlen, J. T., Stokes, A. W., and Winsor, C. P. (1948). The rate of recovery of decimated populations of brown rats in nature. *Ecology* **29**, 133–145. doi:10.2307/1932809
- Engeman, R. M., and Campbell, D. L. (1999). Pocket gopher reoccupation of burrow systems following population reduction. *Crop Protection* **18**, 523–525. doi:10.1016/S0261-2194(99)00055-1
- Esler, D., Bowman, T. D., Trust, K. A., Ballachey, B. E., Dean, T. A., Jewett, S. C., and O'Clair, C. E. (2002). Harlequin duck population recovery following the 'Exxon Valdez' oil spill: progress, process and constraints. *Marine Ecology Progress Series* **241**, 271–286. doi:10.3354/meps241271

- Fabrizio, M. C., Dorazio, R. M., and Schram, S. T. (2001). Dynamics of individual growth in a recovering population of lake trout (*Salvelinus namaycush*). *Canadian Journal of Fisheries and Aquatic Sciences* **58**, 262–272. doi:10.1139/f00-232
- Fahrig, L. (2001). How much habitat is enough? *Biological Conservation* **100**, 65–74. doi:10.1016/S0006-3207(00)00208-1
- Fleming, T. H. (1979). Life-history strategies. In: 'Ecology of Small Mammals'. (Ed. D. M. Stoddart.) pp. 1–61. (Springer: Dordrecht.)
- Fletcher, T., and Morris, K. (2003). 'Captive Breeding and Predator Control: A Successful Strategy for Conservation in Western Australia.' (Cambridge University Press: New York.)
- Fox, B. J., and Fox, M. D. (1984). Small-mammal recolonization of open-forest following sand mining. *Australian Journal of Ecology* **9**, 241–252. doi:10.1111/j.1442-9993.1984.tb01361.x
- Franklin, J. F., Lindenmayer, D., MacMahon, J. A., McKee, A., Magnuson, J., Perry, D. A., Waide, R., and Foster, D. (2000). Threads of continuity. *Conservation in Practice* **1**, 8–17. doi:10.1111/j.1526-4629.2000.tb00155.x
- Friend, G. R. (1993). Impact of fire on small vertebrates in mallee woodlands and heathlands of temperate Australia: a review. *Biological Conservation* **65**, 99–114. doi:10.1016/0006-3207(93)90439-8
- Frost, K. J., Lowry, L. F., and Hoef, J. M. (1999). Monitoring the trend of harbor seals in Prince William Sound, Alaska, after the Exxon Valdez oil spill. *Marine Mammal Science* **15**, 494–506. doi:10.1111/j.1748-7692.1999.tb00815.x
- Fu, C., Mohn, R., and Fanning, L. P. (2001). Why the Atlantic cod (*Gadus morhua*) stock off eastern Nova Scotia has not recovered. *Canadian Journal of Fisheries and Aquatic Sciences* **58**, 1613–1623. doi:10.1139/f01-095
- Gaines, M. S., and McClenaghan, L. R. (1980). Dispersal in small mammals. *Annual Review of Ecology and Systematics* **11**, 163–196. doi:10.1146/annurev.es.11.110180.001115
- Gardmark, A., Enberg, K., Ripa, J., Laakso, J., and Kaitala, V. (2003). The ecology of recovery. *Annales Zoologici Fennici* **40**, 131–144.
- Garrett, M. G. (1982). 'Dispersal of Black-Tailed Prairie Dogs (*Cynomys ludovicianus*) in Wind Cave National Park, South Dakota.' (Iowa State University of Science and Technology: Ames, IA.) 76 pp.
- Garrott, R. A., Eberhardt, L. L., and Burn, D. M. (1993). Mortality of sea otters in Prince William Sound following the Exxon Valdez oil spill. *Marine Mammal Science* **9**, 343–359. doi:10.1111/j.1748-7692.1993.tb00468.x
- Gassner, F., Takken, W., Lombaers-van der Plas, C., Kastelein, P., Hoetmer, A. J., Holdinga, M., and van Overbeek, L. S. (2013). Rodent species as natural reservoirs of *Borrelia burgdorferi sensu lato* in different habitats of *Ixodes ricinus* in the Netherlands. *Ticks and Tick-Borne Diseases* **4**, 452–458. doi:10.1016/j.ttbdis.2012.11.017
- George, D. B., Webb, C. T., Pepin, K. M., Savage, L. T., and Antolin, M. F. (2013). Persistence of black-tailed prairie-dog populations affected by plague in northern Colorado, USA. *Ecology* **94**, 1572–1583. doi:10.1890/12-0719.1
- Getz, L. L., McGuire, B., Pizzuto, T., Hofmann, J. E., and Frase, B. (1993). Social-organization of the prairie vole (*Microtus ochrogaster*). *Journal of Mammalogy* **74**, 44–58. doi:10.2307/1381904
- Getz, L. L., McGuire, B., and Carter, C. S. (2005). Social organization and mating system of free-living prairie voles *Microtus ochrogaster*: a review. *Acta Zoologica Sinica* **51**, 178–186.
- Golet, G. H., Hunt, J. W., and Koenig, D. (2013). Decline and recovery of small mammals after flooding: implications for pest management and floodplain community dynamics. *River Research and Applications* **29**, 183–194. doi:10.1002/rra.1588
- Greenwood, P. J. (1980). Mating systems, philopatry and dispersal in birds and mammals. *Animal Behaviour* **28**, 1140–1162. doi:10.1016/S0003-3472(80)80103-5
- Halle, S. (1993a). Wood mice (*Apodemus sylvaticus* L.) as pioneers of recolonization in a reclaimed area. *Oecologia* **94**, 120–127. doi:10.1007/BF00317312
- Halle, S. (1993b). Diel pattern of predation risk in microtine rodents. *Oikos* **68**, 510–518. doi:10.2307/3544919
- Hamar, M., and Tuta, A. (1971). Rhythm of recovery of *Microtus arvalis* populations and effectiveness of some insecticide treatments. *Organisation Europeenne et Mediterraneenne pour la Protection des Plantes Publications Serie A* **58**, 65–72.
- Hayes, L. D. (2000). To nest communally or not to nest communally: a review of rodent communal nesting and nursing. *Animal Behaviour* **59**, 677–688. doi:10.1006/anbe.1999.1390
- Heiberg, A. C., Sluydts, V., and Leirs, H. (2012). Uncovering the secret lives of sewer rats (*Rattus norvegicus*): movements, distribution and population dynamics revealed by a capture–mark–recapture study. *Wildlife Research* **39**, 202–219. doi:10.1071/WR11149
- Ims, R. A., Henden, J.-A., and Killengreen, S. T. (2008). Collapsing population cycles. *Trends in Ecology & Evolution* **23**, 79–86. doi:10.1016/j.tree.2007.10.010
- Jacob, J. (2003a). The response of small mammal populations to flooding. *Mammalian Biology* **68**, 102–111. doi:10.1078/1616-5047-00068
- Jacob, J. (2003b). Short-term effects of farming practices on populations of common voles. *Agriculture, Ecosystems & Environment* **95**, 321–325. doi:10.1016/S0167-8809(02)00084-1
- Jacob, J. (2013). Vertebrate pest management: science and application. *Pest Management Science* **69**, 321–322. doi:10.1002/ps.3496
- Jacob, J., and Hempel, N. (2003). Effects of farming practices on spatial behaviour of common voles. *Journal of Ethology* **21**, 45–50.
- Jacob, J., and 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., Singleton, G. R., and Hinds, L. A. (2008). Fertility control of rodent pests. *Wildlife Research* **35**, 487–493. doi:10.1071/WR07129
- Jacob, J., Sudarmaji, , Singleton, G. R., Rahmini, , Herawati, N.A., and Brown, P. R. (2010). Ecologically based management of rodents in lowland irrigated rice fields in Indonesia. *Wildlife Research* **37**, 418–427. doi:10.1071/WR10030
- Jacob, J., Manson, P., Barfknecht, R., and Fredricks, T. (2014). Common vole (*Microtus arvalis*) ecology and management: implications for risk assessment of plant protection products. *Pest Management Science* **70**, 869–878. doi:10.1002/ps.3695
- Jo Manning, C., Dewsbury, D. A., Wakeland, E. K., and Potts, W. K. (1995). Communal nesting and communal nursing in house mice, *Mus musculus domesticus*. *Animal Behaviour* **50**, 741–751. doi:10.1016/0003-3472(95)80134-0
- Kamarudin, K. A., Lee, C. H., and Munir, A. A. (1991). Wood-rat (*Rattus tiomanicus* Miller) population build-up in a cocoa-coconut plantation after field-poisoning. *MARDI Research Journal* **19**, 239–249.
- Klemola, T., Korpimäki, E., and Koivula, M. (2002). Rate of population change in voles from different phases of the population cycle. *Oikos* **96**, 291–298. doi:10.1034/j.1600-0706.2002.960211.x
- Knowles, C. J. (1986). Population recovery of black-tailed prairie dogs following control with zinc phosphide. *Journal of Range Management* **39**, 249–251. doi:10.2307/3899060
- Korpimäki, E., Klemola, T., Norrdahl, K., Oksanen, L., Oksanen, T., Banks, P. B., Batzli, G. O., and Henttonen, H. (2003). Voles cycles and predation. *Trends in Ecology & Evolution* **18**, 494–495. doi:10.1016/S0169-5347(03)00159-9
- Korpimäki, E., Brown, P. R., Jacob, J., and Pech, R. P. (2004). The puzzles of population cycles and outbreaks of small mammals solved? *Bioscience* **54**, 1071–1079. doi:10.1641/0006-3568(2004)054[1071:TPOPCA]2.0.CO;2

- Krebs, C. J., and Myers, J. H. (1974). Population cycles in small mammals. *Advances in Ecological Research* **8**, 267–399. doi:10.1016/S0065-2504(08)60280-9
- Krebs, C. J., Gaines, M. S., Keller, B. L., Myers, J. H., and Tamarin, R. H. (1973). Population cycles in small mammals. *Science* **179**, 35–41. doi:10.1126/science.179.4068.35
- Krebs, C. J., Wingate, I., LeDuc, J., Redfield, J. A., Taitt, M., and Hilborn, R. (1976). *Microtus* population biology: dispersal in fluctuating populations of *M. townsendii*. *Canadian Journal of Zoology* **54**, 79–95. doi:10.1139/z76-009
- Lambin, X., Petty, S. J., and Mackinnon, J. L. (2000). Cyclic dynamics in field vole populations and generalist predation. *Journal of Animal Ecology* **69**, 106–119. doi:10.1046/j.1365-2656.2000.00380.x
- Lambin, X., Bretagnolle, V., and Yoccoz, N. G. (2006). Vole population cycles in northern and southern Europe: is there a need for different explanations for single pattern? *Journal of Animal Ecology* **75**, 340–349. doi:10.1111/j.1365-2656.2006.01051.x
- Lawton, C., and Rochford, J. (2007). The recovery of grey squirrel (*Sciurus carolinensis*) populations after intensive control programmes. *Biology and Environment: Proceedings of the Royal Irish Academy* **107B**, 19–29. doi:10.3318/BIOE.2007.107.1.19
- Le Conte, Y., Ellis, M., and Ritter, W. (2010). Varroa mites and honey bee health: can Varroa explain part of the colony losses? *Apidologie* **41**, 353–363. doi:10.1051/apido/2010017
- Letnic, M., Dickman, C. R., Tischler, M. K., Tamayo, B., and Beh, C. L. (2004). The responses of small mammals and lizards to post-fire succession and rainfall in arid Australia. *Journal of Arid Environments* **59**, 85–114. doi:10.1016/j.jaridenv.2004.01.014
- Leukers, A., and Jacob, J. (2010). Dispersal dynamics of common voles (*Microtus arvalis*) in agro-ecosystems. *Mammalian Biology* **75**, 17.
- Leukers, A., Heckel, G., and Jacob, J. (2012). Genotypisierung einer Feldmaus-Population zur Aufklärung von Ausbreitungsprozessen in Kulturlandschaften. *Julius-Kühn-Archiv* **438**, 233–234.
- Lindenmayer, D. B., Cunningham, R. B., and Peakall, R. (2005). The recovery of populations of bush rat *Rattus fuscipes* in forest fragments following major population reduction. *Journal of Applied Ecology* **42**, 649–658. doi:10.1111/j.1365-2664.2005.01054.x
- Liu, H., Jin, Z., Chen, Y., and Zhang, F. (2012). Population dynamics of plateau pika under lethal control and contraception control. *Advances in Difference Equations* **2012**, 1–13. doi:10.1186/1687-1847-2012-1
- LoGiudice, K. (2006). Toward a synthetic view of extinction: a history lesson from a North American rodent. *Bioscience* **56**, 687–693. doi:10.1641/0006-3568(2006)56[687:TASVOE]2.0.CO;2
- MacArthur, R. H. (1962). Some generalized theorems of natural selection. *Proceedings of the National Academy of Sciences of the United States of America* **48**, 1893–1897. doi:10.1073/pnas.48.11.1893
- MacArthur, R. H., and Wilson, E. O. (1967). 'The Theory of Island Biogeography.' (Princeton University Press: Princeton, NJ.)
- MacMahon, J. A., Parmenter, R. R., Johnson, K. A., and Crisafulli, C. M. (1989). Small mammal recolonization on the Mount St. Helens Volcano: 1980–1987. *American Midland Naturalist* **122**, 365–387. doi:10.2307/2425924
- Martin, G. (2003). The role of small ground-foraging mammals in topsoil health and biodiversity: implications to management and restoration. *Ecological Management & Restoration* **4**, 114–119. doi:10.1046/j.1442-8903.2003.00145.x
- Meaney, M. J., and Stewart, J. (1981). A descriptive study of social development in the rat (*Rattus norvegicus*). *Animal Behaviour* **29**, 34–45. doi:10.1016/S0003-3472(81)80149-2
- Montgomery, W. I., Wilson, W. L., and Elwood, R. W. (1997). Spatial regulation and population growth in the wood mouse *Apodemus sylvaticus*: experimental manipulations of males and females in natural populations. *Journal of Animal Ecology* **66**, 755–768. doi:10.2307/5926
- Mutschmann, F., Berger, L., Zwart, P., and Gaedicke, C. (2000). Chytridiomycosis on amphibians: first report from Europe. *Berliner und Münchener Tierärztliche Wochenschrift* **113**, 380–383.
- Myers, R. A., Mertz, G., and Fowlow, P. S. (1997). Maximum population growth rates and recovery time for Atlantic cod, *Gadus morhua*. *Fishery Bulletin* **95**, 762–772.
- Nakagiri, N., Tainaka, K.-i., and Tao, T. (2001). Indirect relation between species extinction and habitat destruction. *Ecological Modelling* **137**(2–3), 109–118. doi:10.1016/S0304-3800(00)00417-8
- Oli, M. K. (2003). Population cycles of small rodents are caused by specialist predators: or are they? *Trends in Ecology & Evolution* **18**, 105–107. doi:10.1016/S0169-5347(03)00005-3
- Parker, K. R., and Wiens, J. A. (2005). Assessing recovery following environmental accidents: environmental variation, ecological assumptions, and strategies. *Ecological Applications* **15**, 2037–2051. doi:10.1890/04-1723
- Perry, R. D., and Fetherston, J. D. (1997). *Yersinia pestis*: etiologic agent of plague. *Clinical Microbiology Reviews* **10**, 35–66.
- Peterson, C. H., Rice, S. D., Short, J. W., Esler, D., Bodkin, J. L., Ballachey, B. E., and Irons, D. B. (2003). Long-term ecosystem response to the Exxon Valdez oil spill. *Science* **302**, 2082–2086. doi:10.1126/science.1084282
- Pianka, E. R. (1974). Niche overlap and diffuse competition. *Proceedings of the National Academy of Sciences of the United States of America* **71**, 2141–2145. doi:10.1073/pnas.71.5.2141
- Pikula, J., Tremil, F., Beklova, M., Holesovska, Z., and Pikulova, J. (2002). Geographic information systems in epidemiology: ecology of common vole and distribution of natural foci of Tularemia. *Acta Veterinaria* **71**, 379–387. doi:10.2754/avb200271030379
- Pita, R., Mira, A., and Beja, P. (2014). *Microtus cabreræ* (Rodentia: Cricetidae). *Mammalian Species* **46**, 48–70. doi:10.1644/912.1
- Reichstein, H. (1960). Untersuchungen zum Aktionsraum und zum Revierverhalten der Feldmaus *Microtus arvalis* (Pall.). *Zeitschrift für Säugetierkunde-International Journal of Mammalian Biology* **25**, 150–169.
- Reznick, D., Bryant, M. J., and Bashey, F. (2002). r- and K-selection revisited: the role of population regulation in life-history evolution. *Ecology* **83**, 1509–1520. doi:10.1890/0012-9658(2002)083[1509:RAK SRT]2.0.CO;2
- Samia, N. I., Kausrud, K. L., Heesterbeek, H., Ageyev, V., Begon, M., Chan, K.-S., and Stenseth, N. C. (2011). Dynamics of the plague-wildlife-human system in Central Asia are controlled by two epidemiological thresholds. *Proceedings of the National Academy of Sciences of the United States of America* **108**, 14 527–14 532. doi:10.1073/pnas.1015 946108
- Shi, D., Wan, X., Davis, S. A., Pech, R. P., and Zhang, Z. (2002). Simulation of lethal control and fertility control in a demographic model for Brandt's vole *Microtus brandti*. *Journal of Applied Ecology* **39**, 337–348. doi:10.1046/j.1365-2664.2002.00716.x
- Shilova, S. A., and Tchabovsky, A. V. (2009). Population response of rodents to control with rodenticides. *Current Zoology* **55**, 81–91.
- Sinclair, A. R. E., Pech, R. P., Dickman, C. R., Hik, D., Mahon, P., and Newsome, A. E. (1998). Predicting effects of predation on conservation of endangered prey. *Conservation Biology* **12**, 564–575. doi:10.1046/j.1523-1739.1998.97030.x
- Singleton, G. R. (2003). 'Impacts of Rodents on Rice Production in Asia.' IRRI Discussion Paper Series, Series Volume ID no. 45. (International Rice Research Institute: Los Baños, Philippines)
- Singleton, G. R., Hinds, L. A., Krebs, C. J., and Spratt, D. M. (2003). 'Rats, Mice and People: Rodent Biology and Management.' (Australian Centre for International Agricultural Research: Canberra.)
- Singleton, G. R., Brown, P. R., Jacob, J., and Aplin, K. P. (2007). Unwanted and unintended effects of culling: a case for ecologically-based rodent management. *Integrative Zoology* **2**, 247–259. doi:10.1111/j.1749-4877.2007.00067.x

- Sinski, E., Pawelczyk, A., Bajer, A., and Behnke, J. (2006). Abundance of wild rodents, ticks and environmental risk of *Lyme borreliosis*: a longitudinal study in an area of Mazury Lakes district of Poland. *Annals of Agricultural and Environmental Medicine* **13**, 295–300.
- Smith, K. R., Barthman-Thompson, L., Gould, W. R., and Mabry, K. E. (2014). Effects of natural and anthropogenic change on habitat use and movement of endangered salt marsh harvest mice. *PLoS ONE* **9**(10), e108739. doi:10.1371/journal.pone.0108739
- Smyser, T. J., Johnson, S. A., Page, L. K., and Rhodes, O. E. (2012). Synergistic stressors and the dilemma of conservation in a multivariate world: a case study in Allegheny woodrats. *Animal Conservation* **15**, 205–213. doi:10.1111/j.1469-1795.2011.00505.x
- St. Romain, K., Tripp, D. W., Salkeld, D. J., and Antolin, M. F. (2013). Duration of plague (*Yersinia pestis*) outbreaks in black-tailed prairie dog (*Cynomys ludovicianus*) colonies of Northern Colorado. *EcoHealth* **10**, 241–245. doi:10.1007/s10393-013-0860-4
- Stein, G. H. W. (1958). 'Die Feldmaus.' (Franckh'sche Verlagshandlung: Stuttgart.)
- Stenseth, N. C., Bjornstad, O. N., and Falck, W. (1996). Is spacing behaviour coupled with predation causing the microtine density cycle? A synthesis of current process-oriented and pattern-oriented studies. *Proceedings of the Royal Society of London. Series B, Biological Sciences* **263**, 1423–1435. doi:10.1098/rspb.1996.0208
- Stenseth, N. C., Leirs, H., Skonhofs, A., Davis, S. A., Pech, R. P., Andreassen, H. P., Singleton, G. R., Lima, M., Machang'u, R. S., and Makundi, R. H. (2003). Mice, rats, and people: the bio-economics of agricultural rodent pests. *Frontiers in Ecology and the Environment* **1**, 367–375. doi:10.1890/1540-9295(2003)001[0367:MRAPT]2.0.CO;2
- Sullivan, T. P., Sullivan, D. S., and Hogue, E. J. (2001). Reinvasion dynamics of northern pocket gopher (*Thomomys talpoides*) populations in removal areas. *Crop Protection* **20**, 189–198. doi:10.1016/S0261-2194(00)00126-5
- Sutherland, E. F., and Dickman, C. R. (1999). Mechanisms of recovery after fire by rodents in the Australian environment: a review. *Wildlife Research* **26**, 405–419. doi:10.1071/WR97045
- Telle, H. J. (1966). Beitrag zur Kenntnis der Verhaltensweise von Ratten, vergleichend dargestellt bei *Rattus norvegicus* und *Rattus rattus*. *Zeitschrift für angewandte Zoologie* **53**, 129–196. doi:10.1071/WR97045
- Tew, T. E., and Macdonald, D. W. (1994). Dynamics of space use and male vigor amongst wood mice, *Apodemus sylvaticus*, in the cereal ecosystem. *Behavioral Ecology and Sociobiology* **34**, 337–345. doi:10.1007/BF00197004
- Turner, M. G., Baker, W. L., Peterson, C. J., and Peet, R. K. (1998). Factors influencing succession: lessons from large, infrequent natural disturbances. *Ecosystems* **1**, 511–523. doi:10.1007/s100219900047
- Vacanti, P. L., and Geluso, K. N. (1985). Recolonization of a burned prairie by meadow voles (*Microtus pennsylvanicus*). *Prairie Naturalist* **17**, 15–22.
- Westemeier, R. L., Brawn, J. D., Simpson, S. A., Esker, T. L., Jansen, R. W., Walk, J. W., Kershner, E. L., Bouzat, J. L., and Paige, K. N. (1998). Tracking the long-term decline and recovery of an isolated population. *Science* **282**, 1695–1698. doi:10.1126/science.282.5394.1695
- Witmer, G., Eisemann, J. D., and Howald, G. (2007a) 'The Use of Rodenticides for Conservation Efforts.' USDA National Wildlife Research Center—Staff Publications, Paper 780. (U.S. Department of Agriculture: Washington, D.C.)
- Witmer, G. W., Boyd, F., and Hillis-Starr, Z. (2007b). The successful eradication of introduced roof rats (*Rattus rattus*) from Buck Island using diphacinone, followed by an irruption of house mice (*Mus musculus*). *Wildlife Research* **34**, 108–115. doi:10.1071/WR06006
- Woinarski, J. C. Z., Legge, S., Fitzsimons, J. A., Traill, B. J., Burbidge, A. A., Fisher, A., Firth, R. S. C., Gordon, I. J., Griffiths, A. D., Johnson, C. N., McKenzie, N. L., Palmer, C., Radford, I., Rankmore, B., Ritchie, E. G., Ward, S., and Ziembecki, M. (2011). The disappearing mammal fauna of northern Australia: context, cause, and response. *Conservation Letters* **4**, 192–201. doi:10.1111/j.1755-263X.2011.00164.x
- Wood, B. J., and Liau, S. S. (1984). A long-term study of *Rattus tiomanicus* population in an oil palm plantation in Johore, Malaysia. 2. Recovery from control and economic aspects. *Journal of Applied Ecology* **21**, 465–472. doi:10.2307/2403422
- Zhang, Z. (2000). Mathematical models of wildlife management by contraception. *Ecological Modelling* **132**, 105–113. doi:10.1016/S0304-3800(00)00308-2
- Zhang, Z. B., Hinds, L., Singleton, G., and Wang, Z. W. (1998). Rodent biology and management. Abstracts of papers presented at the International Conference on Rodent Biology and Management, held at Beijing, China, 5–9 October 1998. *ACIAR Technical Reports* **45**, 1–146.
- Zhang, M., Wang, Y., Li, B., Guo, C., and Chen, A. (2004). The population recovery of rodent pests after application of anticoagulant in agro-ecosystem in the middle and lower reaches of Yangtze Valley. *Acta Phytotaxonomica Sinica* **31**, 138–147. [In Chinese]
- Zhang, M., Wang, K., Wang, Y., Guo, C., Li, B., and Huang, H. (2007). Recovery of a rodent community in an agro-ecosystem after flooding. *Journal of Zoology* **272**, 138–147. doi:10.1111/j.1469-7998.2006.00248.x
- Zhang, J., Yang, K., and Li, P. (2011). Preliminary study on the rodent population dynamics in farmland in the earthquake-stricken area of Beichuan county. *Chinese Journal of Vector Biology and Control* **22**(2), 121–123. [In Chinese]
- Zub, K., Jedrzejewska, B., Jedrzejewski, W., and Barton, K. A. (2012). Cyclic voles and shrews and non-cyclic mice in a marginal grassland within European temperate forest. *Acta Theriologica* **57**, 205–216. doi:10.1007/s13364-012-0072-2