Rodent outbreaks in North America

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Fluctuations in rodent population densities in North America are a reality. Our understanding of the factors causing such fluctuations is incomplete; therefore, it is important to monitor populations to increase our understanding of natural wildlife communities so as to avoid substantial damage to agriculture, forestry, and urban infrastructures, and to prevent rodent-borne disease transmission to humans. There is a need to establish integrated pest management programs in which monitoring, preventive cultural practices, and various control methods (mechanical, physical, biological, and chemical) are strategically coordinated to maintain rodent population densities at acceptable pest levels.

Keywords: agriculture, damage, land use, management, North America, outbreaks, rodents

North America has more than 400 species of rodents (Hall 1981). They are found in all ecoregions, from high arctic tundra to forests, prairies, and arid deserts. They inhabit subterranean, terrestrial, arboreal, and aquatic habitats. Most of these species do not cause significant problems for humans. However, many rodents have adapted to and taken advantage of human environments, and are considered pests in urban settings, agriculture, and forestry. Rodent populations can reach high densities, often considered outbreaks, under diverse environmental conditions. Also, many species have cyclic fluctuations related to various biological factors. Whether or not all these high densities qualify as "outbreaks" and "cyclic-high" peaks, such fluctuations in rodent numbers result in significant conflicts with humans (Marsh 1988, Hygnstrom et al 1994). In this chapter, we argue that many rodent species experience population outbreaks with similar characteristics and effects on natural and anthropogenic environments.

High rodent densities reported in North America

Rodents are characterized by high intrinsic rates of increase (Batzli 1999). When they have the required food, water, and cover to survive and reproduce, they thrive; when these resources are in short supply, animals either emigrate or die (Tobin and Fall 2004). Greater reproduction and immigration may lead to population increases and peaks (Miller 1946, Proulx 1997). All rodent populations, independent of their size, life history, and habitat, can fluctuate in numbers. Table 1 shows some examples of high densities for various rodent species reported in North America. Many of these species occupy agricultural fields under some conditions.

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Table 1. Some high rodent densities reported in North America and average characteristics of those rodent species. Compiled from Banfield (1974), Feldhamer et al (2003), Hygnstrom et al (1994), and Marsh (1988).

Species	Body mass (g)	Lifespan (years)	Litters per year	Litter size	High density ha^{-1}	Cyclic populations (yes/no)	Primary habitats	Additional references
Brown lemming (*Lemmus sibiricus*)	100	1	1–3	4–9	320	Yes	Tundra	Pitelka and Batzli (1993)
Voles (*Microtus* spp.)	65	1	1–5	3–6		Yes	Grassland	Beck et al (1958), Boonstra and Krebs (1978), Murray (1965)
Ground squirrels (*Spermophilus* spp.)	500	4–5	1	4–9	330	Yes?	Grassland	Proulx (2010), Rickart (1988)
Muskrat (*Ondatra zibethicus*)	1,100	2–3	2–3	4–8	100	Yes	Marsh, wetlands	Errington (1954)
Deer mice (*Peromyscus* spp.)	30	<1	2–4	3–5	100	No	Many habitats	Sullivan and Krebs (1981), Vessey and Vessey (2007), Hoffman (1955)
Pocket gophers (*Thomomys* spp.)	250	1–3	1–2	3–6	153	No	Forest, grassland	Witmer and Engeman (2007), Aldous (1957), Proulx (1997)
Cotton rats (*Sigmodon* spp.)	200	<1	2–6	5–7	373	No	Grassland	Hawthorne (1994)
Rice rats (*Oryzomys* spp.)	80	<1	5–6	2–5	50	No	Marsh, grassland	Smith and Vrieze (1979)
Grey squirrel (*Sciuris carolinensis*)	800	3–4	2	3	50	No	Forest	Jackson (1961)
Nutria[a] (*Myocastor coypu*)	5,400	2–3	2–3	4–5	138	No?	Marsh, wetlands	Wentz (1971)
Norway rat[a] (*Rattus norvegicus*)	450	1	4–6	6–12	150	No?	Urban/suburban	S. Stopak (USDA, pers. comm.), Brooks and Barnes (1972), Colvin and Kaukeinen (2008), Proulx, unpubl. data
House mouse[a] (*Mus musculus*)	30	1	5–10	5–6	500	No?	Urban/suburban	Pearson (1963)

[a]Introduced to the U.S.

For the most part, population fluctuations are irregular. But, the fluctuations of some populations are more regular than one would expect by chance. These are commonly called cycles (Smith 1974). The two most common intervals between oscillations are 3 to 4 years, typified by lemmings (Stenseth 1999, Wilson et al 1999) and voles (Krebs 1996, Ylonen et al 2003), and 6 to 10 years, typified by muskrats (McLeod 1950, Errington 1954, Butler 1962) and ground squirrels (Erlien and Tester 1984, Byrom et al 2000). However, there is no clear distinction between small mammal populations that are cyclic and those that fluctuate irregularly (Hansson and Henttonen 1985, Taitt and Krebs 1985). Within the same habitat or region, rodent populations often irrupt and reach numbers that are manyfold those of “normal” densities (Table 2).

Table 2. Temporal fluctuations in the density of rodents from a single population.

Species	Densities ha^{-1}		References
	General range	High	
Columbian ground squirrel (*Spermophilus columbianus*)	10–30	43–78	Dobson and Kjelgaard (1985)
Fox squirrel (*Sciurus niger*)	0.05	2.1–5.1	Brown and Yeager (1945)
Northern pocket gopher (*Thomomys talpoides*)	47	183	Hansen (1960)
Muskrat (*Ondatra zibethicus*)	20–40	>80	Lynch et al (1947), Errington (1963)
Voles (*Microtus* spp.)	0	427	Myers and Krebs (1974), Taitt and Krebs (1985)
Mountain beaver (*Aplodontia rufa*)	<1	15–20	Hooven (1977)

Factors associated with rodent outbreaks in North America

Many factors can cause high densities or outbreaks of rodent populations in North America. Some are density-independent (abiotic), for example, weather, and others are density-dependent (biotic), for example, predation. Some factors act synergistically (e.g., loss of cover and increased predation), while others may be interrelated (e.g., frequent precipitations and forage increase). Although a variety of factors may be responsible for population fluctuations, weather, food, social interactions, and predation are often identified as the main causes.

Weather. The two most commonly measured forms of biological response to climate change are adjustments in species’ geographical distributions and in timing of activity (Parmesan et al 2000, Parmesan and Yohe 2003). Extremes of temperature have a direct impact on the distribution of kangaroo rats (*Dipodomys* spp.), some species not being able to maintain their body temperatures in cold weather, and others being overly sensitive to high temperatures (Dawson 1955, Gaby 1972).

Abundant rainfall, especially after a period of drought, can result in a flush of vegetation growth. Rodent populations can respond quickly to the improved forage and cover provided in these situations. Abundant rainfall when combined with a mild winter and a warm spring can lead to high reproduction and survival in some species of rodents. Such conditions have led to house-mouse outbreaks in California (Pearson 1963) and vole outbreaks in Oregon (Beck et al 1958). Tomich (1986) noted similar house mouse outbreaks in Hawaii and Singleton et al (2007) noted similar responses in house mouse populations in Australia so the phenomenon appears to occur worldwide, especially in mild climate (subtropical, Mediterranean) areas. Weather events (mild temperatures and abundant precipitation) can lead to abundant acorn crops (i.e., mast production) a year or two later, resulting in dramatic increases in mice and vole populations (Schnurr et al. 2002, Clotfelter et al. 2007). Oceanic weather events (El Niño Southern Oscillation) can cause increased precipitation that results in increases in rodent populations for the reasons previously discussed (Hjelle and Glass 2000, Rodriguez-Moran et al 1998, Glass et al 2000).

Drought impacts on vegetation growth may affect the composition of rodent communities. Rodents often respond to decreased vegetation height with reduced movements and increased risk sensitivity in their feeding behavior (Jacob 2008), and their productivity may be affected. Conversely, low vegetation height may attract rodents that monitor the movements of their con-specifics and predators. Population outbreaks of Richardson's ground squirrel in grasslands and pastures with low vegetation in southern Saskatchewan were the result of a widespread drought (Proulx 2010).

Food. When rodents have access to high quality and/or quantity of food, the percent of the population in reproductive condition may increase (Reichman and Van De Graaf 1975), yearlings may breed earlier than usual (Lair 1985), the proportion of females weaning a litter augments (Karels and Boonstra 2000), and litter size may increase considerably (Table 3).

Predation. Where predators are abundant, and particularly where they have coevolved with the prey species, density-dependent or delayed density-dependent predation will either prevent outbreaks or generate cycles (Klemola et al 2003). In the Canadian tundra, predation mortality was sufficient to prevent summer population growth of noncyclic lemming populations (Reid et al 1995) and may have been sufficient to regulate cyclic lemming populations (Wilson et al 1999).

Predators may be considered specialists or generalists and they may respond in a numerical or functional way to fluctuations in prey abundance. Generalist predators are believed to stabilize prey numbers, whereas specialist predators should cause fluctuations in numbers (Andersson and Erlinge 1977). For example, ferruginous hawks (*Buteo regalis*) are specialist predators feeding almost exclusively on Richardson's ground squirrels (Lokemoen and Duebbert 1976, Schmutz et al 1980). Least weasels (*Mustela nivalis*) and short-tailed weasels (*M. ermine*) are vole specialists (Simms

Table 3. Effect of food quality and/or supply on the litter size of rodent populations.

Species	Number of young per litter[a]		References
	Lower food quality or supply	Higher food quality or supply	
Northern pocket gopher (*Thomomys talpoides*)	3–5 (native grass lands)	5–7 (alfalfa fields)	Hansen (1960), Hansen and Ward (1966), Andersen (1978), Proulx (2002)
Pine vole (*Microtus pinetorum*)	1.6 (abandoned orchard)	2.0 (managed orchard)	Cengel et al (1978)
Belding's ground squirrel (*Spermophilus beldingi*)	3.6	4.1 (supple mental feeding)	Trombulak (1991)

[a]Statistically significant differences between litter sizes.

1979, Korpimäki et al 1991). Long-tailed weasels (*M. frenata*) may become specialist predators of Richardson's ground squirrels from April to July, when adults and juveniles are active above ground, but thereafter switch to other prey (Proulx et al 2010). In other regions, they may systematically investigate fields to find and kill northern pocket gopher (Proulx 2005a). Thus, some predators of small mammals can change from being specialists to being generalists in a seasonal and regional fashion (Korpimäki and Krebs 1996).

Multiple factors. Despite intensive research efforts, ecologists still disagree about what causes population cycles (Korpimäki et al 2004, Krebs 1996, Ylonen et al 2003). Researchers have suggested the cycles are related to resource limitation (Ford and Pitelka 1984, Hornfeldt et al 1986), predation pressures (Korpimäki et al 1991, Korpimaki and Norrdahl 1998), vegetation cover (Birney et al 1976), density-dependent season length (Smith at al 2006), breeding performance (Mihok et al 1985), defense mechanisms from food plants (Massey et al 2008), disease outbreaks (Wolff and Edge 2003), and the body condition of individuals in a population (Agrell et al 1992), but perhaps not to stress hormone levels (Boonstra and Boag 1992). Lambin et al (2006) suggested that the reasons for cycles likely differ by geographic region, and multiple reasons should be considered.

Urban settings and land-use practices

Environmental conditions (e.g., food supplies, low predator numbers, cover, etc.) that are associated with rodent population fluctuations are often identified in urban settings, agricultural land, and forest operations. We briefly discuss such environments because these are the areas where significant conflicts with humans can occur.

Urban settings. Commensal species of rats and mice commonly occur in urban settings in North America as in other urban areas of the world. Occasionally, they reach high densities. Millions of commensal rats may live in the larger cities (Corrigan 2001). Recently, Colvin and Kaukeinen (2008) ranked the major cities of the U.S. for their rodent risk. A number of human-caused factors make the urban setting very supportive of commensal rodent populations, and populations are maintained at low densities if continuous management actions are taken, typically with the use of rodenticides.

In many situations, urban settings inadvertently provide the basic needs of commensal rodents: food, harborage (cover), water, and a relatively predator-free environment (with the occasional exception of pets and feral cats). The urban environment also provides a relatively stable thermal environment year-round. Food comes from a variety of sources: stored foods, pet food, food spillage, and wastes. Harborage or cover comes from the many interstitial spaces in buildings, burrowing under foundations, outbuildings, sewer systems, debris piles, and other areas. Water is available from kitchens and bathrooms, leakage inside and outside of buildings, intentional or unintentional catchment devices, yard watering, pools and ponds, pet water bowls, and other sources.

Proper sanitation and exclusion integrated with inspection and management activities are all important elements of keeping urban rodent populations at low levels so that significant damage or disease hazards are not issues of concern. Specific recommendations and comprehensive municipal programs were presented by Colvin and Jackson (1999), Corrigan (2001), and Colvin and Kaukeinen (2008). Colvin and Kaukeinen (2008) described the development and use of an environmental management system (EMS) to reduce the risk of rodent infestations in urban settings. The EMS system included

- Have a solid policy and legal basis
- Assess risks and associated mitigation
- Establish specific objectives and targets
- Plan and organize necessary resources (personnel, budget, equipment)
- Acquire and train competent personnel
- Implement and monitor management actions
- Document all aspects of the EMS
- Assess EMS effectiveness with audits and reviews

Agricultural production. Farms and ranches can support large populations of commensal rodents in and around buildings for the same reasons described above for urban settings. Beyond this, however, are factors involved with the creation and maintenance of agroecosystems that can be very supportive of rodent populations. No-till agriculture can conserve soil and water resources, but provides good habitat (food and cover) for rodents (Witmer et al 2007). The grassy edges or fallow fields surrounding crop fields provide refugia for rodents, which can then take advantage of crop fields once they grow to stages that produce abundant forage and cover. Additionally, certain crops provide better conditions and resources for rodents: corn fields support more rodents than soybean fields (Witmer et al 2007, Witmer and Fantinato 2003), and alfalfa fields provide pocket gophers with higher quality food supplies than do native grasslands (Proulx 2002, 2005b). Poor grassland management and overgrazing create favorable living conditions for ground squirrels (Proulx 2010).

In some settings (e.g., agricultural areas and airports), predators are controlled or excluded for various reasons, which can result in abundant rodent populations (Kim et al 2007, Witmer and Fantinato 2003). These predator populations would otherwise dampen rodent population outbreaks (Andersson and Erlinge 1977, Baker and Brooks 1982).

Forestry operations. Clearcut logging (removal of entire forest canopy) generally results in a large response in growth by understory vegetation. This provides abundant ground cover and nutritious forage for rodents (as well as rabbits and ungulates) that take advantage of the situation. These herbivores can cause substantial damage to reforestation efforts, especially when nursery-raised, fast-growing seedlings are planted. Sullivan and Krebs (1981) documented outbreaks of deer mice (*Peromyscus* spp.) after logging, and Witmer and Engeman (2007) noted increases of pocket gophers after logging. In years of peak populations of meadow vole (*Microtus pennsylvanicus*), Buckner (1972) reported young stands of Scotch pine being completely girdled.

Rodent problems in North America

The types and levels of damage associated with high rodent population densities have been discussed by Marsh (1988) and Witmer et al (1995). Commensal rodents, for example, Norway rats, roof rats (*Rattus rattus*), Polynesian rats (also called Kiore, *R. exulans*), and house mice, cotton rats and rice rats, ground squirrels, pocket gophers, voles, and sometimes lemmings all may cause losses to crops and pasture and rangeland forage. Many of these species will also cause significant damage to orchards and young forest plantations. Deer mice are mainly seed-eaters and can adversely affect reforestation efforts. Rats and mice cause physical damage to structures and wiring when they move into buildings. Tree squirrels cause damage to electrical wiring and transformers (causing power outages), and to structures and wiring when they move into building attics. Muskrats and nutria (*Myocastor coypus*) damage marsh vegetation, dikes and levees, and nearby crops. Beaver (*Castor canadensis*) damage includes flooding of roads and pastures, cutting and eating crops and ornamental plants, damaging fish ponds by plugging overflow pipes, and flooding of forested areas (Baker and Hill 2003). Once introduced to islands, commensal rodents have also caused significant damage to endemic flora and fauna, including the extinction of numerous species (Howald et al 2007).

High rodent population densities can result in increased cases of rodent-borne disease (e.g., hantavirus) transmission to humans (Hjelle and Glass 2000, Rodriguez-Moran et al 1998, Glass et al 2000), and in increased plague outbreaks (Stapp et al 2009). Ground squirrels are reservoirs of hantavirus and several zoonotic diseases, including leptospirosis, tularemia, and plague. Water-borne tularemia is a zoonotic disease occurring in beavers and muskrats. For an overview of the many diseases carried, and potentially transmitted, by rodents, see Meerburg et al (2009).

Case history: Richardson's ground squirrels in Canada

The range of Richardson's ground squirrel (*Spermophilus richardsonii*) includes the southern prairies of Canada and extends south into the prairie region of the north-central United States. The animals are buffy-gray and average 36 cm in total length, with a mass of 450 g. They produce one litter of 6–8 young per year and live to 3–4 years. They live in colonies and build and occupy elaborate burrow systems. They feed on a variety of natural green vegetation and seeds, but also various crops. The Richardson's ground squirrel is second in prominence only to the grasshopper in the rogue's gallery of agricultural pests in the Canadian plains. Reliable and comprehensive data are scarce, but it is certain that this rodent did severe damage to crops over large areas of the Canadian prairies in the last century, and generations of farmers waged battles to control this species (Banfield 1974).

In 2000-01, western and central Canadian prairies experienced a severe drought with warm winter and low precipitation (Liu et al 2004). As Richardson's ground squirrels prefer to establish their burrow systems in fields with shorter vegetation and good visibility (Yensen and Sherman 2003), dry weather and depressed plant growth created ideal conditions for a population outbreak (Proulx 2010), with densities often exceeding 40 animals ha^{-1} in spring (Proulx et al 2010). An increase in cattle numbers in the late 1990s (Statistics Canada 2001) because of a valuable market, and a huge livestock oversupply due to import restrictions on live ruminant animals and meat products from Canada caused by the discovery of bovine spongiform encephalopathy (mad cow disease) in 2003 (Mitura and Di Piétro 2004), led to overgrazing and persistence of favorable environmental conditions for ground squirrels (Proulx 2010). Although there was an obvious lack of effective control methods available to farmers at the beginning of the population outbreak (Proulx 2010), the adoption and misuse of a variety of poison baits during the 2000s (e.g., strychnine baits spread on surface, alteration of registered baits with other toxicants and attractants, excessive use of anticoagulants in poor bait station designs, etc.) resulted in an increase in moribund and poisoned ground squirrels and nontarget animals on the surface, and the subsequent poisoning of predators that further contributed to a lack of effective control of ground-squirrel populations (Proulx 2010). The Richardson's ground squirrel population outbreak was therefore due to an agricultural drought and poor grassland management following socioeconomic changes, and the depletion of predator populations (Proulx 2010).

The control of Richardson's ground squirrel populations requires a long-term management program, integrating sustainable grassland management techniques with an effective conservation of mammalian and avian predators, and the sensible use of effective rodenticides. The success of such a multifaceted management program will depend on the establishment of an effective education program, the institution of incentive programs for better management of grassland ecosystems, and the implementation and enforcement of rules to better monitor the production and distribution of effective poisons, and minimize their excessive use (Proulx 2010).

Case history: voles in Washington State

Voles occur over a large part of North America (Witmer et al 2009). These animals are grayish brown, and average 15–16 cm in length, with a mass of 40–50 g. They produce 1–5 litters of 3–6 young per year, but live only about a year. They build and occupy simple burrow systems with many openings. They feed on a variety of natural green vegetation and seeds, but also various crops. They are active year-round and feed on tubers and roots during the winter. When densities are high, they cause substantial damage to agriculture (Witmer and VerCauteren 2001). In no-till agricultural crop fields in the state of Washington, montane voles (*Microtus montanus*) and long-tailed voles (*M. longicaudus*) are the main damaging species.

Vole studies began at the Palouse Conservation Farm because of the damage being sustained in experimental no-till crop fields. Unfortunately, the land management practices used in no-till agriculture to conserve water and soil (no annual tillage, no burning, and leaving plant stubble) all benefit small rodent populations (Witmer and VerCauteren 1991). Initially, rodent population densities were high, with as many as 70 captures overnight in 10 by 10-m grids of 100 Sherman live traps (Witmer, unpublished data). As much as a 15% loss of pea plants occurred over winter (Witmer et al 2007). This can happen because voles remain active all winter under snow cover. A food habits study revealed that the voles were feeding mainly on grain crops (barley and wheat) as well as pea plants (Witmer et al 2007). It was clear that vole populations abandoned fields after harvest and that the surrounding fallow fields provided refugia for survivors and a source population that could later reinvade fields once crops were growing again.

Experimental population and damage control methods were started (Witmer et al 2007), but, unfortunately, the vole population crashed of its own accord so the study results were equivocal. Metal barriers extending about 38 cm above and below ground did not prevent rodent access to crops. Zinc phosphide–treated grain reduced populations, but they rebounded within a year. This suggests that rodenticide baiting would need to be a long-term vole management requirement to keep populations below significant damage thresholds.

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