

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.

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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.

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 (<i>Lemmus sibiricus</i>)	100	1	1–3	4–9	320	Yes	Tundra	Pitelka and Batzli (1993)
Voles (<i>Microtus</i> spp.)	65	1	1–5	3–6		Yes	Grassland	Beck et al (1958), Boonstra and Krebs (1978), Murray (1965)
Ground squirrels (<i>Spermophilus</i> spp.)	500	4–5	1	4–9	330	Yes?	Grassland	Proulx (2010), Rickart (1988)
Muskrat (<i>Ondatra zibethicus</i>)	1,100	2–3	2–3	4–8	100	Yes	Marsh, wetlands	Errington (1954)
Deer mice (<i>Peromyscus</i> spp.)	30	<1	2–4	3–5	100	No	Many habitats	Sullivan and Krebs (1981), Vessey and Vessey (2007), Hoffman (1955)
Pocket gophers (<i>Thomomys</i> spp.)	250	1–3	1–2	3–6	153	No	Forest, grassland	Witmer and Engeman (2007), Aldous (1957), Proulx (1997)
Cotton rats (<i>Sigmodon</i> spp.)	200	<1	2–6	5–7	373	No	Grassland	Hawthorne (1994)
Rice rats (<i>Oryzomys</i> spp.)	80	<1	5–6	2–5	50	No	Marsh, grassland	Smith and Vrieze (1979)
Grey squirrel (<i>Sciurus carolinensis</i>)	800	3–4	2	3	50	No	Forest	Jackson (1961)
Nutria ^a (<i>Myocastor coypu</i>)	5,400	2–3	2–3	4–5	138	No?	Marsh, wetlands	Wentz (1971)
Norway rat ^a (<i>Rattus norvegicus</i>)	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 (<i>Mus musculus</i>)	30	1	5–10	5–6	500	No?	Urban/suburban	Pearson (1963)

^aIntroduced 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 (<i>Spermophilus columbianus</i>)	10–30	43–78	Dobson and Kjelgaard (1985)
Fox squirrel (<i>Sciurus niger</i>)	0.05	2.1–5.1	Brown and Yeager (1945)
Northern pocket gopher (<i>Thomomys talpoides</i>)	47	183	Hansen (1960)
Muskrat (<i>Ondatra zibethicus</i>)	20–40	>80	Lynch et al (1947), Errington (1963)
Voies (<i>Microtus</i> spp.)	0	427	Myers and Krebs (1974), Taitt and Krebs (1985)
Mountain beaver (<i>Aplodontia rufa</i>)	<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 world-wide, 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 (<i>Thomomys talpoides</i>)	3–5 (native grass lands)	5–7 (alfalfa fields)	Hansen (1960), Hansen and Ward (1966), Andersen (1978), Proulx (2002)
Pine vole (<i>Microtus pinetorum</i>)	1.6 (abandoned orchard)	2.0 (managed orchard)	Cengel et al (1978)
Belding's ground squirrel (<i>Spermophilus beldingi</i>)	3.6	4.1 (supplemental feeding)	Trombulak (1991)

^aStatistically 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, Korpimäki and Norrdahl 1998), vegetation cover (Birney et al 1976), density-dependent season length (Smith et 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 Kioere, *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 Piéto 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

Voies 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.

References

- Agrell J, Erlinge S, Nelson J, Sandell M. 1992. Body weight and population dynamics: cyclic demography in a noncyclic population of the field vole (*Microtus agrestis*). *Can. J. Zool.* 70:494-501.
- Aldous CM. 1957. Fluctuations in pocket gopher populations. *J. Mammal.* 38:266-267.
- Andersen DC. 1978. Observation on reproduction, growth and behavior of the northern pocket gopher (*Thomomys talpoides*). *J. Mammal.* 59:418-422.
- Andersson M, Erlinge S. 1977. Influence of predation on rodent populations. *Oikos* 29:591-597.
- Baker BW, Hill EP. 2003. Beaver *Castor canadensis*. In: Feldhamer GA, Thompson BC, Chapman JA, editors. *Wild mammals of North America: biology, management, and conservation*. Baltimore, Maryland (USA): The Johns Hopkins University Press. p 288-310.

- Baker JA, Brooks RJ. 1982. Impact of raptor predation on a declining vole population. *J. Mammal.* 63:297-300.
- Banfield A. 1974. *The mammals of Canada*. University of Toronto Press, Toronto. 438 p.
- Batzli GO. 1999. Can seasonal changes in density dependence drive population cycles? *Trends Ecol. Evol.* 14:129-131.
- Beck RJ, Osgood SB, Smith MD, editors. 1958. *The Oregon Meadow Mouse irruption of 1957-1958*. Corvallis, Oregon (USA): Federal Cooperative Extension Service, Oregon State College. 88 p.
- Birney EC, Grant WE, Baird DD. 1976. Importance of vegetative cover to cycles of *Microtus* populations. *Ecology* 57:1043-1051.
- Boonstra R, Boag PT. 1992. Spring declines in *Microtus pennsylvanicus* and the role of steroid hormones. *J. Animal Ecol.* 61:339-352.
- Boonstra R, Krebs C. 1978. Pitfall trapping of *Microtus townsendii*. *J. Mammal.* 59:136-148.
- Brooks JE, Barnes AM. 1972. An outbreak and decline of Norway rat populations in California rice fields. *California Vector Views* 19:5-14.
- Brown LG, Yeager LE. 1945. Fox squirrels and gray squirrels in Illinois. *Illinois Nat. Hist. Survey Bull.* 23:449-535.
- Buckner CH. 1972. The strategy for controlling rodent damage to pines in the Canadian mid-west. In: Marsh RE, editor. *Proceedings of the 5th Vertebrate Pest Conference*. Davis, California (USA): University of California. p 43-48.
- Butler L. 1962. Periodicities in the annual muskrat population figures for the Province of Saskatchewan. *Can. J. Zool.* 40:1277-1286.
- Byrom AE, Karels TJ, Krebs CJ, Boonstra R. 2000. Experimental manipulation of predation and food supply of arctic ground squirrels in the boreal forest. *Can. J. Zool.* 78:1309-1319.
- Cengel DJ, Estep JE, Kirkpatrick RL. 1978. Pine vole reproduction in relation to food habits and body fat. *J. Wildlife Manage.* 42:822-833.
- Clotfelter ED, Pederson AB, Cranford JA, Ram N, Snajdr EA, Nolan V Jr, Ketterson ED. 2007. Acorn mast drives long-term dynamics of rodent and songbird populations. *Oecologia* 154:493-503.
- Colvin BA, Jackson WB. 1999. Urban rodent control programs for the 21st century. In: Singleton GR, Hinds LA, Krebs CJ, Spratt DM, editors. *Rats, mice and people: rodent biology and management*. Canberra (Australia): Australian Centre for International Agricultural Research. p 243-257.
- Colvin BA, Kaukeinen DE. 2008. Using an environmental management system to improve vertebrate pest programs. In: Timm RM, Madon MB, editors. *Proceedings of the 23rd Vertebrate Pest Conference*. Davis, California (USA): University of California. p 186-193.
- Corrigan RM. 2001. *Rodent control: a practical guide for pest management professionals*. Cleveland, Ohio (USA): GIE Media. 355 p.
- Dawson WR. 1955. The relation of oxygen consumption to temperature in desert rodents. *J. Mammal.* 36:543-553.
- Dobson FS, Kjelgaard JD. 1985. The influence of food resources on population dynamics in Columbian ground squirrels. *Can. J. Zool.* 63:2095-2104.
- Erlien DA, Tester JR. 1984. Population ecology of sciurids in north-western Minnesota. *Can. Field-Naturalist* 98:1-6.
- Errington PL. 1954. On the hazards of overemphasizing numerical fluctuations in studies of "cyclic" phenomena in muskrat populations. *J. Wildlife Manage.* 18:66-90.

- Errington PL. 1963. Muskrat populations. Ames, Iowa (USA): Iowa State University Press.
- Feldhamer G, Thompson B, Chapman J. 2003. Wild mammals of North America. 2nd ed. Baltimore, Md. (USA): The Johns Hopkins University Press.
- Ford RG, Pitelka FA. 1984. Resource limitation in populations of the California vole. *Ecology* 65:122-136.
- Gaby R. 1972. Differential niche utilization by two species of kangaroo rat (genus *Dipodomys*). Dissertation. Las Cruces, N.M. (USA): New Mexico State University. 71 p.
- Glass GE, Cheek JE, Patz JA, Shields TM, Doyle TJ, Thoroughman DA, Hunt DK, Ensore RE, Gage KL, Irland C, Peters CJ, Bryan R. 2000. Using remotely sensed data to identify areas at risk for Hantavirus Pulmonary Syndrome. *Emerging Infectious Diseases* 6:238-247.
- Hall ER. 1981. Mammals of North America. 2nd ed. New York, New York (USA): John Wiley & Sons. 2 vols.
- Hansen RM. 1960. Age and reproductive characteristics of mountain pocket gophers in Colorado. *J. Mammal.* 41:323-335.
- Hansen RM, Ward AI. 1966. Some relations of pocket gophers to rangelands on Grand Mesa, Colorado. Fort Collins, Col. (USA): Colorado Agricultural Experimental Station Technical Bulletin Number 88. 22 p.
- Hansson I, Henttonen H. 1985. Gradients in density variations of small rodents: the importance of latitude and snow cover. *Oecologia* (Berlin) 67:394-402.
- Hawthorne D. 1994. Cotton rats. In: Hygnstrom SE, Timm RM, Larson GE, editors. Prevention and control of wildlife damage. Lincoln, Nebraska (USA): University of Nebraska Cooperative Extension. p B-97-B-99.
- Hjelle B, Glass GE. 2000. Outbreak of Hantavirus infection in the Four Corners region of the United States in the wake of the 1997-1998 El Niño-southern oscillation. *J. Infectious Diseases* 181:1569-1573.
- Hoffman RS. 1955. A population-high for *Peromyscus maniculatus*. *J. Mammal.* 36:571-572.
- Hooven EF. 1977. The mountain beaver in Oregon: its life history and control. Oregon State University, Corvallis (USA): Forest Research Laboratory, Research Paper 30. 20 p.
- Hornfeldt B, Logren O, Carlsson BG. 1986. Cycles in voles and small game in relation to variations in plant production indices in northern Sweden. *Oecologia* 68:496-502.
- Howald G, Donlan C, Galvan J, Russell J, Parkes J, Samaniego A, Wandy Y, Veitch D, Genovesi P, Pascal M, Saunders A, Tershy B. 2007. Invasive rodent eradication on islands. *Conserv. Biol.* 21:1258-1268.
- Hygnstrom SE, Timm RM, Larson GE, editors. 1994. Prevention and control of wildlife damage. Lincoln, Nebraska (USA): University of Nebraska Cooperative Extension. 2 vols.
- Jackson H. 1961. Mammals of Wisconsin. Madison, Wis. (USA): University of Wisconsin Press. 504 p.
- Jacob J. 2008. Response of small rodents to manipulations of vegetation height in agro-ecosystems. *Integr. Zool.* 3:3-10.
- Karels TJ, Boonstra R. 2000. Concurrent density dependence and independence in populations of arctic ground squirrels. *Nature* 408:460-463.
- Kim S, Tschirhart J, Buskirk SW. 2007. Reconstructing past population processes with general equilibrium models: house mice in Kern County, California, 1926-1927. *Ecol. Model.* 209:235-248.
- Klemola T, Pettersen T, Stenseth NC. 2003. Trophic interactions in population cycles of voles and lemmings: a model-based synthesis. *Adv. Ecol. Res.* 33:75-160.
- Korpimäki E, Krebs CJ. 1996. Predation and population cycles of small mammals. *BioScience* 46:754-764.

- Korpimäki E, Norrdahl K. 1998. Experimental reduction of predator reverses the crash phase of small-rodent cycles. *Ecology* 79:2448-2455.
- Korpimäki E, Norrdahl K, Rinta-Jaskari T. 1991. Response of stoats and least weasels to fluctuating food abundances: is the low phase of the voles cycle due to mustelid predation? *Oecologia* 88:552-561.
- Korpimäki E, Brown PR, Jacob J, Pech RP. 2004. The puzzles of population cycles and outbreaks of small mammal solved? *BioScience* 54:1071-1079.
- Krebs C. 1996. Population cycles revisited. *J. Mammal.* 77:8-24.
- Lair H. 1985. Mating seasons and fertility of red squirrels in southern Québec. *Can. J. Zool.* 63:2323-2327.
- Lambin X, Bretagnolle V, Yoccoz NG. 2006. Vole population cycles in northern and southern Europe: is there a need for different explanations for single pattern? *J. Animal Ecol.* 75:340-349.
- Liu J, Stewart RE, Szeto K. 2004. Moisture transport and other hydrometeorological features associated with the severe 2000/01 drought over the Western and Central Canadian Prairies. *Am. Meteorol. Soc.* 17:305-319.
- Lokemoen JT, Duebbert HF. 1976. Ferruginous hawk nesting ecology and raptor populations in northern South Dakota. *Condor* 78:464-470.
- Lynch IJ, O'Neil T, Lay DW. 1947. Management significance of damage by geese and muskrats to Gulf Coast marshes. *J. Wildlife Manage.* 1:50-76.
- Marsh RE. 1988. Rodent problems on the North American continent. In: Prakash I, editor. *Rodent pest management*. Boca Raton, Fla. (USA): CRC Press, Inc. p 1-11.
- Massey FP, Smith MJ, Lambin X, Hartley SE. 2008. Are silica defenses in grasses driving vole population cycles? *Biol. Lett.* 4:419-422.
- McLeod JA. 1950. A consideration of muskrat populations and population trends in Manitoba. *Trans. Royal Soc. Can.* 44:69-79.
- Meerburg BG, Singleton GR, Kijlstra A. 2009. Rodent-borne diseases and their risks for public health. *Crit. Rev. Microbiol.* 35:221-270.
- Mihok S, Turner BN, Iverson SL. 1985. The characterization of vole population dynamics. *Ecol. Monographs* 55:399-420.
- Miller MA. 1946. Reproductive rates and cycles in the pocket gopher. *J. Mammal.* 27:335-358.
- Mitura V, Di Piéto L. 2004. Canada's beef cattle sector and the impact of BSE on farm family income, 2000-2003. Ottawa, Ontario (Canada): Statistics Canada, Agriculture Division, Catalogue No. 21-601-MIE. 6 p.
- Murray KF. 1965. Population changes during the 1957-58 vole (*Microtus*) outbreak in California. *Ecology* 46:163-171.
- Myers JH, Krebs CJ. 1974. Population cycles in small mammals. *Adv. Ecol. Res.* 8:267-399.
- Parnesan C, Root TL, Wilig MR. 2000. Impacts of extreme weather and climate on terrestrial biota. *Bull. Am. Meteorol. Soc.* 81:443-450.
- Parnesan C, Yohe G. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Science* 421:37-42.
- Pearson OP. 1963. History of two local outbreaks of feral house mice. *Ecology* 44:540-549.
- Pitelka F, Batzli G. 1993. Distribution, abundance and habitat use by lemmings on the north slope of Alaska. In: Stenseth N, Ims R, editors. *The biology of lemmings*. New York, NY (USA): Academic Press. p 213-236.
- Proulx G. 1997. A northern pocket gopher (*Thomomys talpoides*) border control strategy: promising approach. *Crop Prot.* 16:279-284.

- Proulx G. 2002. Reproductive characteristics of northern pocket gophers, *Thomomys talpoides*, in Alberta alfalfa fields. *Can. Field-Naturalist* 116:319-321.
- Proulx G. 2005a. Long-tailed weasel, *Mustela frenata*, movements and diggings in alfalfa fields inhabited by northern pocket gophers, *Thomomys talpoides*. *Can. Field-Naturalist* 119:175-180.
- Proulx G. 2005b. Body weights of adult and juvenile northern pocket gophers, *Thomomys talpoides*, in central Alberta alfalfa fields. *Can. Field-Naturalist* 119:551-555.
- Proulx G. 2010. Factors contributing to the outbreak of Richardson's ground squirrel populations in the Canadian Prairies. In: Timm RM, editor. Proceedings of the 24th Vertebrate Pest Conference. Davis, California (USA): University of California. (In press.)
- Proulx G, MacKenzie N, MacKenzie K, Proulx B, Stang K. 2010. The Richardson's ground squirrel (*Spermophilus richardsonii*) research & control program 2009-2010. Alpha Wildlife Research & Management Ltd. Report prepared for Saskatchewan Association Rural Communities (SARM), Regina, Saskatchewan (Canada). 50 p.
- Reichman OJ, Van De Graaf KM. 1975. Association between ingestion of green vegetation and desert rodent reproduction. *J. Mammal.* 56:503-506.
- Reid DG, Krebs CJ, Kenney A. 1995. Limitation of collared lemming population growth at low densities by predation mortality. *Oikos* 73:387-398.
- Rickart E. 1988. Population of the Piute ground squirrel (*Spermophilus mollis*). *Southwest. Nat.* 33:91-96.
- Rodriguez-Moran P, Kelly C, Williams TM, Hjelle B. 1998. Hantavirus infection in the Four Corners region of USA in 1998. *Lancet* 352:1353.
- Schmutz JK, Schmutz SM, Boag DA. 1980. Coexistence of three species of hawks (*Buteo* spp.) in the prairie-parkland ecotone. *Can. J. Zool.* 58:1075-1089.
- Schnurr JL, Ostfeld RS, Canham CD. 2002. Direct and indirect effects of masting on rodent populations and tree seed survival. *Oikos* 96:402-410.
- Simms DA. 1979. North American weasels: resource utilization and distribution. *Can. J. Zool.* 57:504-520.
- Singleton GR, Tann CR, Krebs CJ. 2007. Landscape ecology of house mouse outbreaks in south-eastern Australia. *J. Appl. Ecol.* 44:644-652.
- Smith A, Vrieze M. 1979. Population structure of everglades rodents: responses to a patchy environment. *J. Mammal.* 60:778-794.
- Smith RL. 1974. Ecology and field biology. 2nd ed. New York, New York (USA): Harper & Row Publishers.
- Smith MJ, White A, Lambin X, Sherratt JA, Begon M. 2006. Delayed density-dependent season length alone can lead to rodent population cycles. *Am. Nat.* 167:695-704.
- Stapp P, Salkeld DJ, Franklin HA, Kraft JP, Tripp DW, Antolin MF, Gage KL. 2009. Evidence for the involvement of an alternate rodent host in the dynamics of introduced plague in prairie dogs. *J. Animal Ecol.* 78:807-817.
- Statistics Canada. 2001. Record levels of cattle and hogs. Ottawa, Ontario (Canada): 2001 Census of Agriculture. www.statcan.gc.ca/ca-ra2001/first-premier/farmop-explagri/03livestock-beta1-eng.htm. Accessed January 2010.
- Stenseth NC. 1999. Population cycles in voles and lemmings: density dependence and phase dependence in a stochastic world. *Oikos* 87:427-461.
- Sullivan TP, Krebs CJ. 1981. An irruption of deer mice after logging of coastal coniferous forest. *Can. J. Forestry Res.* 11:586-592.

- Taitt MJ, Krebs CJ. 1985. Population dynamics and cycles. In: Tamarin RH, editor. *Biology of New World Microtus*. Pittsburgh, Penn. (USA): The American Society of Mammalogists. p 567-620.
- Tobin ME, Fall MW. 2004. *Pest control: rodents*. Fort Collins, Colorado (USA): Wildlife Damage Management, Internet Center for USDA National Wildlife Research Center. Available at http://digitalcommons.unl.edu/icwdm_udanwrc/67.
- Tomich PQ. 1986. *Mammals in Hawai'i*. Honolulu, Hawai'i (USA): Bishop Museum Press. 375 p.
- Trombulak SC. 1991. Maternal influence on juvenile growth rates in Belding's ground squirrel (*Spermophilus beldingi*). *Can. J. Zool.* 69:2140-2145.
- Vessey S, Vessey K. 2007. Linking behavior, life history and food supply with the population dynamics of white-footed mice (*Peromyscus leucopus*). *Integr. Zool.* 2:123-130.
- Wentz W. 1971. The impact of nutria (*Myocastor coypus*) on marsh vegetation in the Willamette Valley, Oregon. M.S. thesis. Corvallis, Oregon (USA): Oregon State University. 41 p.
- Wilson DJ, Krebs CJ, Sinclair T. 1999. Limitation of collared lemming populations during a population cycle. *Oikos* 87:382-398.
- Witmer GW, Engeman RM. 2007. Subterranean rodents as pests: the case of the pocket gopher. In: Begall S, Burda H, Schleich CE, editors. *Subterranean rodents: news from underground*. Berlin, Heidelberg (Germany): Springer-Verlag. p 287-299.
- Witmer GW, Fall MW, Fiedler LA. 1995. Rodent control, research needs, and technology transfer. In: Bissonette J, Krausman P, editors. *Integrating people and wildlife for a sustainable future*. Bethesda, Md. (USA): Proceedings of the First International Wildlife Management Congress. p 693-697.
- Witmer G, Snow N, Humberg L, Salmon T. 2009. Vole problems, management options, and research needs in the United States. In: Boulanger J, editor. *Ithaca, New York (USA): Proceedings of the 13th Wildlife Damage Management Conference*. p 235-249.
- Witmer G, Fantinato J. 2003. Management of rodents at airports. In: Fagerstone K, Witmer G, editors. *Fort Collins, Col. (USA): Proceedings of the 10th Wildlife Damage Management Conference*. p 350-358.
- Witmer G, Saylor R, Huggins D, Capelli J. 2007. Ecology and management of rodents in no-till agriculture in Washington, USA. *Integr. Zool.* 2:154-164.
- Witmer GW, VerCauteren K. 2001. Understanding vole problems in direct seeding: strategies for management. In: Veseth R, editor. *Pasco, Wash. (USA): Proceedings of the Northwest Direct Seed Conference*. p 104-110.
- Wolff JO, Edge WD. 2003. A retrospective analysis of a vole population decline in western Oregon, USA. In: Singleton GR, Hinds LA, Krebs CJ, Spratt DM, editors. *Rats, mice and people: rodent biology and management*. Canberra (Australia): Australian Centre for International Agricultural Research. p 47-50.
- Yensen E, Sherman PW. 2003. Ground squirrels: *Spermophilus* and *Ammospermophilus* species. In: Feldhammer GA, Thompson BC, Chapman JA, editors. *Wild mammals of North America: biology, management, and conservation*. Baltimore, Md. (USA): The Johns Hopkins University Press. p 211-231.
- Ylonen H, Eccard J, Sundell J. 2003. Boreal vole cycles and vole life histories. In: Singleton G, Hinds L, Krebs C, Spratt D, editors. *Rats, mice, and people: rodent biology and management*. Canberra (Australia): Australian Centre for International Agricultural Research. p 137-142.

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Witmer, Gary and Gilbert Proulx. Rodent outbreaks in North America. (2010. Pages 253-267 in Grant R. Singleton, Steve R. Belmain, Peter R. Brown, and Bill Hardy, editors. Rodent outbreaks: ecology and impacts. Los Baños (Philippines): International Rice Research Institute. 289p.

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