Long-tailed vole (*Microtus longicaudus*) population outbreaks and refugia after clearcutting of coniferous forests: The search for fluctuations and hotspots

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ABSTRACT

Some species of *Microtus* voles exhibit multi-annual population fluctuations with peak numbers every 3–5 years, and these periods may be interspersed with annual fluctuations in abundance. Populations of long-tailed voles (*M. longicaudus* Merriam) increase during the first 3–4 years after clearcutting of coniferous forests, and it is during this population outbreak that voles may feed on newly planted tree seedlings. It is unclear if *M. longicaudus* has multi-annual population fluctuations similar to other *Microtus* species, and we do not know the location of refuge habitats during low years of abundance. We describe changes in abundance of *M. longicaudus* during the first 5–10 years after clearcut harvesting near Golden, British Columbia, Canada, and evaluated four hypotheses (H) that long-tailed voles will (H₁) have peak populations at 3–4 years post-harvest, decline to low numbers, with outbreak populations appearing again on newly clearcut sites; (H₂) occur at very low (< 1 vole/ha) numbers in uncut forest; (H₃) persist at low numbers (< 5 voles/ha) in riparian refuge sites; and (H₄) be at lower abundance when *M. pennsylvanicus* (Ord) is present at equal or higher numbers.

Long-tailed vole populations increased in abundance on newly clearcut sites and reached independent peak numbers (62, 96, and 134/ha) at 3–4 years post-harvest in three different areas and time periods, thus supporting H₁. Long-tailed voles were consistently at very low numbers in uncut forest, and hence this habitat did not provide a refuge or source area for voles, thereby supporting H₂. We had some evidence to support H₃ that long-tailed voles seemed to persist at low numbers (< 5/ha) in riparian refuge sites. Where both species of voles were present, results tended to not support H₄. We conclude that *M. longicaudus* did not have a multi-annual population fluctuation in abundance, at least for the 9- to 11-year periods post-harvest that we investigated. Thus, tree mortality from an outbreak population of *M. longicaudus*, occurring at 3–4 years post-harvest, could be avoided by planning regeneration planting after this single peak population has subsided. Some long-tailed voles may persist past the peak population in, or near, riparian sites. These voles did not occupy old-growth forest, and hence they presumably migrate to new clearcuts via road networks facilitated by linear grass-dominated habitats.
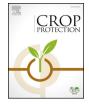
1. Introduction

Multi-annual population fluctuations of voles in the genera *Microtus* and *Myodes* in many north temperate and boreal ecosystems may occur synchronously over large geographical areas and were first described by Elton (1924). Populations of some species of voles reach peak populations every 3–5 years, although these periods may be interspersed with annual fluctuations in abundance (Körpimaki and Krebs, 1996; Krebs, 2013). The amplitude for numerical change is typically less than 5-fold for annual fluctuations and usually over 10-fold for multi-annual cycles (Taitt and Krebs, 1985). Much controversy exists in ecology over the

causes of these population fluctuations with food and predation likely major factors driving vole dynamics (Boonstra et al., 1998; Krebs, 1996, 2013). Voles are the main prey for a wide variety of predators including owls, raptors, small mustelids, and a host of other mammalian carnivores (Pugh et al., 2003). A major question asked by Ylonen et al. (2003), and many other researchers, is how do populations of voles and their predators survive such large population fluctuations? Presumably there are "refuge" habitats where low numbers of voles may persist after a major population decline. It is possible that voles disappear from "optimum" habitats such as meadows and old fields, but are able to survive at low numbers in "sub-optimal" wet habitats where perhaps

they are relatively safe from predation (Ylonen et al., 2003).

The long-tailed vole (*Microtus longicaudus* Merriam) occurs throughout most of the western United States (US) and Canada to eastern Alaska, and may occupy various forest successional habitats, as well as shrub-dominated and riparian sites (Smolen and Keller, 1987). Forest sites harvested by clearcutting have created variable-quality habitats for long-tailed voles in Montana (Halvorson, 1982), Alaska (Van Horne, 1982), and British Columbia (BC) (Sullivan et al., 1999; Sullivan and Sullivan, 2001; Klenner and Sullivan, 2003). *M. longicaudus* seems to have an annual population cycle that is tied to changes in early successional vegetation and availability of coarse woody debris, after clearcutting (Van Horne, 1982; Sullivan and Sullivan, 2010; Craig et al., 2015). Long-tailed voles, as well as other *Microtus* such as the meadow vole (*M. pennsylvanicus* Ord), require a given threshold of cover to occupy a habitat and increase in abundance (Birney et al., 1976; Van Horne, 1982; Adler and Wilson, 1989; Jacob, 2008). The long-tailed vole and meadow vole often occur together in early post-harvest forest sites if grass-dominated habitats are available for both species and a variety of successional habitats for *M. longicaudus* (Reich, 1981; Smolen and Keller, 1987; Zwolak, 2009). Presumed competition suggests that *M. pennsylvanicus* may behaviourally exclude *M. longicaudus* in at least some situations and this is likely habitat-dependent (Colvin, 1973; Randall, 1978; Anich and Hadly, 2013).

There is a 20-year history of plantation failures, owing to severe feeding damage from *M. longicaudus*, in young forest plantations in the Rocky Mountains near Golden in south-central BC, Canada (Sullivan and Sullivan, 2010). A 6-year study of population changes from the time of clearcutting indicated that populations of long-tailed voles seemed to rise and then decline with the abundance of herbaceous plants during the first 3–4 years after clearcutting of coniferous forests (Sullivan and Sullivan, 2010). Annual peaks of 49–84 voles/ha were recorded in the third year before declining in the fourth year. This decline deepened in the fifth post-harvest year and reached local extinction in the sixth year. This outbreak was the first recorded event of voles appearing in high numbers and consuming tree seedlings in this area of BC. Based on "snapshot" samples of habitat characteristics based on time since harvest, long-tailed voles were uncommon on older (> 6 years) successional sites at Golden (Sullivan and Sullivan, 2010), as they were elsewhere in south-central BC (Sullivan et al., 2008). It would have been ideal for continued sampling of long-tailed vole populations on these various cutover sites for several additional years to determine if a multi-annual population fluctuation might have occurred. *M. longicaudus* had an annual population cycle in Alaska at maximum numbers of 30–50 voles/ha in successional stages 2, 7, and 23 years post-harvest (Van Horne, 1982). Similarly, there were annual maximum numbers of 50–70 voles/ha in clearcut sites 9–13 years post-harvest in northwestern BC (Sullivan et al., 1999).

Voles may cause significant damage to trees in young forests in temperate and boreal ecosystems (Gill, 1992; Baxter and Hansson, 2001). In particular, the long-tailed vole is a major consumer of tree seedlings planted on cutover forest land in inland areas of the Pacific Northwest (PNW) of North America (Sullivan and Sullivan, 2010). In addition, the meadow vole also damages newly planted trees in various inland parts of North America (Bergeron and Jodoin, 1989; Ostfeld and Canham, 1993). It is primarily during overwinter periods when microtines feed on bark, vascular tissues (phloem and cambium), and sometimes roots of forest plantation trees and fruit trees in orchards. Direct mortality may result from girdling and clipping of tree stems, and reduced growth of trees that survive sub-lethal feeding injuries (Byers, 1984; Huitu et al., 2009). Newly planted seedlings are primarily damaged in the first winter when their nursery fertilization regime renders them particularly palatable to voles (Sullivan and Martin, 1991; Ostfeld and Canham, 1993). Feeding damage to trees may still occur in subsequent winters, but tends to be minor by 5 years post-planting. At Golden, this pattern was likely related to vole populations starting to decline by 4–5 years after harvest (Sullivan and Sullivan, 2010).

Feeding damage to trees in older plantations tended to be in "hotspots" where presumably a few long-tailed voles persist.

Identification and location of refuge habitats for voles that are pests of forest and agricultural crops would greatly assist management efforts in protecting trees from feeding damage. The question of refuge habitats in agricultural areas has focused on grassy linear habitats and hedgerows that border crop fields and sustain voles during population lows (Edge et al., 1995; Martinelli and Neal, 1995; Witmer et al., 2007; Sullivan and Sullivan, 2009; Rodriguez-Pastor et al., 2016). In forested habitats, most *Microtus* species respond favourably to moisture-bearing (often riparian) sites that have enhanced growth of herbaceous plants (Gashwiler, 1970; Hooven, 1973; Getz, 1985; Lehmkuhl et al., 2008; Bagne and Finch, 2010).

We report on three relatively long-term (5–10 years) datasets of changes in abundance of *M. longicaudus* during the first 10 years after clearcut harvesting near Golden. Our objectives were 1) to provide a description of population outbreaks and refugia of *M. longicaudus* associated with forest plantations; and 2) evaluate four hypotheses (H) that may help explain population changes in these forest habitats. Based on evidence, to date, we predicted that long-tailed voles will (H_1) have peak populations at 3–4 years post-harvest, decline to low numbers, with outbreak populations appearing again on newly clearcut sites; (H_2) occur at very low (< 1 vole/ha) numbers and not persist in uncut forest; (H_3) persist at low numbers (< 5 voles/ha) in riparian refuge sites; and (H_4) be at lower abundance when *M. pennsylvanicus* is present at equal or higher numbers.

Continued sampling of *M. longicaudus* in older plantations (> 6-year-old post-harvest clearcuts), beyond the initial population outbreak, should determine if multi-annual population fluctuations occur in these changing habitats. In addition, sampling of undisturbed habitats such as uncut mature forest will determine if long-tailed vole populations change in abundance independently of vegetative succession. Sampling of uncut forest and seepage (riparian) sites might yield clues as to the location of possible refuge habitats to provide a source of voles to colonize new clearcuts. If there is some degree of competitive exclusion between meadow and long-tailed voles, we would predict that fewer *M. longicaudus* would occur on post-harvest sites of any age if *M. pennsylvanicus* was present in substantial numbers.

2. Methods

2.1. Study areas

Three study areas were located at Roth Creek (51°18′N; 116°45′W), West Palliser (51°15′13″ N; 116°43′57″ W), and East Palliser (51°14′39″ N; 116°41′27″ W) at 25–30 km east of Golden. Roth Creek study sites were within the Montane Spruce (MS$_{dk}$ dry and mild) biogeoclimatic (BEC) subzone; the West Palliser and East Palliser sites were in the Interior Cedar-Hemlock (ICH$_{mk}$ moist cool) subzone (Meidinger and Pojar, 1991). Topography ranged from hilly to very steep terrain at 1060–1350 m elevation; Roth Creek had a south aspect and both West Palliser and East Palliser had a north aspect.

The MS has a cool, continental climate with cold winters and moderately short, warm summers. The average temperature is below 0 °C for 2–5 months, and above 10 °C for 2–5 months, with mean annual precipitation ranging from 30 to 90 cm. The MS landscape has extensive young and maturing seral stages of lodgepole pine (*Pinus contorta* Dougl. ex Loud. var *latifolia* Engelm.), which have regenerated after wildfire. Hybrid interior spruce (*Picea glauca* x *P. engelmannii* (Moench) Voss) and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) are the dominant shade-tolerant climax trees. Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco. var *glauca* (Beissn.) Franco) is an important seral species in zonal ecosystems and is a climax species on warm south-facing slopes in the driest ecosystems. Trembling aspen (*Populus tremuloides* Michx.) is a common seral species and black cottonwood (*Populus trichocarpa* T. & G.) occurs on some moist sites (Meidinger and