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Reinvasion dynamics of northern pocket gopher (*Thomomys talpoides*) populations in removal areas[☆]

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Abstract

This study was designed to test the hypothesis that continuous removal of northern pocket gophers (*Thomomys talpoides*) from natural habitats and tree fruit orchards would result in successful population reduction. A secondary objective was a detailed analysis of demographic responses (reinvasion dynamics) of gopher populations in control and removal sites. Pocket gopher populations were intensively live-trapped in replicate control and removal sites in natural and orchard habitats at Summerland and Vernon, British Columbia, Canada. New pocket gophers readily colonized removal sites in the natural habitats, particularly during spring, summer, and fall months. Fewer gophers colonized vacant sites during winter months ($\leqslant 1$ per ha at Summerland and $\leqslant 9$ per ha at Vernon). Mean abundance of gophers ranged from 15 to 31 per ha on control sites. Population increases due to recruitment on control sites were reflected in periods of high reinvasion of removal sites. Spring reproduction and subsequent dispersal of juvenile gophers resulted in high colonization of vacant habitat. The recovery ratio (colonization rate) of gophers in natural habitats averaged 26.9% in summer and 0.9% in winter at Summerland, and averaged 44.2% in summer and 40.4% in winter at Vernon. Recovery ratios to previous densities on removal sites averaged $> 100\%$ in summer at Summerland and in both seasons at Vernon. A relative recruitment index also followed this pattern at both study areas. New adult gophers that reinvaded removal sites produced young there despite continuous removal of animals. Mean body mass of gophers was significantly higher in control than removal populations at Summerland, but not Vernon. This study is the first intensive live-trapping evaluation of reinvasion dynamics of northern pocket gophers in removal sites. It seems likely that colonization of sites treated with toxicants or kill-trapping will be at least as high as the reinvasion rates recorded in our study. The timing of removals is crucial to achieving an overwinter reduction in gopher abundance.

Keywords: Agro-ecosystems; Feeding damage; Natural habitats; Northern pocket gopher; Old fields; Orchards; Population reduction; Recovery ratios; Reinvasion dynamics; Removal sites; *Thomomys talpoides*; Toxicants

1. Introduction

Pocket gophers (*Thomomys* spp.), in the family Geomyidae, are a group of fossorial rodents that inhabit burrow systems and inflict feeding damage to agricultural and forest crops in North America. The northern pocket gopher (*T. talpoides*) has the widest distribution of all pocket gophers extending from central Alberta and southern British Columbia (BC), Canada to northern New Mexico and Arizona, and from the Dakotas to eastern Washington, Oregon, and northeastern California (Chase et al., 1982). This species is a major vertebrate pest in the fruit-growing regions of BC (Anderson, 1980; Sullivan et al., 1987), Washington, and Oregon, as well as in alfalfa (*Medicago sylvatica*) and other cultivated crops throughout its range (Turner et al., 1973; Foster and Stubbendieck, 1980; Luce et al., 1981; Case, 1989). Pocket gophers feed on the bark, vascular tissues, and roots of orchard trees and vines. This feeding may lead to direct mortality or reduced growth and yield. Pocket gophers are also considered the most serious animal hazard to reforestation efforts in the western United States (Barnes, 1973; Crouch and Frank, 1979; Crouch, 1982). These rodents are likely the limiting factor to regeneration of pine regions throughout the Pacific Northwest because of their feeding on recently planted coniferous seedlings (Bonar, 1995).

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The use of toxicants is the primary method to alleviate feeding damage by pocket gophers. Although this technique is used extensively, there are continuing issues of resistance to formulations, hazard to non-target species, a general desire to reduce the use of pesticides in food and fiber production, and the resiliency of many rodent species to depopulation (Sullivan, 1986; Proulx, 1997). Resiliency or "reinvasion dynamics" of pocket gopher populations is the least understood process of these issues.

Rodents such as voles (*Microtus* spp.) and deer mice (*Peromyscus maniculatus*) readily colonize depopulated areas (Van Vleck, 1968; Myers and Krebs, 1971; Krebs et al., 1976; Martell and Radvanyi, 1977; Sullivan, 1979). However, studies of pocket gopher responses to removal areas include movements in burrow systems (Howard and Childs, 1959; Reichman et al., 1982; Proulx et al., 1995), impact on vegetation (Williams and Cameron, 1986), and dispersal (Williams and Cameron, 1984; Loeb, 1990). Proulx (1997) reported on immigration of pocket gophers by mound counts, in depopulated areas with and without perimeter trap lines. Considering the extensive use of toxicants and other removal methods to reduce pocket gopher populations, there is a dearth of studies investigating the responses of these rodents to depopulation.

This study was designed to test the hypothesis that continuous removal of northern pocket gophers from natural habitats and tree fruit orchards would result in successful population reduction. We provide a detailed analysis of demographic responses (reinvasion dynamics) of gopher populations in control and removal sites.

2. Material and methods

2.1. Study areas and experimental design

The Summerland study area was located at the Pacific Agri-Food Research Centre, Summerland, BC. One control (untreated) site (A) and one removal site (B) were each located in separate natural forb habitats (Table 1). An apple (*Malus domestica*) orchard habitat was located near the forb control site (A) and constituted a toxicant removal site (D). Thus, site A served as a control for both a forb removal site and an orchard removal site. Another control site (C) was located in an old field habitat with a nearby pear (*Pyrus* sp.) orchard habitat which acted as a second toxicant removal site (E) (Table 1). Both 1.2-ha orchards were located within a 90 ha mosaic of tree fruits and vineyards which had strychnine-treated oats (Gopher Getter®) applied to burrow systems 3–4 times a year. Common plant species in the forb habitats at Summerland were diffuse knapweed (*Centaurea diffusa*), baby's breath (*Gypsophila paniculata*), arrow leaved balsamroot (*Balsamorhiza sagittata*), and bunchgrass (*Agropyron spicatum*); and in the orchard and old field habitats were orchard grass (*Dactylis glomerata*), quack grass (*A. repens*), bluegrass (*Poa* spp.), smooth brome (*Bromus inermis*), and crested wheatgrass (*A. cristatum*). The orchards were mowed 5 or 6 times each summer. The old field control habitat was not mowed.

Table 1
Design of control and removal sites at the Summerland and Vernon study areas. Letters designate control-removal pairs

Study area	Control habitat	Removal habitat
Summerland	Forb-A	Forb-B
	Forb-A	Orchard-D
	Old field-C	Orchard-E
Vernon	Old field-G	Old field-H
	Orchard-I	Orchard-J

A second study area was located in Kalamalka Lake Park (old field habitat) and at the Coldstream Ranch (apple orchard habitat), near Vernon, BC. Each of the old field and orchard habitats had one control site and one removal site (Table 1). Plant species in the old field habitats were similar to those at Summerland; and in the orchards were orchard grass, dandelion (*Taraxacum officinale*), and other forbs in minor abundance. These orchards were mowed two or three times each summer. Toxicants were not applied to gopher burrow systems in these orchards. In those removal sites where toxicants were not applied, pocket gophers were removed permanently from the sites.

Our experimental design had two true replicates of control and removal sites in natural habitats. A third replicate pair would clearly have strengthened the study. Because all orchard control sites at Summerland were treated with toxicants for pocket gophers, we had to use nearby forb and old field sites as controls for the orchard removal sites. These control sites were different from the orchard sites and this was an important limitation for our results and conclusions. All control and removal sites were spatially segregated to ensure independence of experimental units (Hurlbert, 1984).

2.2. Pocket gopher populations

Gophers were live-trapped on 1-ha checkerboard grids with Longworth live-traps. Each grid (except for Summerland removal at 6 × 8) had 49 (7 × 7) stations at 14.3-m intervals. Live-traps were set within recently used tunnels or burrows indicated by fresh excavations of soil. Thus, traps did not usually have permanent stations but were moved in response to gopher activity. Traps were baited with whole oats, peanut butter, and carrot; coarse brown cotton was supplied as bedding. Traps were set on day 1, checked on the morning and afternoon of day 2, and morning of day 3, and then locked open between trapping periods. The Summerland and Vernon grids had 20–35 and 40–45 traps, respectively, set in a given trapping period.

Pocket gopher populations at Summerland were live-trapped at 3-week intervals from July 1982 to September 1983 in the orchard-old field habitats and from March 1983 to September 1984 in the forb habitats. The control-removal comparison in the forb habitats was terminated in September 1984 because of loss of these experimental units to land development. Gopher populations at Vernon were also live-trapped at 3-week intervals from May 1983 to November 1985 in the old field habitats, and from April 1985 to November 1985 in the orchard habitats. Trapping was conducted at 4-week intervals in winter. Summerland populations were not sampled between December 1983 to February 1984 nor Vernon populations between December 1983 to March 1984 and November 1984 to April 1985 because of snowfall and frozen ground conditions.

All gophers captured were ear-tagged with serially numbered tags, breeding condition noted, weighed on Pesola spring balances, and point of capture recorded. Reproductive performance was measured by palpation of male testes and the condition of mammaries of females (Krebs et al., 1969). New animals appearing in traps for the first time were called recruits. Age at sexual maturity was used to determine age classes of gophers with body weight used as an index of age. The percentage of sexually mature animals in a series of weight classes was used to determine the weight limitations for juveniles and adults. Our age classes have assumed juveniles to be young of the year which do not breed until the next year, and hence are seldom if ever sexually mature. Individuals of which $< 50\%$ are mature in the upper weight class are called subadults. Adults must have at least 50% of gophers sexually mature in the lowest weight class. Age classes of gophers were determined by body weight: juveniles < 49 g; subadults 49–60 g; adults $\geqslant 61$ g.

2.3. *Demographic and reinvasion parameters*

Complete enumeration using minimum number alive (MNA) (Krebs, 1966) provided the density values for each trapping period. MNA takes into account animals that are known to be alive but are not captured at a given sampling time. If x number of animals captured at time t are not caught at $t + 1$ but are recaptured at $t + 2$, then those x animals are alive but not censused at $t + 1$ and are included in the density estimate for that time. This technique yields reasonably accurate estimates when trappability of animals is $\geqslant 70\%$ (Hilborn et al., 1976). Mean unweighted trappability (susceptibility to capture) treats each individual animal as one sample, regardless of how long it occurred in a given population (Krebs and Boonstra, 1984). Population densities for the control populations were also estimated by the Jolly–Seber model (Seber, 1982) for reasons outlined by Jolly and Dickson (1983). All gophers captured during each trapping period on the three removal sites were removed permanently from the grids by transport to release areas $\geqslant 5$ km away from sites.

Reinvasion rate of the removal and toxicant sites was measured in three ways: number of new gophers, recovery ratio, and relative recruitment index (Krebs et al., 1976). Recovery ratio = number of gophers colonizing removal grid at time '*i*'/population size on control grid at time '*i*'. Relative recruitment index = number of gophers colonizing removal grid at time '*i*'/number of new recruits tagged on control grid at time '*i*'. The recovery ratio was used as a measure of the resiliency (Holling, 1973) of the control populations as well as that of the number of gophers that have reinvaded the removal and toxicant grids during the previous trapping period. Data have been grouped into summer (April–September) and winter (October–March) periods.

Reproductive performance was based on number of successful pregnancies. A pregnancy was considered successful if a female was lactating during the period following the estimated time of birth of a litter (Sullivan, 1990). Average body mass, with 95% confidence limits, was calculated for male and female gophers in control and removal populations.

3. Results

3.1. *Pocket gopher populations*

Trappability estimates of pocket gophers ranged from 60.8 to 77.4% and from 51.4 to 86.1% in the Summerland forb and old field control sites, respectively (Table 2). These estimates were lower at the Vernon old field control site with a range of 41.2–61.1%. Totals of individual pocket gophers captured on the Summerland forb control and removal grids were 58 and 80, respectively, and on the Vernon old field control and removal grids were 175 and 345, respectively.

Population changes on control and removal forb sites at Summerland indicated that new pocket gophers readily colonized the removal site during the months of May through August (Fig. 1). The control population of gophers peaked at 21 per ha in 1983 and 19 per ha in 1984. Continuous removal of gophers during summer months resulted in few, if any, animals available to colonize the depopulated area during fall and winter months. At Vernon, in old field habitat, new gophers continued to disperse into the vacant area from May through October, with fewer colonist gophers appearing during winter months. The control population of gophers peaked at 22 per ha in 1983, 38 per ha in 1984, and 25 per ha in 1985. Pocket gopher populations showed a clear annual cycle of abundance on the control site at each study area.

Table 2
Mean estimates (%) of minimum unweighted trappability (MUT) for northern pocket gopher populations in control sites of forb and old field habitats during summer and winter periods (sample size in parentheses)

Period	Summerland		Vernon
	Forb	Old field	Old field
Summer 1983			
MUT	77.4 (22)	86.1 (13)	61.1 (20)
Winter 1983–1984			
MUT	60.8 (17)	74.7 (10)	50.0 (16)
Summer 1984			
MUT	69.9 (22)	51.4 (11)	50.6 (38)
Winter 1984–1985			
MUT	—	—	41.2 (17)
Summer 1985			
MUT	—	—	46.5 (26)

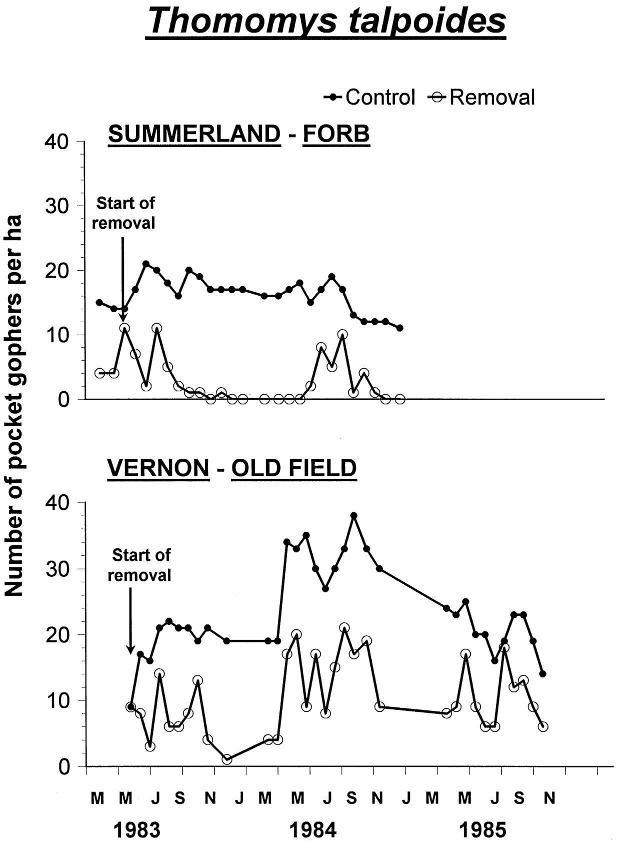

Fig. 1. Population densities (MNA) of northern pocket gophers on control and removal sites in forb and old field habitats at Summerland and Vernon, respectively, during the study. Arrow indicates start of removal experiments.

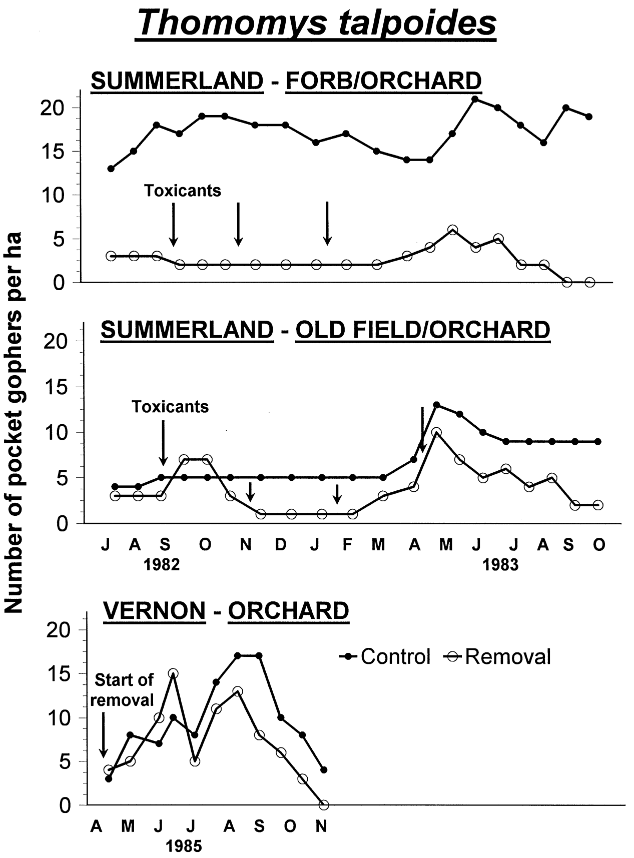

Fig. 2. Population densities (MNA) of northern pocket gophers on control and removal sites in the forb/orchard and old field/orchard habitats at Summerland and the orchard habitat at Vernon during the study. Arrows indicate time of application of toxicants to orchard sites at Summerland and start of removal in orchard sites at Vernon.

Periods of high reinvasion of the respective removal sites appeared to follow a similar pattern of population increases on control sites (Fig. 1). Mean density of gophers per ha was similar at Summerland (S) and Vernon (V) during summer 1983 (18.1) and in winter 1983–1984 ($S = 16.7$ and $V = 19.5$) (Table 3). Mean densities increased to 15.4 (S) and 31.0 (V) during summer 1984 and 31.5 (V) during winter 1984–1985 before declining to 21.3 (V) gophers per ha in summer 1985. Overall, Jolly–Seber estimates averaged 10.9 and 39.5% higher than the MNA values for the control sites at Summerland and Vernon, respectively. Jolly–Seber and MNA calculations showed similar changes in abundance of pocket gophers over time.

Population changes in orchard habitats and their respective controls indicated lower number of pocket gophers in the orchard environments than those recorded in the forb and old field habitats at Summerland and Vernon, respectively (Fig. 2). This difference was most pronounced at Summerland where the gopher population was, on average, 6.7 times higher in the forb control than orchard habitat. This major difference was likely due to the use of forb habitat as a control for orchard habitat. However, the mean abundance of gophers in the Summerland old field control was only 1.8 times higher than that in the orchard habitat (Fig. 2). At Vernon, mean abundance of pocket gophers per ha was 9.7 and 7.3 in the control and removal orchard habitats, respectively (Table 4).

3.2. Reinvasion dynamics

The recovery ratio (colonization rate), with respect to the control population, averaged 26.9% in summer and was 0.9% in winter at Summerland, and averaged 44.2% in summer and 40.4% in winter at Vernon (Table 3). The recovery ratio to the density at the previous trapping period on the removal grid averaged 131.4% in summer and was 0% in winter at Summerland. This same comparison averaged 138.5% in summer and 105.2% in winter periods at Vernon (Table 3). The relative recruitment index averaged 2.09 in summer and was 0.2 in winter at Summerland, and averaged 1.90 in summer and 2.85 in winter periods at Vernon. This measure means that the number of colonist gophers on the removal grids was 90–109% above the number of new gophers captured on the control grids at the two study areas. In winter periods at Vernon, this comparison indicated that, on average, the number of removal colonists was 185% above the number of new gophers appearing on the control grid. Thus, in spite of continuous removal, which should have prevented most reproduction on these removal sites, more new pocket gophers still appeared on these sites than on the controls.

The reinvasion dynamics of gophers on the orchard sites at Summerland was based on use of toxicants as removal agents rather than capture and physical removal of animals from the live-trapping grids. This was not the case at the Vernon orchard sites where physical removal of animals was implemented rather than toxicants. The forb control and orchard removal at Summerland were clearly different in carrying capacity for gophers (Fig. 2). Therefore, the best evaluation of reinvasion capacity was the recovery ratio to previous density which averaged 91.3% on the orchard site (Table 4). The old field control and orchard removal at Summerland were somewhat similar habitats despite the regular mowing of the orchard site (Fig. 2). The mean number of gophers colonizing the removal grid as a percentage of the control density averaged 36.5% in summer and was 5.7% in winter (Table 4). Recovery ratio to previous density averaged 121.2% and the relative recruitment index averaged 1.67 over the three periods, despite four applications of toxicants (Fig. 2).

At Vernon, physical removal of pocket gophers over the summer 1985 period resulted in an 82.5% influx of immigrant animals relative to the control, recovery ratios of 71.9% to the control population and 103.3% to previous density, and a relative recruitment index of 2.22 (Table 4). More new gophers colonized the removal grid than were present on the control during trapping periods in June 1985 (Fig. 2). Totals of individual pocket gophers captured on the Vernon orchard control and removal grids during the one summer period were 37 and 80, respectively.

3.3. Demographic parameters

The breeding season for pocket gophers, based on reproductive condition of males, extended from as early as February at Summerland to the end of May each year at both study areas. Based on incidence of lactating females, there was a maximum of two litters produced per reproductive female during this period. Young of the year gophers appeared as recruits on two occasions during May and June in accordance with approximate weaning times of the two litters. This spring influx of juvenile gophers was reflected in the increase in gopher

Table 3
Average density for control populations and reinvasion data (per 3 weeks) for removal populations of northern pocket gophers during summer and winter periods for Summerland forb habitats and Vernon old field habitats. Sample size (n = number of trapping periods) in parentheses

Study area and period	Control populations (MNA[a]) ± SE	Removal populations			
		Number of immigrants	Recovery ratios (%)		Relative recruitment index
			Control	To previous density	
Summerland forb A + B					
Summer 1983 ($n = 8$)	18.1 ± 0.8	5.00	29.5	125.4	2.11
Winter 1983–1984 ($n = 7$)	16.7 ± 0.2	0.14	0.9	0.0	0.20
Summer 1984 ($n = 8$)	15.4 ± 1.0	3.88	24.3	137.3	2.07
Vernon old field G + H					
Summer 1983 ($n = 7$)	18.1 ± 1.8	7.71	37.8	145.0	1.32
Winter 1983–1984 ($n = 4$)	19.5 ± 0.5	2.75	28.3	154.8	2.00
Summer 1984 ($n = 9$)	31.0 ± 1.8	14.22	44.9	148.1	1.88
Winter 1984–1985 ($n = 2$)	31.5 ± 1.5	3.50	44.0	79.5	1.87
Summer 1985 ($n = 8$)	21.3 ± 1.1	10.63	50.0	122.3	2.50
Fall 1985 ($n = 3$)	18.7 ± 2.6	9.33	49.0	81.3	4.67

[a] MNA = minimum number alive.

Table 4
Average density for control populations and reinvasion data for toxicant (Summerland) and removal (Vernon) populations of pocket gophers in orchards during summer and winter periods. Control sites at Summerland were located in forb and old field habitats, not orchards. Sample size (n = number of trapping periods) in parentheses

Study area and period	Control populations (MNA[a]) ± SE	Removal populations			
		Number of immigrants	Recovery ratios (%)		Relative recruitment index
			Control	To previous density	
Summerland orchard A + D					
Summer 1982 ($n = 4$)	15.8 ± 1.1	1.50	17.9	89.0	0.22
Winter 1982-83 ($n = 7$)	17.4 ± 0.6	0.00	11.5	100.0	0.00
Summer 1983 ($n = 9$)	17.7 ± 0.9	1.11	17.0	85.0	0.50
Summerland orchard C + E					
Summer 1982 ($n = 4$)	4.5 ± 0.3	2.25	50.0	144.3	1.50
Winter 1982-83 ($n = 7$)	5.0 ± 0.0	0.29	5.7	110.8	2.00
Summer 1983 ($n = 9$)	9.7 ± 0.6	2.33	22.9	108.5	1.50
Vernon orchard I + J					
Summer 1985 ($n = 11$)	9.7 ± 1.4	8.00	71.9	103.3	2.22

[a] MNA = minimum number alive.

populations on control sites and the pulses of dispersers which appeared on removal sites during this time (Fig. 1). The second period of increased recruitment and dispersal on these respective sites occurred in the fall each year and was likely related to subadult gophers seeking a place to overwinter.

The number of successful pregnancies for control and removal forb sites at Summerland was 4 and 5 in 1983, and 12 and 0 in 1984, respectively. This measure of reproductive performance for control and removal old field sites at Vernon was 1 and 2 in 1983, 19 and 15 in 1984, and 14 and 9 in 1985, respectively. Thus, except for a complete lack of litter production in the Summerland removal in 1984, new adult pocket gophers reinvaded the removal sites and produced young there despite continuous removal of animals through time.

Mean body mass of pocket gophers was significantly (non-overlapping 95% confidence intervals) higher in control than removal populations for males in summer 1983 and for males and females in summer 1984 in the Summerland forb habitats (Fig. 3). This pattern was not evident in the Vernon old field habitats where mean body masses of males and females were similar (overlapping 95% confidence intervals) in control and removal populations of gophers (Fig. 3). The only exception was in summer 1984 when mean body mass of males was higher in the control than removal populations.

Mean body mass of pocket gophers was similar in control and removal populations in the Summerland forb/orchard, old field/orchard, and Vernon orchard comparisons (Table 5). An exception was in summer 1982 when male gophers at Summerland were significantly heavier in the forb control than on the orchard removal.

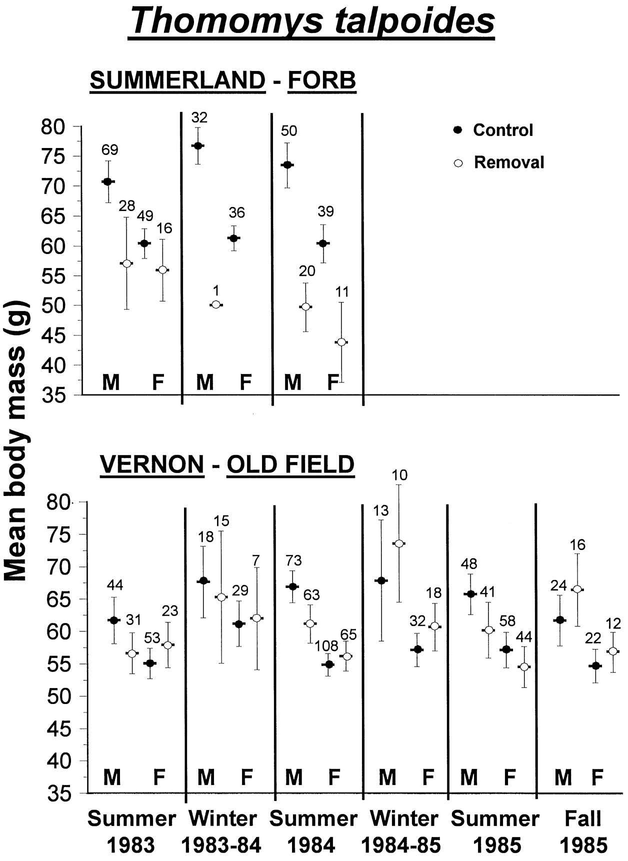

Fig. 3. Mean body mass (g) ± 95% confidence intervals for male (M) and female (F) northern pocket gophers in control and removal sites in forb and old field habitats at Summerland and Vernon, respectively, during summer and winter periods in the study. Sample size is given above upper interval bar.

Table 5
Mean body mass (g) ± 95% confidence intervals for male and female northern pocket gophers in control and removal populations in Summerland forb/orchard and old field/orchard habitats and Vernon orchard habitats during summer and winter periods. Sample size is given in parentheses

Study area and period		Males		Females	
		Control	Removal	Control	Removal
Summerland-Forb/orchard					
Summer 1982	χ	68.9	55.7	68.3	66.3
	95% C.I.	65.3–72.6	48.1–63.3	64.4–72.2	61.9–70.7
	(*n*)	(28)	(3)	(23)	(7)
Winter 1982–1983	χ	78.5	—	63.6	66.5
	95% C.I.	75.3–81.8	—	61.6–65.5	61.2–71.8
	(*n*)	(36)	(0)	(35)	(10)
Summer 1983	χ	70.7	63.0	60.4	63.1
	95% C.I.	67.2–74.2	46.9–79.1	57.9–62.9	58.2–67.9
	(*n*)	(69)	(6)	(49)	(17)
Summerland-Old field/orchard					
Summer 1982	χ	74.0	64.9	61.8	68.4
	95% C.I.	—	62.5–67.2	57.9–65.7	58.8–78.0
	(*n*)	(2)	(7)	(11)	(8)
Winter 1982–1983	χ	89.9	74.0	63.4	71.9
	95% C.I.	72.7–107.0	—	58.1–68.7	64.5–79.3
	(*n*)	(7)	(1)	(14)	(10)
Summer 1983	χ	60.7	58.1	62.8	62.7
	95% C.I.	52.6–68.9	51.8–64.4	60.5–65.1	54.9–70.4
	(*n*)	(22)	(16)	(58)	(21)
Vernon – Orchard					
Summer 1985	χ	74.4	73.2	64.5	58.7
	95% C.I.	66.7–82.1	68.9–77.6	61.5–67.4	54.6–62.8
	(*n*)	(22)	(49)	(59)	(31)

4. Discussion

4.1. Experimental design

Our study had two true replicates of control and removal sites in forb and old field habitats (Hurlbert, 1984). Unfortunately, the Summerland replicate pair was terminated in October 1984 when the sites were developed for other purposes. The study would have been strengthened with addition of a third replicate of these control-removal treatments in a natural habitat. We did have a third true replicate of control and removal sites in the Vernon orchard, albeit for 1 yr only.

Due to lack of availability of orchard control sites at Summerland, we had to use nearby forb and old field sites. Clearly, these control sites were different from orchard habitat conditions. Thus, the most meaningful measurement of resiliency in the orchard populations was to previous density estimates, which was independent of the control populations. The control-removal sites in orchard habitat at Vernon were appropriate experimental units and indicated the high resiliency and density of gophers in orchards without toxicants, at least compared with Summerland orchards. Again, three true replicates of these orchard sites would have strengthened our study considerably.

There was no movement of pocket gophers between sites as no marked gophers were captured on more than one sampling grid, thereby ensuring spatial segregation of experimental units. In addition, the initial densities of gophers in the paired sites were reasonably similar at the start of the removal experiments. The only exception was the forb–orchard sites at Summerland which were clearly different from each other.

A major assumption of our experimental design to measure reinvasion dynamics was that most, if not all, pocket gophers were captured and removed from the removal sites. Since minimum unweighted trappability in the control populations averaged 70% at Summerland and 50% at Vernon, it could be argued that we did not remove all gophers from a given removal site. However, it is likely that our depopulation of gophers via intensive trapping was at least as effective, or more so, than that achieved by toxicants. The persistence of gophers on the two poisoned orchard sites at Summerland, albeit at low density, support this contention. Similarly, several studies have reported the inconsistency of baiting to control gopher populations because of poor bait acceptance and durability (see review by Bonar, 1995). Thus, our population reduction experiment was likely more direct and effective than those conducted with standard toxicant baiting programs.

A second important assumption was that our 1-ha removal sites provided a meaningful scale allowing extrapolation of results to operational areas. It is likely that rates of reinvasion would have been slower if this experiment had been conducted on a larger scale (e.g. 10–100 ha). However, use of toxicants or kill-trapping on an operational basis is usually conducted for short periods only, particularly in the fall in forest plantations, when gopher abundance is highest, prior to the onset of winter. In agricultural crops, baiting may be more frequent as in our orchard sites at Summerland. Regardless, it is unlikely that any operational program would keep a target site devoid of gophers in a manner similar to our experimental results. If this is the case, it seems likely that reinvasion of operationally treated sites is at least as high as recorded in our study, regardless of scale.

4.2. *Reinvasion dynamics*

Our study is the first intensive live-trapping evaluation of the reinvasion dynamics of northern pocket gophers in removal sites. Because toxicants and kill-trapping are the primary methods to reduce populations to alleviate feeding damage by gophers (Bonar, 1995), it seemed prudent to provide a detailed experimental assessment of how these burrowing rodents respond to depopulated areas. Clearly, pocket gophers will readily colonize vacant habitat and in many cases will breed there and produce litters. Alternatively, females may have been pregnant prior to dispersal (Daly and Patton, 1990). Our measurements of resiliency of gopher populations were based on continuous removal of animals in "natural" forb and old field habitats, as well as in the Vernon orchard habitat. The "pulse removal" method through use of toxicants in orchards at Summerland represented one current management regime for these rodent pests. Depending on the durability of toxicant baits or period of kill-trapping, these methods may remove gophers for several weeks or even months under the right conditions (Crouch and Frank, 1979; Tunberg et al., 1984; Marsh and Steele, 1992). However, continuous removal of colonist gophers is not likely under current management scenarios. Thus, our measurements of resiliency represent an ideal situation whereby removal areas are continuously depleted of gophers.

Our hypothesis, that continuous removal of northern pocket gophers from natural habitats and tree fruit orchards would result in successful population reduction, appears to be partially acceptable based on the results from winter months. Abundance of gophers was reduced to $\leqslant 1$ animal/ha in the Summerland forb removal and to $\leqslant 9$ animals/ha in the Vernon old field removal during the winter periods. In summer and fall, numbers of gophers on these removal sites were, on average, 25–50% of the abundance of gophers on control sites. Recovery ratios to previous densities on the removal sites were greater than 100% in most cases, except in some fall and winter months.

The higher population resiliency in Vernon old field sites than in Summerland forb sites was that the forb habitats were located within a mosaic of forb, old field, sagebrush (*Artemisia tridentata*) and orchard habitats at Summerland. None of these habitats was more than 2–3 ha in area. The Vernon old field sites were located within a 100-ha area of continuous and relatively homogeneous habitat. Thus, the source area for gophers to colonize vacant habitat appeared much greater at Vernon than Summerland. This difference was also evident when comparing gopher densities in orchards at Summerland and Vernon. The Vernon orchard covered about 60 ha compared with the much smaller unit size at Summerland. The impressive resiliency of gophers to continuous removal in the Vernon orchard habitat supported this premise (see Fig. 2). An alternative explanation might be that the Summerland orchards had ongoing toxicant applications, whereas those at Vernon did not.

4.3. *Pocket gopher populations*

Pocket gopher populations were relatively stable ranging from 15 to 31 animals/ha in the natural habitats and following an annual cycle of abundance: lower densities in spring from cumulative overwinter mortality and higher densities in fall from juvenile recruitment. This pattern was predictable based on reproductive output of 2 litters/year. Teipner et al. (1983) reported maximum population densities of *T. talpoides* ranging from 59 to 89 animals/ha in presumably optimum habitat. Other estimates were 47 northern pocket gophers/ha on grass/forb range (Chase et al., 1982) and 37 to 62 animals/ha was a high population of *Thomomys* on forest lands (Marsh and Steele, 1992). However, these maximum densities are nearly always in a patchy distribution based on soil characteristics, moisture conditions, and plant communities (Marsh and Steele, 1992). In particular, composition of herbaceous vegetation constitutes the most important habitat factor in determining gopher population thresholds (Andersen and MacMahon, 1981). Thus, our populations were at the lower end of the range of densities of this species. If this is the case, it is possible that reinvasion of vacant areas may be more rapid at higher densities of gophers than recorded in our study.

Since young of the year gophers do not breed until they are at least 1 yr of age (Bonar, 1995), the potential for multi-annual fluctuations in abundance, like those of *Microtus*, are limited. Juvenile gophers are forced from the nest by agonistic behaviour at 5–8 weeks after birth (Teipner et al., 1983). These dispersing juvenile and subadult gophers will readily occupy vacated burrow systems, thereby providing the biological drive to fill in "open" habitat (Reichman et al., 1982; Teipner et al., 1983). In addition, young gophers will occupy marginal habitats until better areas become available, as when other gophers disperse or die (Teipner et al., 1983). This factor may explain the increase in gopher recruitment during fall months in our forb and old field habitats.

4.4. Management implications

Our results have demonstrated the considerable capacity of pocket gophers to reinvade vacant habitat, particularly during spring, summer, and fall months. Some relief appears during winter months when abundance is reduced to < 10 animals/ha through a program of continuous removal of gophers. However, current toxicant and kill-trapping programs do not provide continuous removal of gophers, but rather a series of "pulse-removal" interventions. Based on our results, the timing of removals is critical to achieving at least an overwinter reduction in gopher abundance. For those areas where the northern pocket gopher has two litters in the spring, population reduction during the breeding period will reduce the number of reproductive gophers, and consequently the potential number of juveniles available for colonization. A follow-up program in the fall should further reduce abundance of gophers prior to winter.

In terms of crop protection in forest and agricultural settings, management of gophers will continue to rely on toxicants and trapping to combat the resiliency of these burrowing rodents until another method of damage control becomes available. Development of new bait formulations and evaluation of hazards to non-target species will presumably also continue. Alternatively, other approaches should be encouraged such as herbicide-induced habitat alteration which has been effective in protecting forest (Crouch, 1979, 1982; Engeman et al., 1995, 1998), range (Keith et al., 1959; Tietjen et al., 1967), and orchard (Sullivan and Hogue, 1987) crops by rendering the habitat less favorable to gophers. Although untested in large-scale programs, predator odours used as repellents, to generate an avoidance response in gophers, and as attractants for predators, have shown considerable promise (Sullivan et al., 1988, 1990). Two other potential management tools include manipulation of vegetation cover crops and provision of artificial diversionary foods.

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