# Abating pocket gophers (Thomomys spp.) to regenerate forests in clearcuts

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## Summary

Pocket gophers have long suppressed forest regeneration in clearcuts in western North America, despite the application of intensive and costly, large-scale abatement practices, which also kill non-target wildlife and may increase soil erosion. At four national forests in northern California, gophers (Thomomys bottae and T. monticola) on 50 clearcuts were baited with a 0.5% strychnine concentration on wheat or oat groats, which were presented as loose grains or in  $1 \times 2$  cm paraffin pellets for added durability. The various baits and baiting regimes usually reduced gopher abundance by 50-100% within one month. However, gopher populations recovered too quickly to protect seedlings planted for forest regeneration, especially on plots baited with a mechanical burrow-builder. In some plots where abatement was most successful initially, gopher densities increased to levels exceeding those in control plots by 7-13 months later. As gopher populations recovered following abatement, active burrows first appeared at the plot peripheries and advanced toward the plot centres, suggesting that abated territorial residents were replaced by immigrants dispersing from the surrounding landscape.

Whereas conventional abatement practices can reduce gopher abundance in clearcuts, the small spatial and temporal scales of application encourage reinvasion of vacated ecological space. These population responses defeat the goal of forest management by increasing gopher density in clearcuts; at the same time the conifer seedlings are vulnerable to gopher predation. Predation of conifer seedlings might be reduced by not abating gophers or by using alternative harvest regimes. These alternative strategies would avoid creating the conditions under which gophers contribute to slowing forest regeneration following timber harvests, and they would avoid the widespread and possibly long-term environmental damage caused by applying acute poisons and by using the burrowbuilder.

*Keywords*: clearcuts, forest regeneration, pocket gopher abatement, strychnine, *Thomomys* spp.

## Introduction

Managers of forest resources in western North America face a long-standing problem with forest in many clearcuts failing to regenerate (Barnes 1971, 1978; Hooven 1971; Crouch 1982). Many of these failures are due to girdling and consumption of planted conifer seedlings by pocket gophers that encounter the seedlings when they leave their underground burrows to forage in snow tunnels during winter (Barnes et al. 1970; Hooven 1971; Barnes 1978). Some clearcuts have been planted repeatedly for three decades without successful regeneration. On these clearcuts, abatement programmes using poison baits failed to reduce gopher abundance for long enough to prevent damage (Richens 1965; Barnes 1971; Hooven 1971). Besides failing to regenerate the forest, the common use of the tractor-drawn burrow-builder, which deposits bait in artificial tunnels 10-20 cm below ground where most of the gopher burrows occur, also rips up the soil and kills non-target species of wildlife (K.S. Smallwood, unpublished data 1989). A new baiting regime or management plan is needed to solve this costly problem.

Alternative strategies to poisoning to reduce gopher damage to various commodities include the use of vexar plastic netting for seedling protection (Anthony et al. 1978), livestock grazing on forest clearcuts to damage gopher burrows (Kingery et al. 1978), vegetation removal with 2,4-D (Hull 1971) or atrazine (Engeman et al. 1995) to reduce habitat quality, and release of predator odours into gopher burrows (Sullivan et al. 1990). Vegetation removal with atrazine had the longest lasting treatment effect, although 66% of seedlings in treated plots were damaged after 51 months, and the experiment was pseudoreplicated (Engeman et al. 1995). The other strategies listed either achieved little success or were monitored for an insufficient duration to assess longterm success, and vegetation removal by herbicides is becoming a less viable alternative due to environmental concerns.

The goal of the present study was to determine whether poisoning could reduce gopher abundance for long enough for conifer seedlings to mature beyond the size range of greatest vulnerability to gopher predation. Most conifer seedlings escape gopher predation 4–6 years after planting, or when tree height reaches about 1 m (Barnes 1978). Clearcuts are so numerous in western forests that forest managers usually lack the time to attempt gopher abatement for a second time in each clearcut within six years following planting. Various ideas on baits and baiting regimes have been suggested to overcome the persistent failures of poisoning to reduce gopher abundance for sufficiently long time periods. For

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example, Tunberg *et al.* (1984) suggested that poisoned grains set in paraffin might increase their longevity in the burrow, thereby continuing to kill invading gophers. Also, Miller (1953) recommended spring rather than fall baiting because he hypothesized bait acceptance would increase amongst lactating and post-partum females and gophers first emerging after the winter. However, Barnes *et al.* (1970) recommended fall baiting, when sign is most visible and gophers are most numerous.

The specific objectives of the study were to: (1) compare persistence of gopher abatement on clearcuts using various strychnine baits and baiting regimes; (2) test whether paraffin baits would kill additional gophers as they attempt to replace the original burrow occupant(s); (3) test whether recovery of abated populations proceeded from within or outside the plot; and (4) determine the durability of parafbaits with respect to gopher behaviour fin and environmental conditions. For the first objective, I compared abatement levels between paraffin baits made of oat groats or wheat, and when applied in early spring versus summer, prior to the appearance of fresh gopher sign. My objectives tested some ideas on bait delivery, but they were also intended to identify the mechanism for population recovery following abatement efforts. Gopher abatement practices and their environmental effects bear strongly on the conservation and recovery of forest ecosystems in western North America.

#### **Materials and Methods**

#### Study areas

My study was conducted from May 1989 through August 1990 in northern California. The first two months consisted of trials in 15 clearcuts used for developing bait application and experimental design methods. These trials were in the Klamath, Stanislaus and El Dorado National Forests. The hypothesis-testing phase began in July 1989, and involved >2600 gopher burrows on 124 ha distributed amongst 68 experimental plots in 50 clearcuts that were assigned to me by staff from four National Forests, namely Sequoia, El Dorado, Shasta and Tahoe (Table 1). Within each Forest, the clearcuts studied were clustered nearby each other, and all occurred within mature conifer stands. The clearcuts were at 1300 m elevation at Shasta, and 2500 m at the other three Forests. The clearcuts were centred at 36°5'N, 118°30'W at Sequoia, 38°47'N, 120°8'W at El Dorado, 41°30'N,

Table 1 Summary description of experimental plots and amounts of bait applied for gopher abatement.

Treatment	Number	Hectares		Burrows on plot		Bait $(gha^{-1})$	
	of plots	Sum	Low-high	Sum	Low-high	Mean	
El Dorado National Forest							
Paraffin wheat, diffuse <sup>1</sup>	4	6.2	1.0 - 2.6	165	31-67	364	131
Control	3	6.0	1.4 - 4.0	124	34-49	0	0
Sequoia National Forest							
Paraffin oats	2	4.0	2.0	56	25-31	200	0
Paraffin wheat <sup>2</sup>	2	8.0	4.0	?	?	607	66
Paraffin wheat, diffuse <sup>1</sup>	4	13.2	2.0 - 3.2	252	51-70	161	44
Control for all	4	10.0	2.0 - 3.2	159	29-60	0	0
Shasta-Trinity National Forest							
Experiment 1							
Paraffin wheat	5	8.0	1.6	200	40	469	49
Loose grain wheat	5	10.4	1.6-3.2	200	40	391	125
Mixed bait wheat	4	9.6	1.6-3.2	147	27-40	549	79
Control for wheat	5	8.0	1.6	200	40	0	0
Experiment 2							
Paraffin oats, summer	4	6.0	1.2 - 1.6	166	30-56	421	28
Control for summer	3	4.8	1.6	79	16-40	0	0
Experiment 3							
Paraffin oats, April	3	4.0	1.2 - 1.6	120	40	419	60
Paraffin oats, May	3	4.6	1.4 - 1.6	116	36-40	371	61
Control for April/May	4	5.4	0.8 - 2.0	150	30-40	0	0
Tahoe National Forest							
Experiment 1							
Paraffin wheat	3	6.0	2.0	109	34-40	300	0
Loose grain wheat	3	6.4	2.0 - 2.4	93	22-40	250	56
Control for wheat	3	5.6	1.6 - 2.0	116	36-40	0	0
Experiment 2							
Paraffin oats	2	3.4	1.6 - 1.8	78	38-40	361	39
Control for oats	2	4.0	2.0	69	27-42	0	0

<sup>1</sup>The diffuse treatment was applied to only 68% of the gopher burrows on a plot.

<sup>2</sup>No initial count of burrows was made on these plots.

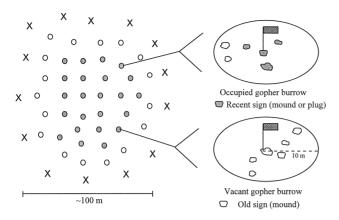


Figure 1 Illustrated example of study design within a baited plot. Open circles symbolize burrows at the plot perimeter, filled circles are burrows in the interior, and 'X' represents burrows that were baited in the buffer, but not marked or monitored.

121°51′W at Shasta, and 39°40′N, 120°34′W at Tahoe. Most of the clearcuts had been managed for gophers and replanted with conifer seedlings repeatedly. Most had been scarified and many were grazed regularly by cattle. They all contained conifer seedlings planted 1–6 years previously. Vegetation was usually sparse, often including forbes, grasses and clusters of lupine. Regardless of the cultural practices previously applied, it was visibly apparent that all of these clearcuts contained higher gopher densities than in surrounding forests and mountain meadows.

## Objectives 1 and 2: persistence of abatement using poison baits, and the multiple-kill effect

The experiments varied in complexity and number of replicates in each Forest (Table 1), depending on the research question being tested and the spatial arrangement of clearcuts in the study areas. Experimental plots of 0.8-4.0 ha were systematically interspersed amongst the clearcuts so that replicated treatments did not occur adjacent to each other, thereby minimizing the likelihood of gradient effects (Hurlbert 1984). Plot sizes varied according to the sizes of clearcuts, but large clearcuts were divided into treatment plots of 4 ha each, which were  $\geq 100$  m apart. The control treatment involved no baiting of gophers within the control plots. In all other plots, except for four at Sequoia and four at El Dorado (described below), poison baits were delivered to all burrows in each plot. An extra 13-15 m-wide circumference was baited outside the boundary of each baited plot (Fig. 1), which equates with the typical diameter of one gopher burrow (Miller 1957; Howard & Childs 1959; Bandoli 1981; Reichman et al. 1982).

Experiment 1 at Shasta and Tahoe tested the persistence of abatement when poisoned wheat grains, both in the conventional loose form and as pellets set by paraffin (described below) were applied. Experiment 2 at the same Forests tested the persistence of paraffin baits composed of oats. Experiment three at Shasta tested the persistence of paraffin baits applied during April and May. Due to gopher inactivity at this time of year, I often relied on old sign to locate burrows for bait application and initial burrow counts. The effectiveness of spring-time baiting was compared qualitatively with that of summer baiting.

To achieve objective 2, a 'diffuse' treatment at El Dorado and Sequoia involved baiting only 68% of the burrows, leaving 32% of the gophers as unbaited neighbours. The diffuse treatment tested whether paraffin baits would kill multiple gophers per baited burrow.

Paraffin baits were made in moulds prepared by bolting together two 2  $\times$  17 cm boards of red fir (*Abies magnifica*), one with 60 1-cm diameter holes. Wax paper between the boards reduced leakage of melted paraffin. All the holes were filled with loose grains of wheat or oat groat coated with green dye and saturated with 1% strychnine solution. The filled mould was baked at 60°C for 5 min to spread heat throughout the mould. Melted household paraffin was then injected into each grain-filled hole until full, yielding about a 0.5% strychnine concentration within the bait. After the paraffin hardened, the boards were unbolted and the 1  $\times$  2 cm baits punched out. Baits with exposed grain were dipped in hot paraffin. Loose grain baits tested in the field were 0.5% strychnine.

Baits were applied in equal amounts through two small holes opened 1-3 m apart in each burrow. The holes were made with a steel probe. Each burrow received six baits in paraffin bait plots, 2 teaspoons of loose grains in loose grain plots, and six paraffin baits and 2 teaspoons of loose grains in the mixed plots. One teaspoon of loose grain bait delivered about the same amount of strychnine as three paraffin baits, so the mixed bait treatment delivered more strychnine (28 g rather than the usual 14 g). All probe holes were then covered by rock and soil.

For objectives 1 and 2, I calculated relative population abundance (RP) with the burrow index (Smallwood & Erickson 1995):

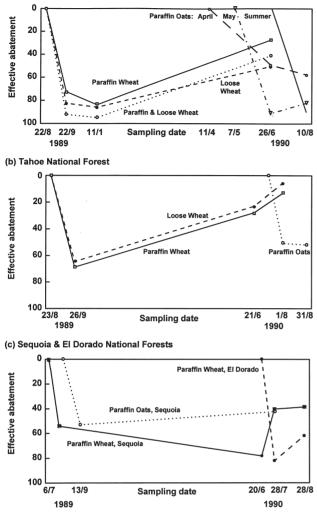
$$RP = \frac{n_s}{N} * 100\%$$

where N was the number of burrows initially marked with survey flags when the abatement experiment was begun (see Table 1 for start dates), and  $n_s$  was the number of flagged burrows with freshly excavated soil  $\leq 10$  m from the flag each time abatement effectiveness was quantified (Fig. 1). Each gopher burrow typically contains one adult gopher (Miller 1946; Bandoli 1981), so the burrow index expressed the abundance of adult gophers. Gopher abatement was measured for up to 13 months using the formula:

$$Effective Abatement = \frac{\overline{RP}_{c} - RP_{A}}{\overline{RP}_{c}} * 100\%,$$

where  $\overline{RP_C}$  was the average of relative population abundance values in the control plots, and  $RP_A$  was the relative population abundance in each abatement plot (Smallwood & Erickson 1995). This measure accounted for the natural, seasonal changes in abundance not due to the abatement

#### (a) Shasta-Trinity National Forest



**Figure 2** Mean effective abatement of different strychnine baits, where effective abatement measures the abundance of the baited populations as a percentage of the average abundance amongst the unbaited, control populations (the value 'O' represents no difference between baited and control populations).

treatments  $(RP_C)$ . Such an accounting of natural dynamics in abundance was important owing to Smallwood and Erickson's (1995) observations of substantial seasonal changes in gopher abundance within the control plots used for this study. I also used the 24 hr open-hole test to detect presence, but the burrow index was more efficient and accounted for 95% of adult gophers in study plots (Smallwood & Erickson 1995). I used one-way ANOVA and Dunnett's t-tests to compare treatment means against the control mean at dates ranging from 1 to 13 months following bait applications.

## Objective 3: plots repopulated by survivors or immigrants?

I monitored gopher burrows in the interior and at the perimeter of three plots during 1990 to test whether immigrants or abatement survivors contributed more to gopher population recovery. The plot perimeters were composed of the outermost burrows receiving the abatement treatment other than the baited buffer (Fig. 1). Burrows of abatement survivors were expected to be homogeneously distributed across each plot following treatment, whereas immigrants were expected to establish burrows at the plot peripheries before new burrows appeared in the plot interiors (Ellison & Aldous 1952).

### Objective 4: durability of paraffin bait

Morphological durability of baits in the field was compared by burying nine paraffin wheat baits and 3 teaspoons of loose grain bait in each of three wire cages 33 cm underground at Tahoe. They were excavated one month later and examined for structural integrity. I also tested whether paraffin baits could endure gopher behaviour. Baits were excavated from 12 burrows 4–5 days after application to assess bait consumption and availability to the gophers.

#### Results

#### Persistence of gopher abatement

Most strychnine bait treatments reduced gopher abundance substantially on clearcuts within two months (p < 0.05 for all one-sided t-test comparisons at Shasta and Tahoe), but gopher abundance in most plots recovered within one year (Fig. 2). Gopher abundance in abatement plots was lower than in control plots through ten months at Shasta, but not at Tahoe (Fig. 2). Paraffin baits for the most part did not prolong abatement beyond that of the conventional loose grain bait (Fig. 2). Mixed baits (more strychnine delivered/burrow) on average accounted for > 90% abatement of gophers after 2.5 months (Fig. 2), but half the burrows showed new activity in these plots within ten months.

Summer (June/July) application of paraffin oat groat bait accounted for equal abatement with the wheat baits of the previous year (Fig. 2). Shasta populations were smaller on oat groat plots than on controls six weeks after baiting (ANOVA F = 181, df = 1,5, p < 0.01). April and May baiting at Shasta did not improve abatement over summertime application of baits (Fig. 2). In plots baited in May, gopher abundance increased substantially from 29 June to 10 August.

Gopher abatement persisted longest where paraffin baits were applied to only 68% of the burrows to test for additional kill of invading neighbours and immigrants (Fig. 2). However, this diffuse bait application at El Dorado and Sequoia failed to abate gophers in more than the 68% of the burrows that had been baited.

In late October 1989, the US Forest Service at two National Forests applied bait on 4 of the study clearcuts with a mechanical burrow-builder, a treatment which was not part of my study design. On two clearcuts at Shasta, the US Forest Service added 3400 g ha<sup>-1</sup> of 0.89% strychnine loose grain wheat bait to the previously-applied 520 g ha<sup>-1</sup> of 0.5% strychnine mixed bait. Despite using 12 times the amount of strychnine per hectare that I used, persistence of abatement did not increase. One year after the original baiting at El Dorado, the burrow-builder added an unknown amount of strychnine on a paraffin bait plot, which accounted for 41%

greater abatement than at other such plots. However, the burrow-builder treatment on one of my control plots effectively increased the population there by 90%. (These plots were removed from the other statistical comparisons of the study.)

### Invasion of plots

New gopher sign typically appeared at the periphery and advanced toward the centre of abatement plots 2–4 months after baiting. By August 1990, sign was more frequent at the periphery of one Sequoia plot baited 2 months earlier ( $\chi^2 = 7.8$ , df = 1, p < 0.01), and at the peripheries of two Shasta plots baited 3–4 months earlier ( $\chi^2 = 5.3$ , df = 1, p < 0.025, and  $\chi^2 = 4.6$ , df = 1, p < 0.05). Based on qualitative monitoring of additional plots, gophers appeared to invade vacant burrows mostly during late spring, one winter after the baits were applied during late summer and fall.

#### Durability

Paraffin baits were morphologically more durable than the loose grains. All loose grain bait in buried wire cages and in gopher burrows sprouted within one month after treatment. Following one treatment at Tahoe, loose grain bait sprouted after only one week of heavy rainfall. All paraffin baits were intact after one month, most with only 1-2 sprouted grains, and some infected with fungus. Most paraffin baits endured gopher behaviour, but some were buried by the gophers in soil plugs, and others were ejected from the burrow up to 0.7 m away.

## Discussion

All the strychnine baits and baiting regimes reduced gopher abundance substantially, but not for the 4-6 years needed to protect regeneration seedlings. Persistence of abatement was too brief in every baiting regime tested, even on plots where gophers were nearly eliminated < 1 month after baiting. Plots where effective abatement was 90-100% one month after baiting had few or no gophers for at least another month, but some then experienced the greatest increases in abundance of all the plots, despite extra bait applications during the first three months. For example, the abundance on one abatement plot at Sequoia increased 330% after 13 months, even though initial abatement was 100% and the plot was baited twice more during 1989. Similarly, the initial > 90% population reduction reported by Barnes et al. (1970) for a burrow-builder treatment was followed by complete population recovery in 3-4 months (Barnes 1971). Because the conifer seedlings are typically planted just after gopher abatement, they are on the clearcut < 8 months before they are covered by the winter snow, which allows immigrant or surviving gophers to burrow right up to the above-ground portions of the seedlings. These seedlings are planted  $\leq 1$ year before gopher populations recover. These recovered gopher populations sometimes exceed the gopher densities in nearby control plots. The mechanisms for this fast recovery

must be understood in order to regenerate conifer forest in clearcut areas with persistent gopher damage.

Several lines of evidence suggest that abatement efforts in western forests actually facilitate immigration by young, dispersing gophers. For example, new burrow activity following bait treatments progressed toward the plot centres from the peripheries. Gophers were less responsive to the open-hole test  $\geq 1$  month after baiting, and similar to Miller's findings (1953), fresh mounds and soil plugs were smaller than normal. Apparent survivors might have been sick, but they were more likely sub-adult immigrants because strychnine is fastacting. Finally, the burrow-builder treatments without prior hand baiting accounted for large population increases after nine months. Fresh gopher sign was more abundant along tracks of the artificial tunnels than on intervening ground, suggesting artificial tunnels encouraged immigration after the strychnine bait decayed. The spatial pattern of population recovery, the types of burrow activity, and the very high densities sometimes reached, all point toward immigration of young animals as the mechanism of population recovery.

The removal of resident gophers clears the way for the steadily dispersing sub-adults (Williams & Cameron 1984; Loeb 1990) which readily take residence in vacant burrows (Howard & Childs 1959; Williams & Baker 1976). Sub-adults can live at higher density because their territories are smaller (Howard & Childs 1959; Patton & Brylski 1978; Reichman et al. 1982; Reichman & Smith 1985) and their inter-burrow spacing equal with that of adults (Reichman et al. 1982). Subadult immigration is probably a function of surrounding habitat quality (Miller 1946; Loeb 1990), the best of which might be meadows, stream courses, road verges and other clearcuts (Barnes 1971). Also, food plants recover during the gopher-free period following bait application (Richens 1965). Increased food availability also reduces territory size (Reichman & Smith 1985), thereby promoting higher density. This rearrangement of gopher burrows requires a greater and critical energy expenditure (Vleck 1979), which demands greater food consumption, perhaps including conifer seedlings.

Whatever the mechanism responsible for the rapid recovery of abated gopher populations in clearcuts, using acute poisons to abate gophers has failed to facilitate forest regeneration in many clearcuts. During August and September 1998, I visited and photographed seven of these clearcuts at Sequoia, two of them at El Dorado, and ten clearcuts containing 17 plots at Shasta. At Sequoia, forest regeneration has failed in one of three clearcuts used as controls, and either failed or only partially succeeded in three of four clearcuts where gophers had been abated 8–9 years previously. Forest regeneration has continued to fail in both of the El Dorado clearcuts I visited, which had received strychnine baits during the study. At Shasta, forest regeneration has continued to fail or only partially succeeded on 3 of the 5 control plots and on 6 of the 12 abatement plots.

Also, despite my careful applications of baits into the gopher burrows, non-target species invaded gopher burrows

following gopher mortality. I sometimes found carcasses of Peromyscus maniculatus and Eutamius spp. next to the bait or above-ground with the bait in their mouths. However, the tractor-drawn burrow-builder treatments applied by the US Forest Service on my plots were far more hazardous to nontarget animal species, because they failed to conceal the poison baits within the artificial tunnels. Soil collapsed into the tunnels along the tracks of the burrow-builder, and the baits were readily visible from above-ground. Many non-target animals perished when they consumed the exposed bait. Furthermore, soil in clearcuts is more likely to erode when it is ripped up by the burrow-builder. The burrow-builder causes all these problems, and it appears to provide the underground pathways for rapid re-invasion of the clearcuts by pocket gophers. The burrow-builder should not be used in forest clearcuts.

In my study, the added durability of paraffin baits may have provided the intended multiple-kill effect, but it failed to prolong gopher abatement long enough to protect seedlings. Furthermore, gophers often ejected paraffin baits to the ground surface, where their durability posed a hazard to wildlife (Anthony *et al.* 1984; K.S. Smallwood, personal observations 1989, 1990). Paraffin baits failed to meet the management objective, and they posed a greater hazard to non-target animals than did the conventional loose grain bait. Paraffin baits should not be used to abate gophers.

#### Management recommendations

Most forest managers lack the time needed to poison gophers at the temporal and spatial scales that would be required to protect conifer seedlings in forest clearcuts. Bait applications would need to be increased in frequency and extended to areas well beyond the individual clearcut. In my opinion, this and other studies have exhausted the possibilities for preventing gopher damage in forest regeneration efforts by removing gophers. The high resiliency of small mammal populations enables quick recolonization and population increase following abatement efforts (Sullivan 1979, 1986). Sullivan (1979) found that deer mice (Peromyscus maniculatus) immigrated onto clearcuts whence deer mice had been abated with poison just the previous season, and these mice destroyed nearly all the conifer seeds distributed by the foresters. The pattern of population recovery following gopher abatement was similar to that of predatory arthropods following application of insecticide across commercial grain fields (Duffield & Aebischer 1994). The conventional gopher management practices in western forests are costly and fail to achieve the intended objectives.

Several of the many preventive strategies reviewed by Van Vuren and Smallwood (1996) might reduce gopher damage to conifer seedlings in seedling plantations. For example, clearcutting might be replaced by selective-cutting, which supports few gophers (Barnes 1971). Planting just after timber harvest might provide the seedlings with time to grow beyond the size range of vulnerability before the gophers in-

vade the plantation (Crouch 1982). Plantations can be located on the landscape to avoid high gopher densities and immigration. Gopher movements are strongly directed by topography and vegetation (Vaughan 1963; Williams & Baker 1976; Tilman 1983), and nearby clearcuts, meadows, streams and roads facilitate recruitment (Barnes 1971). Knowledge of dispersal corridors on the landscape might be exploited by placing gopher fencing (Keith 1961; Williams & Cameron 1984) or drift fence (Howard & Brock 1961) at key locations around the plantation. Aluminium window screen tubes, used effectively to protect oak (Quercus spp.) seedlings from gophers (Adams & Weitkamp 1992), might be modified for conifer seedlings. Finally, damage to conifer seedlings might be prevented by not removing resident gophers, thereby avoiding the spatial coincidence of sub-adult gophers and over-wintering conifer seedlings.

Forest managers should also consider the long-term benefits of gophers to the forest and forest regeneration (Grinnell 1923; Taylor 1935; Mielke 1977; Huntly & Inouye 1988; Litaor et al. 1996). Gopher burrows aerate the soil and channel water below ground, thereby improving conditions for plant growth (Smallwood & Geng 1997). Gophers serve symbiotic roles by transporting spores of mycorrhizal fungi to conifer tree roots (Maser et al. 1978) and by creating burrow habitat used by many other animal species (Vaughan 1961). Gophers also facilitate forest succession (McDonough 1974; Anderson & MacMahon 1985), which is the process that begets forest regeneration on clearcuts. Attempts at gopher abatement in western forests should be replaced with practices that either avoid high gopher densities in close proximity with planted conifer seedlings or that encourage the natural ecological processes needed for forest regeneration.

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## References

- Adams, T.E. & Weitkamp, W.H. (1992) Gophers love oak to death. *California Agriculture* **46**: 27–9.
- Anderson, D.C. & MacMahon, J.A. (1985) Plant succession following the Mount St. Helens volcanic eruption: facilitation by a burrowing rodent, *Thomomys talpoides*. American Midland Naturalist 114: 62–9.
- Anthony, R.M., Barnes, V.G., Jr & Evans, J. (1978) Vexar plastic netting to reduce pocket gopher depredation of conifer seedlings. *Vertebrate Pest Conference* 8: 138–44.

- Anthony, R.M., Lindsey, G.D. & Evans, J. (1984) Hazards to golden-mantled ground squirrels and associated secondary hazard potential from strychnine for forest pocket gophers. *Vertebrate Pest Conference* 11: 25–31.
- Bandoli, J.H. (1981) Factors influencing seasonal burrowing activity in the pocket gopher, *Thomomys bottae*. *Journal of Mammalogy* 62: 293–303.
- Barnes, V.G., Jr (1971) Response of pocket gopher populations to silvicultural practices in Central Oregon. In: Wildlife and Forest Management in the Pacific Northwest, ed. H.C. Black, pp. 167–74. School of Forestry, Oregon State University, Corvallis, USA.
- Barnes, V.G., Jr (1978) Survival and growth of ponderosa pine seedlings injured by pocket gophers. *Tree Planter's Notes* 29: 20–3.
- Barnes, V.G., Jr, Martin, P. & Tietjen, H.P. (1970) Pocket gopher control on Oregon ponderosa pine plantations. *Journal of Forestry* 68: 433–5.
- Crouch, G.L. (1982) Pocket gophers and reforestation on western forests. *Journal of Forestry* 80: 662–4.
- Duffield, S.J. & Aebischer, N.J. (1994) The effect of spatial scale of treatment with dimethoate on invertebrate population recovery in winter wheat. *Journal of Applied Ecology* **31**: 263–81.
- Ellison, L. & Aldous, C.M. (1952) Influence of pocket gophers on vegetation of subalpine grassland in central Utah. *Ecology* 33: 177–86.
- Engeman, R.M., Barnes, V.G., Jr, Anthony, R.M. & Krupa, H.W. (1995) Vegetation management for reducing mortality of ponderosa pine seedlings from *Thomomys* spp. *Crop Protection* 14: 505–8.
- Grinnell, J. (1923) The burrowing rodents of California as agents in soil formation. *Journal of Mammalogy* 4: 137–49.
- Hooven, E.F. (1971) Pocket gopher damage on ponderosa pine plantations in southwestern Oregon. *Journal of Wildlife Management* 35: 346-53.
- Howard, W.E. & Brock, E.M. (1961) A drift-fence pit trap that preserves captured rodents. *Journal of Mammalogy* **42**: 386–91.
- Howard, W.E. & Childs, H.E., Jr (1959) Ecology of pocket gophers with emphasis on *Thomomys Bottae Mewa*. *Hilgardia* 29: 277–358.
- Hull, A.C., Jr (1971) Effect of spraying with 2,4-D upon abundance of pocket gophers in Franklin Basin, Idaho. *Journal of Range Management* 24: 230–2.
- Huntly, N. & Inouye, R. (1988) Pocket gophers in ecosystems: patterns and mechanisms. *Bioscience* 38: 786–93.
- Hurlbert, S.H. (1984) Pseudoreplication and the design of ecological field experiments. *Ecological Monographs* 54: 187–211.
- Keith, J.O. (1961) An efficient and economical pocket gopher exclosure. *Journal of Range Management* 14: 332–4.
- Kingery, J.L., Graham, R.T. & White, J.S. (1978) Damage to firstyear conifers under three livestock grazing intensities in Idaho. US Department of Agriculture, Forest Service, Research Paper INT-376. Intermountain Research Station, Ogden, UT, USA: 8 pp.
- Litaor, M.I., Mancinelli, R. & Halfpenny, J.C. (1996) The influence of pocket gophers on the status of nutrients in alpine soils. *Geoderma* 70: 37–48.
- Loeb, S.C. (1990) Reproduction and population structure of pocket gophers (*Thomomys bottae*) from irrigated alfalfa fields. *Vertebrate Pest Conference* 14: 76–81.
- Maser, C., Trappe, J.M. & Nussbaum, R.A. (1978) Fungal-small mammal interrelationships with emphasis on Oregon coniferous forests. *Ecology* 59: 799–809.

- McDonough, W.T. (1974) Revegetation of gopher mounds on aspen range in Utah. *Great Basin Naturalist* 34: 267-75.
- Mielke, H.W. (1977) Mound building by pocket gophers (Geomyidae): their impact on soils and vegetation in North America. *Journal of Biogeography* 4: 171–80.
- Miller, M.A. (1946) Reproductive rates and cycles in the pocket gopher. *Journal of Mammalogy* 27: 335–58.
- Miller, M.A. (1953) Experimental studies on poisoning pocket gophers. *Hilgardia* 22: 131–66.
- Miller, M.A. (1957) Burrows of the Sacramento Valley pocket gopher in flood-irrigated alfalfa fields. *Hilgardia* 26: 431–52.
- Patton, J.L. & Brylski, V. (1978) Pocket gophers in alfalfa fields: causes and consequences of habitat-related body size variation. *American Naturalist* 130: 493–506.
- Reichman, O.J. & Smith, S.C. (1985) Impact of pocket gopher burrows on overlying vegetation. *Journal of Mammalogy* 66: 720–75.
- Reichman, O.J., Whitham, T.G. & Ruffner, G.A. (1982) Adaptive geometry of burrow spacing in two pocket gopher populations. *Ecology* 63: 687–95.
- Richens, V.B. (1965) An evaluation of control on the Wasatch pocket gopher. *Journal of Wildlife Management* 29: 413–25.
- Smallwood, K.S. & Erickson, W.A. (1995) Estimating gopher populations and their abatement in forest plantations. *Forest Science* 41: 284–96.
- Smallwood, K.S. & Geng, S. (1997) Multi-scale influences of gophers on alfalfa yield and quality. *Field Crops Research* 49: 159–68.
- Sullivan, T.P. (1979) Repopulation of clear-cut habitat and conifer seed predation by deer mice. *Journal of Wildlife Management* 43: 861–71.
- Sullivan, T.P. (1986) Understanding the resiliency of small mammals to population reduction: poison or population dynamics? In: *Control of Mammal Pests*, ed. C.G.J. Richards & T.Y. Ku, pp. 69–82. London: Taylor and Francis Limited.
- Sullivan, T.P., Crump, D.R., Wieser, H. & Dixon, E.A. (1990) Response of pocket gophers (*Thomomys talpoides*) to an operational application of synthetic semiochemicals of stoat (*Mustela* erminea). Journal of Chemical Ecology 16: 941–9.
- Taylor, W.P. (1935) Some animal relations to soils. *Ecology* 16: 127–36.
- Tilman, D. (1983) Plant succession and gopher disturbance along an experimental gradient. *Oecologia* **60**: 285–92.
- Tunberg, A.D., Howard, W.E. & Marsh, R.E. (1984) A new concept in pocket gopher control. *Vertebrate Pest Conference* 11: 7–16.
- Van Vuren, D. & Smallwood, K.S. (1996) Ecological management of vertebrate pests in agricultural systems. *Biological Agriculture* and Horticulture 13: 41–64.
- Vaughan, T.A. (1961) Vertebrates inhabiting pocket gopher burrows in Colorado. *Journal of Mammalogy* **42**: 171–4.
- Vaughan, T.A. (1963) Movements made by two species of pocket gophers. American Midland Naturalist 69: 367–72.
- Vleck, D. (1979) The energy cost of burrowing by the pocket gopher *Thomomys Bottae. Physiological Zoology* 52: 122–36.
- Williams, L.R. & Cameron, G.N. (1984) Demography of dispersal in Attwater's pocket gopher (*Geomys attwateri*). Journal of Mammalogy 65: 67–75.
- Williams, S.L. & Baker, R.J. (1976) Vagility of local movements of pocket gophers (*Geomyidae: Rodentia*). American Midland Naturalist 96: 303–16.

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