

# Influence of removal sampling of small mammals on abundance and diversity attributes: scientific implications

**THOMAS P. SULLIVAN**, Department of Forest Sciences, Faculty of Forestry, University of British Columbia, 2424 Main Mall, Vancouver, British Columbia V6T 1Z4, Canada [tom.sullivan@ubc.ca](mailto:tom.sullivan@ubc.ca)  
**DRUSCILLA S. SULLIVAN**, Applied Mammal Research Institute, 11010 Mitchell Avenue, Sumnerland, British Columbia V0H 1Z8, Canada

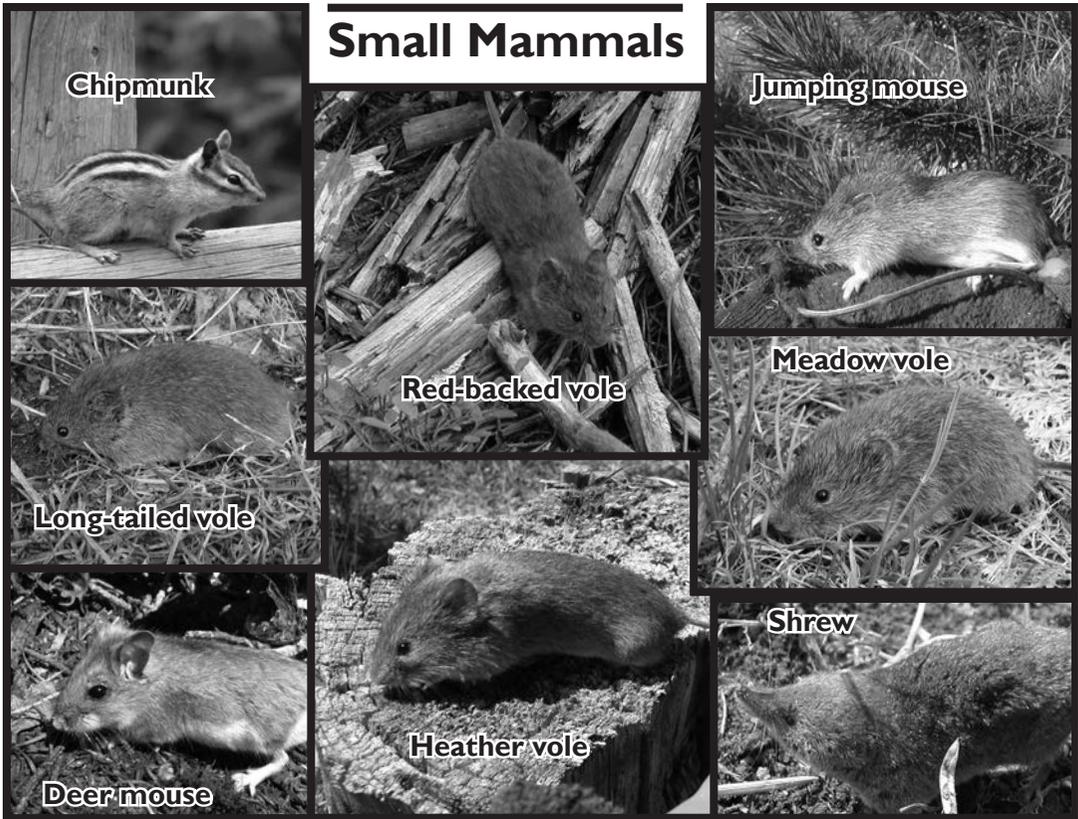
**Abstract.** Terrestrial small mammals occupy a variety of temperate and boreal forests in North America and Eurasia and contribute to biodiversity within these ecosystems. Researchers commonly use a variation of removal trapping to sample small-mammal populations and communities in these systems. However, it is not known if recurrent removal sampling might bias abundance estimates or alter the very populations under study. We addressed 2 questions: (1) are estimates of population size and species richness and diversity gained from removal trapping different from those based on live-trapping? and (2) what residual impact does removal trapping have on small-mammal populations and communities, as revealed by live-trapping? In 2 experiments (summer 2004 and autumn 2005), we compared undisturbed controls (non-removal) with removal sampling for 5-, 10-, and 30-night periods. Total abundance estimates during removal periods were dramatically higher (up to 3-fold) on non-removal than removal sites in both experiments. Mean abundance of the 2 most common species, deer mouse (*Peromyscus maniculatus*) and northwestern chipmunk (*Neotamias amoenus*), were substantially higher on non-removal than removal sites in the autumn experiment. The longer the removal interval, the deeper the degree of departure from non-removal levels of abundance. Species richness during removal periods also followed the pattern of abundance, whereby new, uncommon species appeared on removal sites, but not non-removals, during the autumn experiment. The residual impact of removal trapping, as revealed by live-trapping, indicated that abundance estimates were up to 4.5-fold higher on non-removal than post-removal sites and continued for at least 1 month as the small mammal community reorganized itself via immigration and settlement. Species diversity was still significantly different among removals 8 months after the autumn removal period. Removal-trapping over variable lengths (5 to 30 nights) may not provide an accurate picture of the abundance or diversity of small mammals.

**Key words:** abundance, human–wildlife conflicts, live-trapping, population dynamics, removal trapping, scientific implications, small mammals, species richness and diversity, spurious results

**TERRESTRIAL SMALL MAMMALS** of temperate and boreal forests in North America and Eurasia include many species of mice, voles, shrews, and squirrels. These species contribute to biodiversity within natural and managed forests because they serve as prey for various carnivores, disseminate seeds and spores of plants and fungi, and may regulate some invertebrate populations (Maser et al. 1978, Hansson 1988, Hornfeldt et al. 1990, Carey and Johnson 1995, Carey and Harrington 2001, Pearce and Venier 2005; Figure 1). A major focus to conserve biodiversity in changing forest landscapes has included abundance and species diversity of forest-floor, small-mammal communities (Ruggiero et al. 1991, Zabel and Anthony 2003). Thus, there is a need to accurately sample small-mammal populations across a range of ecosystems and habitats. A

major goal is to capture a representative sample of the small-mammal population or community by using a reliable trapping methodology.

Researchers commonly use a variation on removal trapping to sample small-mammal populations and communities (Corn and Bury 1991, Gilbert and Allwine 1991, Gitzen et al. 2007, Lehmkuhl et al. 2008). Removal trapping is kill-trapping of animals using either snap traps or pitfall removal traps. It has been conventional wisdom that removal of small numbers of animals once or twice a year (e.g., 3-night trapping periods in spring and fall) has little effect on the overall small mammal community (Christensen and Hornfeldt 2003). However, no studies have actually evaluated whether or not recurrent removal of small mammals might bias abundance and diversity estimates or alter the very populations under



**Figure 1.** Examples of forest-floor, small mammal species encountered in our study.

study. Removal trapping provides a static sample for a specific point in time and may be biased by immigrating individuals and species of small mammals that colonize a depopulated area. In addition, there may be a limited ability to resample populations or communities because of this disruption (Farnsworth and Rosovsky 1993).

In a preliminary short-term (4-night) experiment, removal trapping, compared to mark-recapture live trapping, disrupted small mammal populations and yielded spurious values for community characteristics (Sullivan et al. 2003). In addition, Wiewel et al. (2009) reported that mark-recapture population estimates were consistently more precise than removal estimates. Without direct comparison to undisturbed control (non-removal) samples of small-mammal populations and communities, there is no measure of the accuracy of studies using recurrent removal methods. Here, we address 2 scientific issues: (1) whether estimates of population size ( $N$ , and related community metrics) gained from removal

trapping are different from those based on live-trapping; and (2) what residual impact removal trapping has on small-mammal populations and communities, as revealed by live-trapping.

## Methods

### Design and trapping protocol

We chose 12 sites (3 replicates of 4 treatments) of early successional montane spruce (*Picea glauca* × *P. engelmannii*) forest near Summerland, British Columbia, Canada (49° 40'N; 119° 53'W), as our experimental units. Small-mammal communities are most abundant in early successional forests that develop after clearcut harvesting (Fisher and Wilkinson 2005). Determination of a range of commonly used removal periods and seasons was based on a comprehensive review of published forest, small-mammal studies from 1974 to 2010 (Sullivan and Sullivan 2010). The 4 treatments consisted of control (non-removal), 5-, 10-, and 30-night removal trapping. This completely randomized design allowed direct comparison of abundance and diversity attributes of small-

mammal communities subjected to the different sampling regimes.

Two experiments were conducted to compare summer (2004) and autumn (2005) seasons. In each experiment we live-trapped, marked, and released small mammals every 4 weeks from May to October each year on all 12 sites. A second post-removal period in May 2006 was added to the autumn 2005 experiment. Sampling was not conducted from November to April because of snow cover and difficult access. One live-trapping grid (1 ha) per site had 49 ( $7 \times 7$ ) trap stations at 14.3-m intervals with 1 or 2 Longworth-style live-traps (Rogers Manufacturing Co., Peachland, British Columbia) at each station. The number of traps at a station was increased when trap occupancy was  $>60\%$ . Traps were supplied with whole oats, a slice of carrot, and cotton as bedding. Each trap had a 30-  $\times$  30-cm plywood cover for protection from sunlight (heat) and precipitation. Traps were set on the afternoon of day 1, checked on the morning and afternoon of day 2 and morning of day 3, and then locked open between trapping periods. All animals captured were ear-tagged with serially numbered tags. We also recorded the point of capture (Krebs et al. 1969). On non-removal sites, and during pre-removal and post-removal periods on removal sites, we trapped for 2 nights each session. On removal sites, this normal capture-release trapping was replaced by 5, 10, or 30 consecutive nights of removal trapping during the actual removal periods (July 2004 and September 2005). Animals captured during removal-trapping periods were removed permanently from grids and transported to release areas  $\geq 10$  km from study sites. No marked animals emigrated between study sites, because all sites were separated by  $\geq 1$  km or a topographic barrier. Abundance, species richness, and species diversity were calculated for these small-mammal communities.

### Abundance and diversity estimates

Abundance estimates of animals were derived from the Jolly-Seber (J-S) stochastic model for open populations with correction for small sample sizes (Seber 1982, Krebs 1999). The J-S model assumes marked and unmarked animals have the same capture probability in each sampling session (Krebs 1999). Because our

traps were locked open between trap sessions, it seemed plausible that trap responses of animals dissipated between our monthly sampling sessions. J-S estimates were calculated for data from the 2-night trapping sessions on the non-removal sites and pre-removal and post-removal periods on the removal sites. Total number of individuals captured was used to compare populations of the uncommon species and for all species captured during the removal periods. Species richness was the total number of species sampled for the small-mammal community on each site (Krebs 1999). Species diversity was based on the Shannon-Wiener index and log-series alpha (Magurran 2004). All handling of animals followed guidelines approved by the American Society of Mammalogists (Sikes et al. 2011) and the Animal Care Committee, University of British Columbia.

### Statistical analysis

The 2 experiments were analyzed separately by a repeated-measures analysis of variance (RM-ANOVA; Zar 1999) to determine the effect of removal treatments and time on mean total abundance, mean species richness, and mean species diversity of the forest floor small-mammal community, based on the 2-night, live-trapping sample every 4 weeks, for the pre-removal and post-removal periods. Where required, data were transformed with the logarithmic (base 10) to better approximate homogeneity of variance as measured by the Levene statistic (Fowler et al. 1998). Mauchly's *W*-test statistic was used to test for sphericity (independence of data among repeated measures; Littell 1989; Kuehl 1994). Where necessary, *F*-values were calculated using the Huynh-Feldt correction factor (Huynh and Feldt 1976), which decreased the stated degrees of freedom due to correlation of data among repeated measures (periods). A 1-way (univariate) ANOVA was conducted to compare removal periods when a significant site  $\times$  time interaction was detected. This same analysis was used to detect differences in mean abundance of each small mammal species, mean total abundance, mean species richness, and mean species diversity based on captures per 100 trap-nights during the actual removal periods (Skalski and Robson 1992). Data from small mammal removal studies are commonly

**Table 1.** Mean ( $n = 3$  replicate sites)  $\pm$  SE abundance of each small mammal species per 100 trap-nights (TN) during the actual removal period in the summer 2004 experiment and results of ANOVA. Columns of mean values with different letters are significantly different by Duncan's multiple-range test (DMRT), adjusted for multiple contrasts. The total number of unique individuals captured in the 3 replicate grids of each treatment is given in parentheses.

Species	Sites				ANOVA	
	2-night non-removal (TN = 294)	5-night removal (TN = 735)	10-night removal (TN = 1,470)	30-night removal (TN = 4,310)	$F_{3,8}$	$P$
Deer mouse	6.46 $\pm$ 2.66 (19)	4.90 $\pm$ 1.47 (36)	3.47 $\pm$ 1.05 (51)	2.11 $\pm$ 0.33 (93)	1.34	0.33
Northwestern chipmunk	10.54 $\pm$ 5.48 (31)	3.81 $\pm$ 1.30 (28)	2.45 $\pm$ 1.30 (36)	2.04 $\pm$ 0.22 (90)	2.23	0.16
Long-tailed vole	0.68 $\pm$ 0.68 (2)	0.41 $\pm$ 0.24 (3)	0.13 $\pm$ 0.07 (2)	0.66 $\pm$ 0.66 (29)	0.18	0.91
Meadow vole	0.00 $\pm$ 0.00 (0)	0.00 $\pm$ 0.00 (0)	0.34 $\pm$ 0.34 (5)	0.00 $\pm$ 0.00 (0)	1.00	0.44
Heather vole	0.34 $\pm$ 0.34 (1)	0.54 $\pm$ 0.36 (4)	0.34 $\pm$ 0.14 (5)	0.23 $\pm$ 0.06 (10)	0.26	0.85
Montane shrew	0.00 $\pm$ 0.00 (0)	0.54 $\pm$ 0.54 (4)	1.50 $\pm$ 1.11 (22)	0.77 $\pm$ 0.58 (34)	0.88	0.49
Common shrew	0.68 $\pm$ 0.68 (2)	0.00 $\pm$ 0.00 (0)	0.07 $\pm$ 0.07 (1)	0.02 $\pm$ 0.02 (1)	0.91	0.48
Total	18.70 $\pm$ 4.58 (55)A	10.20 $\pm$ 0.23 (75)B	8.30 $\pm$ 2.00 (122)B	5.83 $\pm$ 1.41 (257)B	5.99	0.02
Species richness	3.00 $\pm$ 0.58	3.67 $\pm$ 0.33	5.00 $\pm$ 1.15	4.33 $\pm$ 0.67	1.33	0.33
Species diversity	1.29 $\pm$ 0.51	1.20 $\pm$ 0.16	1.51 $\pm$ 0.35	0.99 $\pm$ 0.16	0.42	0.74

summarized by the number of animals captured per 100 trap nights to standardize trapping effort among sites and times. Duncan's multiple-range test (DMRT) adjusted for multiple contrasts was used to compare mean values based on ANOVAs (Saville 1990). In all cases, the level of significance was  $P \leq 0.05$ .

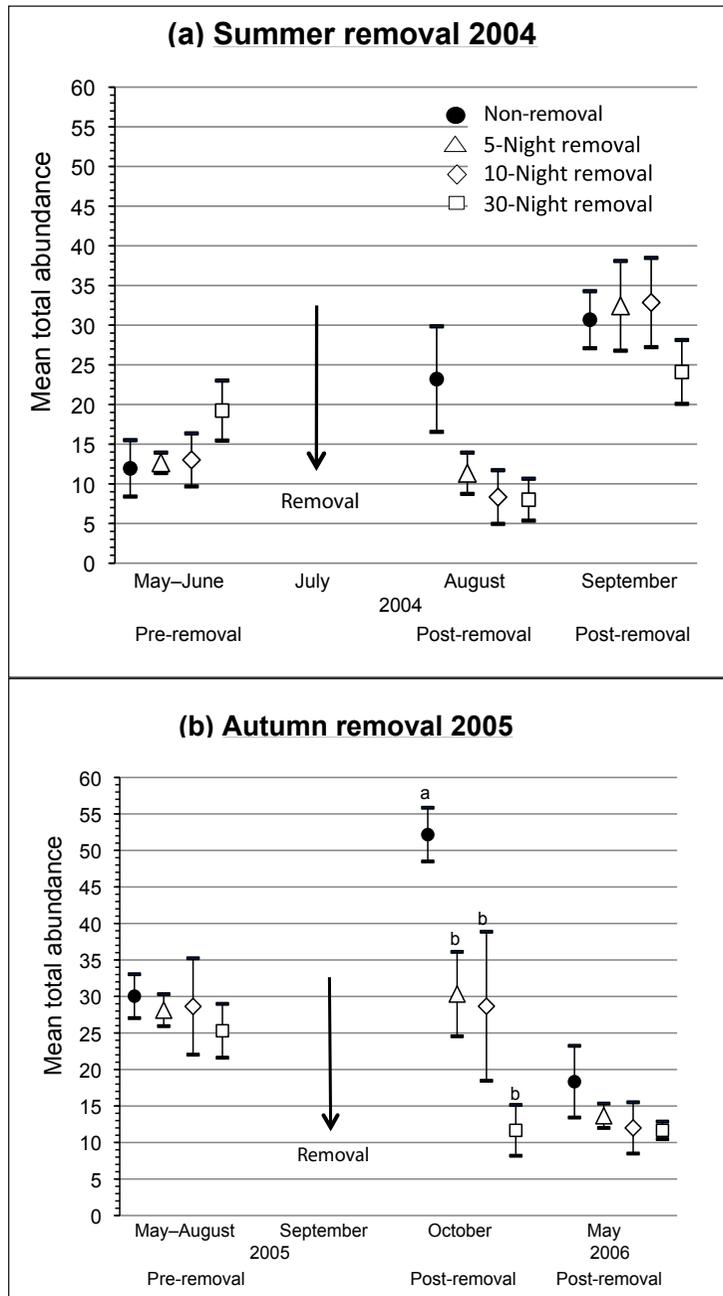
## Results

Overall, 10 species of forest-floor small mammals, composed of 3,017 individuals, were captured. Deer mice (*Peromyscus maniculatus*) were the most common, with 1,223 individuals, followed by 566 long-tailed voles (*Microtus longicaudus*), 534 northwestern chipmunks (*Neotamias amoenus*), 272 montane shrews (*Sorex monticolus*), 193 meadow voles (*Microtus pennsylvanicus*), 143 heather voles (*Phenacomys intermedius*), 54 common shrews (*Sorex cinereus*), 23 southern red-backed voles (*Myodes gapperi*), 8 western jumping mice (*Zapus princeps*), and 1 northern bog-lemming (*Synaptomys borealis*).

In the removal period of the 2004 experiment,

the mean abundance of each small-mammal species was similar among sites, yet, the total number of animals per 100 trap nights was significantly (univariate ANOVA;  $F_{3,8} = 5.99$ ,  $P = 0.02$ ) different, being highest (DMRT,  $P = 0.05$ ) on the non-removal, with values 1.8 to 3.2 times greater than those on the removal sites (Table 1). In the removal period of the 2005 experiment, mean abundance of the 2 most common species per 100 trap nights, the deer mouse and northwestern chipmunk, were highest on the non-removal sites, ranging from 1.5 to 4.2 times and 2.7 to 11.8 times greater, respectively, than their counterparts on the removal sites (Table 2). Again, mean total abundance of small mammals per 100 trap nights was significantly (univariate ANOVA;  $F_{3,8} = 6.18$ ,  $P = 0.02$ ) different, being highest (DMRT,  $P = 0.05$ ) on the non-removal sites (Table 2).

Mean total abundance of small mammals was similar among treatments in the pre-removal period in each of the 2004 and 2005 removal experiments (Figure 2). There was a significant



**Figure 2.** Mean ( $n = 3$  replicate sites)  $\pm$  SE total abundance (Jolly-Seber) of small mammals in non-removal, 5-, 10-, and 30-night removals during the pre-removal and 2 post-removal periods in the (a) summer 2004 removal experiment and (b) autumn 2005 removal experiment. The arrow denotes the actual removal period. Mean values with different letters are significantly different by Duncan's multiple range test (DMRT), adjusted for multiple contrasts.

site  $\times$  time interaction in both experiments, 2004 ( $F_{6,16} = 3.64, P = 0.02$ ) and 2005 ( $F_{6,16} = 9.52, P < 0.01$ ). A dramatic decline occurred in the first post-removal period of each experiment where mean total abundance on the respective non-removals was 2.1 to 2.9 (2004) and 1.7 to 4.5 (2005) times higher than the 3 removal sites

(Figure 2). This comparison was not formally significant (univariate ANOVA;  $F_{3,8} = 2.94, P = 0.10$ ) in 2004, but was significantly (univariate ANOVA;  $F_{3,8} = 6.90, P = 0.01$ ) different between the non-removal and the 3 removal treatments (all similar to one another; DMRT,  $P = 0.05$ ) in 2005 (Figure 2). Much of this difference

**Table 2.** Mean ( $n = 3$  replicate sites)  $\pm$  SE abundance of each small mammal species per 100 trap-nights (TN) during the actual removal period in the autumn 2005 experiment and results of ANOVA. Columns of mean values with different letters are significantly different by Duncan's multiple range test (DMRT), adjusted for multiple contrasts. Total number of unique individuals captured in the 3 replicate grids of each treatment is given in parentheses.

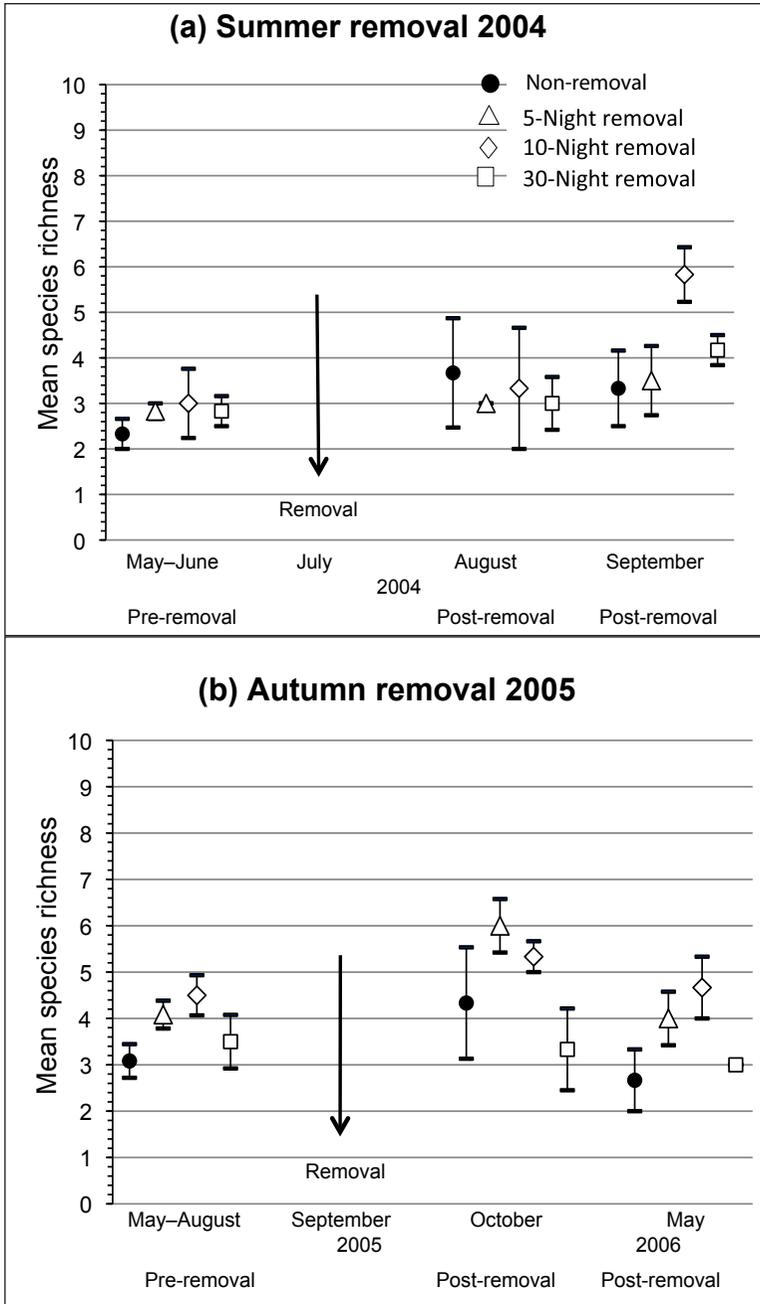
Species	Site				ANOVA	
	2-night non-removal (TN = 294)	5-night removal (TN = 735)	10-night removal (TN = 1,470)	30-night removal (TN = 4,410)	$F_{3,8}$	$P$
Deer mouse	23.81 $\pm$ 4.14 (70)A	15.78 $\pm$ 2.68 (116)AB	8.57 $\pm$ 0.71 (126)BC	5.65 $\pm$ 0.96 (249)C	10.23	<0.01
Northwestern chipmunk	16.32 $\pm$ 5.14 (48)A	5.99 $\pm$ 1.38 (44)B	2.59 $\pm$ 0.49 (38)B	1.38 $\pm$ 0.16 (61)B	19.73	<0.01
Long-tailed vole	2.04 $\pm$ 1.18 (6)	3.27 $\pm$ 2.65 (24)	7.14 $\pm$ 4.90 (105)	5.62 $\pm$ 4.92 (248)	0.37	0.78
Meadow vole	3.06 $\pm$ 3.06 (9)	0.54 $\pm$ 0.54 (4)	3.67 $\pm$ 2.26 (54)	0.75 $\pm$ 0.48 (33)	0.61	0.63
Heather vole	0.68 $\pm$ 0.34 (2)	2.31 $\pm$ 1.34 (17)	0.47 $\pm$ 0.14 (7)	0.57 $\pm$ 0.40 (25)	1.46	0.30
Southern red-backed vole	0.00 $\pm$ 0.00 (0)	0.82 $\pm$ 0.82 (6)	0.41 $\pm$ 0.12 (6)	0.07 $\pm$ 0.04 (3)	0.82	0.52
Western jumping mouse	0.00 $\pm$ 0.00 (0)	0.00 $\pm$ 0.00 (0)	0.07 $\pm$ 0.07 (1)	0.02 $\pm$ 0.02 (1)	0.79	0.53
Montane shrew	1.36 $\pm$ 0.90 (4)	0.27 $\pm$ 0.14 (2)	1.83 $\pm$ 0.43 (27)	1.16 $\pm$ 0.46 (51)	1.39	0.31
Common shrew	0.34 $\pm$ 0.34 (1)	0.41 $\pm$ 0.24 (3)	0.75 $\pm$ 0.27 (11)	0.11 $\pm$ 0.06 (5)	1.10	0.40
Total	47.61 $\pm$ 2.78 (140)A	29.39 $\pm$ 3.67 (216)B	25.50 $\pm$ 8.58 (375)B	15.33 $\pm$ 4.78 (676)B	6.18	0.02
Species richness	4.33 $\pm$ 0.88 A	6.00 $\pm$ 0.58 AB	8.33 $\pm$ 0.33 C	7.33 $\pm$ 0.67 BC	7.20	0.01
Species diversity	1.22 $\pm$ 0.32	1.59 $\pm$ 0.25	2.14 $\pm$ 0.27	1.53 $\pm$ 0.18	2.09	0.18

was attributed to deer mice and northwestern chipmunks that maintained their populations on the non-removal sites. Mean total abundance of small mammals was similar among non-removal and removal sites in the second post-removal period in each experiment.

Mean species richness also showed a significant ( $F_{6,16} = 2.97$ ,  $P = 0.04$ ) site  $\times$  time interaction (RM-ANOVA) in summer 2004 (Figure 3). When periods were analyzed separately (univariate ANOVA), species richness was similar among treatments in the pre-removal and 2 post-removal periods. However, in the removal period, species richness in the 3 removal treatments ranged from 1.2 to 1.7 times higher than the non-removal (Table 1). In the autumn 2005 experiment, mean species richness was similar among removal and non-removal

sites during pre-removal and post-removal periods (Figure 3). However, mean species richness was significantly (univariate ANOVA;  $F_{3,8} = 7.20$ ,  $P = 0.01$ ) different during the actual removal period, with richness highest (DMRT,  $P = 0.05$ ) on the 10- and 30-night removal sites, the 5- and 30-night removal sites were similar, with the lowest value on the non-removal site (Table 2).

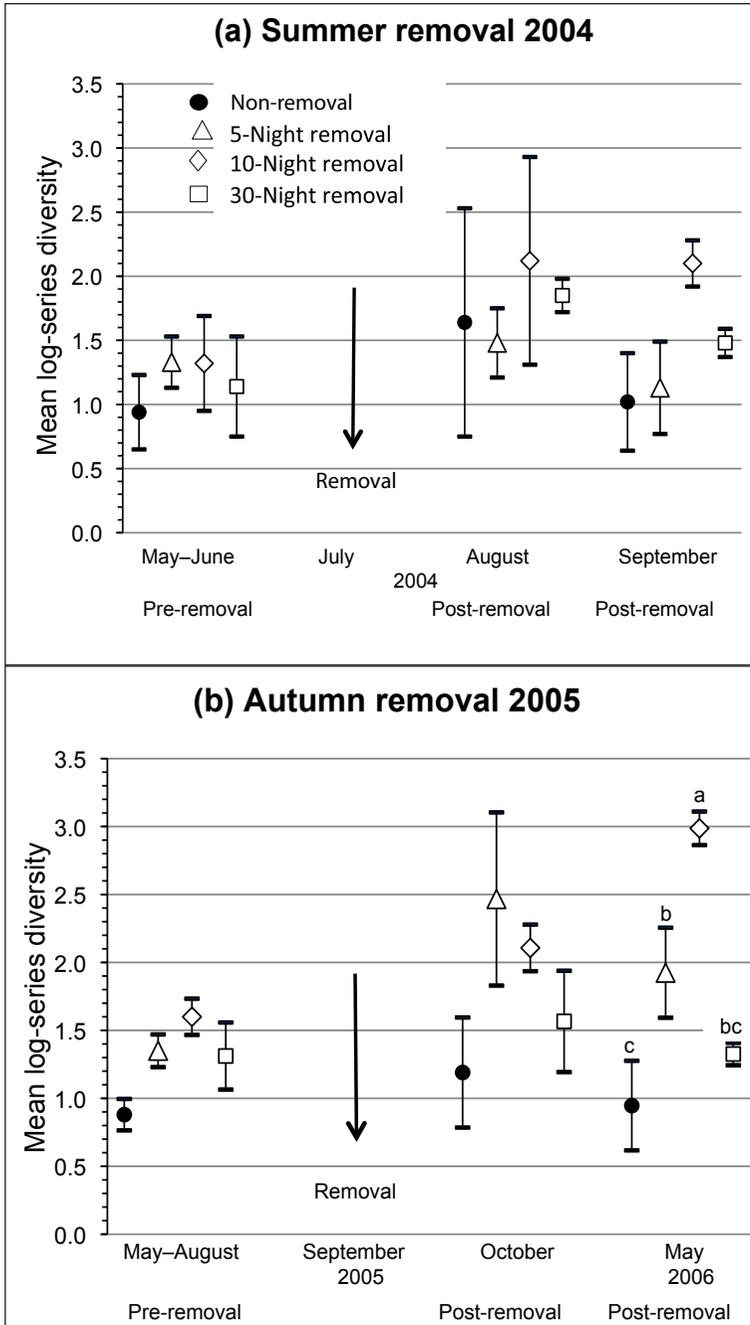
Mean log-series diversity was similar among non-removal and removal sites in 2004 (Figure 4), but then was significantly ( $F_{3,8} = 6.52$ ,  $P = 0.02$ ) different with respect to site, and near significance ( $F_{6,16} = 2.34$ ,  $P = 0.08$ ) for the site  $\times$  time interaction in 2005 (Figure 4). Overall, this measure of diversity was highest on the 5- and 10-night removal sites, similar on the 5- and 30-night removal sites, as well as the



**Figure 3.** Mean ( $n = 3$  replicate sites)  $\pm$  SE species richness of small mammals in non-removal, 5-, 10-, and 30-night removals during the pre-removal and 2 post-removal periods in the (a) summer 2004 removal experiment and (b) autumn 2005 removal experiment. The arrow denotes the actual removal period.

non-removal and 30-night sites. This same pattern of significant differences also occurred in the second post-removal period (May 2006; univariate ANOVA;  $F_{3,8} = 13.18, P < 0.01$ ); however, mean species diversity was similar (univariate ANOVAs) among sites in the pre-removal, removal (Table 2), and first post-

removal periods (Figure 4). Measurements with the Shannon-Wiener index followed the same pattern of results. In both experiments, a significant time factor indicated that mean species richness and diversity measurements increased in the removal and post-removal periods.



**Figure 4.** Mean ( $n = 3$  replicate sites)  $\pm$  SE species diversity (log-series) of small mammals in non-removal, 5-, 10-, and 30-night removals during the pre-removal and 2 post-removal periods in the (a) summer 2004 removal experiment and (b) autumn 2005 removal experiment. The arrow denotes the actual removal period. Mean values with different letters are significantly different by Duncan’s multiple range test (DMRT), adjusted for multiple contrasts.

The increase in richness and diversity indices was related to 2 new species, the meadow vole and montane shrew appearing on the removal sites during the removal period in 2004. In 2005, 2 new species, the red-backed vole and western jumping mouse, appeared

1 and 2). These species were not recorded on the non-removal sites during the respective removal periods. A fifth uncommon species, an individual northern bog-lemming, occurred for the first time in this general study area in the 10-night post-removal period in May 2006.

## Discussion

Our results are the first quantitative investigation of the impact of variable length removal trapping on abundance, richness, and diversity attributes of forest-floor, small-mammal communities. Removal sampling yielded different results for abundance measurements with respect to the first issue of comparing those attributes gained from removal trapping and live-trapping. When converted to number of animals per 100 trap nights, the total abundance estimates during removal periods were dramatically higher (up to 3-fold) on non-removal than on removal sites in both experiments. In the autumn 2005 experiment, mean abundance of the 2 most common species per 100 trap nights, the deer mouse and northwestern chipmunk, were substantially higher on non-removal than removal sites. The longer the removal interval, the greater was the degree of departure from non-removal (undisturbed) levels of abundance. Thus, inferences to abundance from removal trapping in our study would appear to be inaccurate. Mark-recapture population estimates from live-trapping were consistently more precise than removal estimates for several species of Pacific Island small mammals (Wiewel et al. 2009) and for terrestrial small mammals in a coastal coniferous forest (Sullivan et al. 2003). Comparisons for other taxa reported similar results, whereby removal of individuals from a given population may yield biased data (Rodgers et al. 1992, Jung et al. 2002). We acknowledge that evaluation of our abundance estimates, based on monthly live-trapping to assess temporal dynamics in long-term studies, was limited because we do not know the true abundance of the small mammal populations in our study areas. We would require data from populations that are spatially closed and completely enumerated, which has yet to be done (Krebs et al. 2011). We also note that our manual removal of captured individuals from live-traps on removal sites was assumed to be equivalent to past studies where animals were killed by snap-traps or pitfall traps.

Species richness and diversity also followed the different pattern of abundance, whereby new, uncommon species appeared on removal sites, but not on non-removal sites. It could be argued that these temporally uncommon,

or even rare, species require a much larger sampling area than 1-ha grids and that we simply missed them. Such uncommonness may relate to true rarity (e.g., northern bog-lemming), habitat partitioning at a scale larger than our sampling unit (e.g., western jumping mouse), or temporal variability via population fluctuations (e.g., meadow vole) of a given species. Immigration to removal sites was likely stimulated by removal of resident individuals, thereby opening such sites to colonization by uncommon species and subordinate individuals, such as that reported for behavioral interactions among voles (Andrzejewski and Rajska 1972, Boonstra and Krebs 1978, Beacham and Krebs 1980). Other studies have documented that known neighbors (e.g., individually marked animals) colonized areas after the removal of residents (Sullivan 1979, Schieck and Millar 1987). One potential consequence of these interactions may be that live-trap samples are more representative of the dominant resident population and not of the population or community as a whole. It is not clear how kill-trapping would improve on this situation other than removing most, if not all, animals living on the sample site, whether they are resident, transient, dominant, or subordinate.

Our live-trapping regime may also have been biased because *Sorex* spp. survived poorly in traps. Pitfall traps have been recommended as a means to sample shrews and other species that are not as efficiently captured in conventional live-traps (Bury and Corn 1987, Kirkland and Sheppard 1994). However, in the only study evaluating these particular trap types, Stromgren (2007) reported significantly more shrews captured in Longworth live-traps than in pitfalls. Hawes (1977) also used Longworth traps and found that 2 shrew species readily entered traps, and trap mortality was very low with frequent checking. Our sampling regime would have been improved with more frequent checking of traps and use of appropriate shrew food as bait (Stromgren 2007). To this end, it is important to note that all live-trapping studies have some minor degree of mortality of animals, but usually disruption of a population or community is relatively low.

Alternatively, it could be argued that we did not have enough traps on our non-removal grids to capture all animals, whether dominant,

subordinate, common, or uncommon. This premise seems unlikely because even at relatively high densities in summer-fall 2005, we seldom had >60% of live-traps occupied in any single night of trapping. Similarly, the 2 nights of live-trapping on our non-removals may also seem insufficient to capture the majority of animals on a sample site. However, sampling open populations (Krebs et al. 1976) at 2- to 4-week intervals through different seasons and years generates data on demographic variables, such as reproduction and survival, that complement data on abundance. In these cases, short intervals of actual trapping (2 to 4 nights) have been found sufficient to limit capture of transient animals, as well as minimize excessive handling and confinement of animals in traps (Steele et al. 1984, Moreau 2000, Conard et al. 2008). Although our relatively intensive approach to population studies may seem unnecessary for mammalogists studying diversity and conservation issues, data on reproduction and survival provide an often crucial indicator of population and habitat quality that abundance data alone do not (Van Horne 1983, Sullivan and Sullivan 2001).

The second issue of the residual impact of removal trapping on small mammal populations and communities, as revealed by live-trapping, was addressed by monitoring the post-removal populations through time. Abundance estimates in non-removal sites were up to 4.5-fold higher than in post-removal sites. This effect was maintained for at least 1 month as the small mammal community reorganized itself via immigration and settlement. Although abundance patterns seemed to stabilize by the second post-removal period in each experiment, log-series species diversity was still significantly different among treatments 8 months after the removal period. This same pattern was recorded for Shannon-Wiener species diversity. The similarity in diversity of non-removal and 30-night removal communities was likely related to the general dominance of 1 or 2 species (e.g., deer mice, chipmunks, or *Microtus*) on these sites. Thus, even though total abundance estimates suggested that residual effects of removal were relatively short-term (1 month) in nature, the actual impact on species diversity of the small mammal community seemed to last longer.

Measurements of species richness and diversity for forest-floor, small-mammal communities using removal methods may yield questionable results, both during the actual removal periods (richness in 2005) and potentially in some post-removal periods (diversity in 2005). Our results suggested that rare or uncommon species might appear in removal sites and encourage biodiversity surveys using such methodology. However, these results would be spurious in terms of identifying the particular species with the correct habitat or site in which such captures occurred. This dilemma is most pronounced when measuring the responses of small mammals to forestry practices or other habitat alterations. A crucial question is whether an uncommon species occurs naturally in a given habitat or because of disruption from removal trapping. Our results were from relatively productive ecosystems in a temperate forest zone; results from other, less productive ecosystems might yield more severe results in terms of recovery times after removals or capture of rare species.

We ask why this removal sampling continues to be used despite the well-known resiliency of small mammals to depopulation and the consequent immigration of a variety of individuals and species (Martell and Radvanyi 1977, Fairbairn 1978, Sullivan 1986, Sullivan et al. 2001). In a review of forest small-mammal studies over 3 decades, from 1981 to 2010, 69 studies used a form of removal sampling (Sullivan and Sullivan 2010). Indeed, the current edition of *Guidelines of the American Society of Mammalogists for Use of Wild Mammals in Research* still advocates kill-trapping as an acceptable sampling methodology (Sikes et al. 2011). However, Sikes et al. (2011) state that study goals and the potential impact that removing numbers of animals might have on the natural population need to be considered by researchers who adopt kill-trapping as a sampling program.

Killing of mammals or other vertebrates for human welfare and wildlife health issues may be justified, but the continued use of this practice for ecological studies seems highly questionable (Diamond 1987, Vucetich and Nelson 2007). Kill-trapping might be required for some species that are very difficult to live-trap, detailed reproductive and physiological

data may be needed, or, perhaps, some studies have very limited access to sites. As discussed by Sullivan et al. (2003) and Wiewel et al. (2009), the issue of limited funding needs to be carefully considered, because, if the presumed less-costly removal sampling provides data of questionable value, then, perhaps, such funds would be better allocated elsewhere.

The practices of collecting organisms in the field and the impact of this on rare species, not to mention population and community attributes, need to be reevaluated (Farnsworth and Rosovsky 1993). In addition, concerns over the fate of nontarget animals, primarily birds, captured by kill-traps and live-traps have been noted (Waldien et al. 2004, Lane et al. 2009). Short-term removals (e.g., 3 nights in spring and fall) were deemed to have little effect on size of small-mammal populations (Christensen and Hornfeldt 2003). Although we did not have a 3-night removal period, the impact of this standard approach to estimates of abundance and composition seemingly would be similar to the 4-night removals reported by Sullivan et al. (2003) and perhaps our 5-night removals. But, what about longer-term removals, such as the 30 nights examined in our study? Several large-scale studies ranging from 2 to 4 years in duration and 28 to 40 consecutive nights per year had removals of small-mammal individuals totaling 8,704, 16,892, and 21,351 (Martin and McComb 2002, Suzuki and Hayes 2003, Gitzen et al. 2007). What impact do these removals of biomass have on the predator community, species at risk, and other ecosystem functions of which forest-floor small mammals play vital roles? Even relatively small proportional declines in biomass or individuals of common species may trigger significant disruption in ecosystem structure, function, and services (Gaston and Fuller 2007).

Assuming that our live-trapping results provide accurate measurements of abundance, species richness and diversity of resident small mammal communities through time, then, those data using repeated removal-sampling protocols (5- to 30-night removals) should be clearly identified as disrupted populations or communities. All removal intervals yielded significantly lower total abundance estimates than non-removals during removal periods in both experiments. The same pattern was evident

for deer mice and northwestern chipmunks in the autumn experiment. Species richness (during the removal period) and species diversity (in the post-removal periods) in the autumn experiment also followed this pattern, although not consistently. Recovery periods were similar across removal methods: 1 month for abundance estimates and up to 8 months for diversity measurements.

Results of many small mammal studies are integrated into policy or management decisions regarding natural resources, crop protection, or conservation of species at risk. Thus, it is imperative that the methodology used accurately reflects the condition of the resident small-mammal communities. Removal-trapping over variable lengths (5 to 30 nights) may not provide an accurate picture of the abundance or diversity of small mammals. Except in specific circumstances, removal methods are a poor choice for ecological studies.

### Acknowledgments

We thank the Applied Mammal Research Institute for financial and logistical support. We thank H. Sullivan for assistance with the fieldwork and D. Fraser, C. J. Krebs, and V. J. Craig for constructive comments on an earlier version of the manuscript.

### Literature cited

- Andrzejewski, R., and E. Rajska. 1972. Trappability of bank voles in pitfall and live traps. *Acta Theriologica* 17:41–56.
- Beacham, T. D., and C. J. Krebs. 1980. Pitfall versus live-trap enumeration of fluctuating populations of *Microtus townsendii*. *Journal of Mammalogy* 61:486–499.
- Boonstra, R., and C. J. Krebs. 1978. Pitfall trapping of *Microtus townsendii*. *Journal of Mammalogy* 59:136–148.
- Bury, R. B., and P. S. Corn. 1987. Evaluation of pitfall trapping in northwestern forests: trap arrays with drift fences. *Journal of Wildlife Management* 51:112–119.
- Carey A. B., and M. L. Johnson. 1995. Small mammals in managed, naturally young, and old-growth forests. *Ecological Applications* 5:336–352.
- Carey, A. B., and C. A. Harrington. 2001. Small mammals in young forests: implications for management for sustainability. *Forest Ecology and Management* 154:289–309.

- Christensen, P., and B. Hornfeldt. 2003. Long-term decline of vole populations in northern Sweden: a test of the destructive sampling hypothesis. *Journal of Mammalogy* 84:1292–1299.
- Conard, J. M., J. A. Baumgardt, P. S. Gipson, and D. P. Althoff. 2008. The influence of trap density and sampling duration on the detection of small mammal species richness. *Acta Theriologica* 53:143–156.
- Corn, P. S., and R. B. Bury. 1991. Small mammal communities in the Oregon Coast Range. Pages 241–254 in L. F. Ruggiero, K. B. Aubry, A. B. Carey, and M. H. Huff, technical coordinators. *Wildlife and vegetation of unmanaged Douglas-fir forests*. U.S. Department of Agriculture, Forest Service General Technical Report PNW-GTR-285. Portland, Oregon, USA.
- Diamond, J. M. 1987. Justifiable killing of birds? *Nature* 330:423.
- Fairbairn, D. J. 1978. Dispersal of deer mice, *Peromyscus maniculatus*: proximal causes and effects of fitness. *Oecologia* 32:171–193.
- Farnsworth, E. J., and J. Rosovsky. 1993. The ethics of ecological field experimentation. *Conservation Biology* 7:463–472.
- Fisher, J. T., and L. Wilkinson. 2005. The response of mammals to forest fire and timber harvest in the North American boreal forest. *Mammal Review* 35:51–81.
- Fowler, J. L. Cohen, and P. Jarvis. 1998. *Practical statistics for field biology*. Wiley, New York, New York, USA.
- Gaston, K. J., and R. A. Fuller. 2007. Commonness, population depletion and conservation biology. *Trends in Ecology and Evolution* 23:14–19.
- Gilbert, F. F., and R. Allwine. 1991. Small mammal communities in the Oregon Cascade Range. Pages 257–267 in L. F. Ruggiero, K. B. Aubry, A. B. Carey, and M. H. Huff, technical coordinators. *Wildlife and vegetation of unmanaged Douglas-fir forests*. U.S. Department of Agriculture, Forest Service General Technical Report PNW-GTR-285. Portland, Oregon, USA.
- Gitzen, R. A., D. W. Stephen, C. C. Maguire, T. Manning, and C. B. Halpern. 2007. Response of terrestrial small mammals to varying amounts and patterns of green-tree retention in Pacific Northwest forests. *Forest Ecology and Management* 251:142–155.
- Hansson, L. 1988. Grazing impact by small rodents in a steep cyclicity gradient. *Oikos* 51:31–42.
- Hawes, M. L. 1977. Home range, territoriality, and ecological separation in sympatric shrews, *Sorex vagrans* and *Sorex obscurus*. *Journal of Mammalogy* 58:354–367.
- Hornfeldt, B., B. G. Carlsson, O. Lofgren, and U. Eklund. 1990. Effects of cyclic food supply on breeding performance in Tengmalm's owl. *Canadian Journal of Zoology* 68:522–530.
- Huynh, H., and L. S. Feldt. 1976. Estimation of the box correction for degrees of freedom from sample data in the randomized block and split-plot designs. *Journal of Educational Statistics* 1:69–82.
- Jung, R. E., G. H. Dayton, S. J. Williamson, J. S. Sauer, and S. Droege. 2002. An evaluation of population index and estimation techniques for tadpoles in desert pools. *Journal of Herpetology* 36:465–472.
- Kirkland, G. L. J., and P. K. Sheppard. 1994. Proposed standard protocol for pitfall sampling of small mammal communities. Pages 277–283 in J. F. Merritt, G. L. J. Kirkland, and R. K. Rose, editors. *Advances in the biology of shrews*, Carnegie Museum of Natural History special publication no. 18. Pittsburgh, Pennsylvania, USA.
- Krebs, C. J. 1999. *Ecological Methodology*. Longman, Menlo Park, California, USA.
- Krebs, C. J., R. Boonstra, S. Gilbert, D. Reid, A. J. Kenney, and E. J. Hofer. 2011. Density estimation for small mammals from livetrapping grids: rodents in northern Canada. *Journal of Mammalogy* 92:974–981.
- Krebs, C. J., B. L. Keller, and R. H. Tamarin. 1969. *Microtus* population biology: demographic changes in fluctuating populations of *M. ochrogaster* and *M. pennsylvanicus* in southern Indiana. *Ecology* 50:587–607.
- Krebs, C. J., I. Wingate, J. LeDuc, J. A. Redfield, M. Taitt, and R. Hilborn. 1976. *Microtus* population biology: dispersal in fluctuating populations of *M. townsendii*. *Canadian Journal of Zoology* 54:79–95.
- Kuehl, R. C. 1994. *Statistical principles of research design and analysis*. Duxbury Press, Belmont, California, USA.
- Lane, V. R., K. V. Miller, S. B. Castleberry, D. A. Miller, and T. B. Wigley. 2009. Methods to reduce avian bycatch in small mammal studies using snap traps. *Journal of Wildlife Management* 74:595–599.
- Lehmkuhl, J. F., R. D. Pepper, and M. A. O'Connell.

2008. Riparian and upland small mammals on the east slope of the Cascade range, Washington. *Northwest Science* 82:94–107.
- Littel, R. C. 1989. Statistical analysis of experiments with repeated measures. *Hortscience* 24:36–40.
- Magurran, A. E. 2004. *Measuring Biological Diversity*. Blackwell, Oxford, United Kingdom.
- Martell, A. M., and A. Radvanyi. 1977. Control of small mammals on a hardwood plantation by poison-bait feeders. *Forestry Chronicle* 53:96–99.
- Martin, K. J., and W. C. McComb. 2002. Small mammal habitat associations at patch and landscape scales in Oregon. Pages 77–88 in S. DeStefano and R. G. Haight, editors. *Forest-wildlife habitat relationships*. Society of American Foresters, Bethesda, Maryland, USA.
- Maser C., J. M. Trappe, and R. A. Nussbaum. 1978. Fungal–small mammal interrelationships with emphasis on Oregon coniferous forests. *Ecology* 59:799–809.
- Moreau, F. 2000. A comparison of trapping methodologies and grid size for small mammal research. Thesis, University of British Columbia. Vancouver, British Columbia, Canada.
- Pearce J., and L. Venier. 2005. Small mammals as bioindicators of sustainable boreal forest management. *Forest Ecology and Management* 208:153–175.
- Rodgers, J. D., M. F. Solazzi, S. L. Johnson, and M. A. Buckman. 1992. Composition of three techniques to estimate juvenile coho salmon populations in small streams. *North American Journal of Fisheries Management* 12:79–86.
- Ruggiero, L. F., K. B. Aubry, A. B. Carey, and M. H. Huff. 1991. Wildlife and vegetation of unmanaged Douglas-fir forests. U.S. Department of Agriculture, Forest Service General Technical Report PNW-GTR-285. Portland, Oregon, USA.
- Saville, D. J. 1990. Multiple comparison procedures: the practical solution. *American Statistician* 44:174–180.
- Schieck, J. O., and J. S. Millar. 1987. Can removal areas be used to assess dispersal of red-backed voles? *Canadian Journal of Zoology* 65:2575–2578.
- Seber, G. A. 1982. *The estimation of animal abundance and related parameters*. Charles Griffin, London, United Kingdom.
- Sikes, R. S., W. L. Gannon, and the Animal Care and Use Committee of the American Society of Mammalogists. 2011. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *Journal of Mammalogy* 92:235–253.
- Skalski, J. R., and D. S. Robson. 1992. *Techniques for wildlife investigations: design and analysis of capture data*. Academic Press, San Diego, California, USA.
- Steele, B. B., R. L. Bayn Jr., and C. V. Grant. 1984. Environmental monitoring using populations of birds and small mammals: analyses of sampling effort. *Biological Conservation* 30:157–172.
- Stromgren, E. J. 2007. Pitfall versus Longworth live trapping of shrews. Thesis, Agroecology Program, Faculty of Land and Food Systems, University of British Columbia, Vancouver, British Columbia, Canada.
- Sullivan, T. P. 1979. Repopulation of clearcut habitat and conifer seed predation by the deer mouse. *Journal of Wildlife Management* 43:861–871.
- Sullivan, T. P. 1986. Understanding the resiliency of small mammals to population reduction: poison or population dynamics? Pages. 69–82 in C. G. J. Richards, and T. Y. Ku, editors. *Control of mammal pests, supplement no. 1 to Tropical pest management* 32. Taylor and Francis, London, United Kingdom.
- Sullivan, T. P., and D. S. Sullivan. 2001. Influence of variable retention harvests on forest ecosystems. II. Diversity and population dynamics of small mammals. *Journal of Applied Ecology* 38:1234–1252.
- Sullivan, D. S., and T. P. Sullivan. 2010. A comprehensive review of trapping designs and methodology in published forest-small mammal studies, 1974–2010, information report. Applied Mammal Research Institute. Summerland, British Columbia, Canada.
- Sullivan, T. P., D. S. Sullivan, and E. J. Hogue. 2001. Reinvasion dynamics of northern pocket gopher (*Thomomys talpoides*) populations in removal areas. *Crop Protection* 20:189–198.
- Sullivan, T. P., D. S. Sullivan, D. B. Ransome, and P. M. F. Lindgren. 2003. Impact of removal-trapping on abundance and diversity attributes in small-mammal communities. *Wildlife Society Bulletin* 31:464–474.
- Suzuki, N., and J. P. Hayes. 2003. Effects of thinning on small mammals in Oregon coastal forests. *Journal of Wildlife Management* 67:352–371.

Van Horne, B. 1983. Density as a misleading indicator of habitat quality. *Journal of Wildlife Management* 47:893–901.

Vucetich, J. A., and M. P. Nelson. 2007. What are 60 warblers worth? Killing in the name of conservation. *Oikos* 116:1267–1278.

Waldien, D. L., et al. 2004. Incidental captures of birds in small mammal traps: a cautionary note for interdisciplinary studies. *Wildlife Society Bulletin* 32:1260–1268.

Wiewel, A. S., A. A. Y. Adams, and G. H. Rodda. 2009. Evaluating abundance estimation precision and the assumption of a count-based index for small mammals. *Journal of Wildlife Management* 73:761–771.

Zabel C. A., and R. M. Anthony. 2003. *Mammal community dynamics: management and conservation in the coniferous forests of western North America*. Cambridge University Press, Cambridge, United Kingdom.

Zar, J. H. 1999. *Biostatistical Analysis*. Prentice-Hall, Englewood Cliffs, New Jersey, USA.



**THOMAS P. SULLIVAN** (right) is a professor of wildlife ecology and conservation in the Department of Forest Sciences, Faculty of Forestry, and Food and Environment Program, Faculty of Land and Food Systems, University of British Columbia (UBC). He is also director and research scientist with the Applied Mammal Research Institute. He has M.Sc. (1976) and Ph.D. (1978) degrees from UBC. His current research programs involve interactions of small mammals with forestry and agriculture.

**DRUSCILLA S. SULLIVAN** (left) is a research associate with the Applied Mammal Research Institute and has conducted studies on small mammal populations in forest- and agro-ecosystems since 1978. She has B.Sc. (1975) and M.Sc. (1977) degrees from University of British Columbia. She is a premier mouse-trapper and fieldworker in new and ongoing small-mammal studies.