

# Effects of Blowdown on Small Mammal Populations

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**ABSTRACT.**—Over 150,000 ha of standing forest was altered as a result of a large-scale blowdown in the Boundary Waters Canoe Area Wilderness, Minnesota in 1999. We collected data in summers 2000 and 2001 to assess the effects of windthrow perturbation on small mammal communities in northern coniferous forests. Small mammal diversity, as well as density of the two most common species, red-backed voles (*Clethrionomys gapperi*) and woodland jumping mice (*Napaeozapus insignis*), were determined in three different treatments with varying proportions of blowdown (<33%, 33–66% and >66% blowdown). Diversity of small mammals increased from 2000 to 2001 and was highest in forest stands with <33% blowdown. The density of the two most abundant species of small mammals also differed among blowdown categories. Red-backed voles predominated at all sites, but exhibited peak densities (>25 individuals/ha) at sites most affected by blowdown. In contrast, density of woodland jumping mice exhibited an inverse relationship with red-backed voles, attaining peak densities (8 individuals/ha) in stands with <33% blowdown. Age ratios (juveniles: adults) were not influenced by year for either woodland jumping mice or red-backed vole populations, but differed for vole populations among blowdown categories. Juvenile red-backed voles predominated at sites with 33–66% (2.2: 1) and <33% blowdown (1.2: 1). Red-backed voles selected for blowdown and appeared to displace other small mammal species from this habitat. Because red-backed voles feed on coniferous seedlings, are primary dispersers of mycorrhizae and are prey for many predators, their selection of blowdown habitat could significantly influence community assemblages and forest succession following blowdowns.

## INTRODUCTION

Small mammals are critical members of conifer-northern hardwood forests because of the multiple ecological roles they fulfill as prey (Hayward and Phillipson, 1979) predators (Maxson and Oring, 1978) and dispersers of seeds and of spores of mycorrhizae (Maser *et al.*, 1978; Terwilliger and Pastor, 1999). Small mammal populations are particularly influential in northern forests following large-scale disturbances by altering subsequent successional processes (Sullivan and Sullivan, 2001; Howe and Lane, 2004). Understanding how small mammal communities adjust to major alterations in their habitat enhances our understanding of the ecology of forest systems (Sousa, 1984) and provides a basis for predicting long-term floral and faunal responses to large-scale disturbances.

Three forces that dramatically alter extensive tracts of forest habitat are clearcuts, fires and wind (Powell and Brooks, 1981). Changes in vegetation and small mammal populations are well documented for clearcuts (Noble *et al.*, 1977; Kirkland, 1990; Sullivan *et al.*, 1999) and burns (Ahlgren, 1966; Krefting and Ahlgren, 1974), but few studies have quantified the effects

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of windthrow on forest structure or mammal populations. Past observations suggest that the vegetational effects of blowdowns do not closely parallel those reported after fire or logging (Powell and Brooks, 1981). Unlike fire and clearcuts, which destroy much of the vegetation, blowdowns leave affected vegetation intact on the forest floor. Different effects on vegetation might cause distinctive perturbations of animal communities. However, only limited data were collected previously concerning mammalian responses to blowdown, even though blowdown events are common in coniferous forests (Dunn *et al.*, 1983; Canham and Loucks, 1984).

Indeed, only two studies have addressed the effects of blowdown on small mammal communities (Powell, 1972; Powell and Brooks, 1981). These studies were limited to just three species [red-backed vole (*Clethrionomys gapperi*), deer mouse (*Peromyscus maniculatus*) and masked shrew (*Sorex cinereus*)], which were investigated by means of kill trapping. In both studies, overall small mammal abundance appeared to increase in response to blowdown, but red-backed voles seemed to benefit most from blowdown, exhibiting the most pronounced increases in density. However, only limited conclusions can be drawn from either study because both assessed only one, relatively small (100 ha) blowdown site.

To better understand the effects of large-scale blowdowns on small mammal communities, we investigated the response of 13 species over a 2 y period to a large-scale blowdown that occurred in the Boundary Waters Canoe Area Wilderness (BWCAW) in 1999. Specifically, our objectives were to compare small mammal diversity and the population size, demographic structure and population dynamics of the most abundant small mammal species among forest stands that experienced varying degrees of blowdown.

#### METHODS

*Study area.*—The BWCAW is a large continuous tract of federally protected boreal forest within the Superior National Forest (SNF), in Northeastern Minnesota (47.9°N, 91.2°W). The wilderness area encloses >430,000 ha and adjoins Quetico National Park in Canada, which encompasses an additional 475,800 ha, making this one of the largest intact and protected northern coniferous forests in the Great Lakes Region. Motorized vehicles are prohibited within the BWCAW, which is accessible only by canoe routes or on hiking trails.

Primary vegetation of the BWCAW includes boreal species such as black and white spruce (*Picea mariana* and *P. gluaca*), jack pine (*Pinus banksiana*), balsam fir (*Abies balsamea*), tamarack (*Larix laricina*), white cedar (*Thuja occidentalis*), quaking aspen (*Populus tremuloides*) and paper birch (*Betula papyrifera*). However, some Great Lakes forest and eastern deciduous forest species such as white and red pine (*Pinus strobus* and *P. resinosa*), red oak (*Quercus rubra*), red maple (*Acer rubrum*), black ash (*Fraxinus nigra*), yellow birch (*Betula allegheniensis*) and large toothed aspen (*Populus grandidentata*) reach their northern limit within the BWCAW (Heinsleman, 1996). Using overstory and understory vegetation characteristics, Grigal and Ohmann (1975) identified 13 distinct upland forest community types within the BWCAW. Similarly, Heinsleman (1996) summarized eight lowland vegetational communities within the BWCAW.

On 4 July 1999 a complex of storms converged in northeastern Minnesota, generating winds >146 km/h and damaging approximately 193,000 ha of standing forest in the SNF. Within the national forest, the BWCAW sustained the most extensive storm damage, losing >150,000 ha of standing trees. In an attempt to quantify the extent of blowdown on public lands, the Minnesota Department of Natural Resources (MN DNR) and the U.S. Forest Service (USFS) mapped the distribution of three blowdown categories based on aerial and ground surveys within the BWCAW: <33% damaged, 33–66% damaged and >66% damaged (Superior National Forest, 2002).

*Design.*—Using maps developed by the USFS and MN DNR, we predetermined sampling sites within the BWCAW by dividing the wilderness evenly into 3 km-wide longitudinal rectangles of varying length. We randomly selected four of these longitudinal rectangles and located potentially suitable sampling sites within each rectangle that encompassed all three categories of blowdown (<33%, 33–66% and >66% damaged). In 2000, we established three trapping grids (one for each blowdown category) at each sampling site. We confirmed the percent blowdown by direct visual assessment in the field both years. We re-established the same trapping grids in 2001. Thus, four sites, each with three categories of blowdown (<33%, 33–66%, and >66% blowdown), were sampled in 2000 and 2001.

*Field methods.*—We conducted field work from 9 July to 4 August 2000 and 20 July–10 August 2001, accessing all trapping grids by foot and canoe. To document vegetative composition, we measured the percent ground cover and density of plant species (number/m<sup>2</sup>) on three random 25 m<sup>2</sup> areas within each trapping grid in 2001. For small mammal sampling, we set Sherman live traps at 10 m intervals in 5 × 5 trapping grids. Traps were baited with peanut butter and oats (Beer *et al.*, 1954) and placed under adequate cover to reduce heat for trapped animals (Powell and Brooks, 1981). At each site, we trapped small mammals at the three blowdown categories simultaneously. We examined traps twice daily (dawn and dusk) for three consecutive days. At the end of each trapping session, we moved traps to other pre-determined areas after they were properly cleaned (Jones *et al.*, 1996). Captured animals were identified to species, weighed, measured and sexed (Kunz *et al.*, 1996). For red-backed voles and woodland jumping mice, we used the mass, total length and presences of teats or scrotal testes as criteria for aging individuals as adults or juveniles (J. F. Merritt, pers. comm.). Captured animals were marked uniquely with non-toxic paint pens and released at the site of capture. Animals were captured and handled following guidelines suggested by the American Society of Mammalogists (ad hoc Committee for Acceptable Field Methods in Mammalogy, 1987).

*Data analysis.*—We compared plant density and the percent of blowdown across blowdown categories using Kruskal-Wallis tests. When significant differences were detected in the omnibus test, we employed the Dunn Procedure for *post hoc* comparisons (Zar, 1999). These non-parametric tests were employed as the vegetation data did not meet the assumption of normality or homoscedasticity required for parametric statistics. Small mammal diversity was determined for each blowdown category and site for both years with the Shannon-Weiner Index. We compared diversity indices across time and among blowdown categories using a repeated measures analysis of variance (RM-ANOVA), where time (2000 and 2001) was the repeated factor and blowdown categories (<33%, 33–66% and >66% blowdown) served as the between-subjects factor (von Ende, 2001).

We used program CAPTURE (Otis *et al.*, 1978; White *et al.*, 1982) to estimate the abundance of the two most abundant species, red-backed voles and woodland jumping mice, within each site and blowdown category for both years. We determined that for both years the most appropriate model for red-backed voles was the null model  $M_0$ , which assumes constant probability of capture. The most appropriate model for woodland jumping mice in 2000 was the null model, but the most appropriate model in 2001 was Jackknife  $M_h$ , which assumes variable probability of capture by animal. We estimated densities for both species by dividing abundance estimates by the effective area trapped (Wilson and Anderson, 1985). We calculated the effective area trapped by adding one-half the mean maximum distance moved (MMDM; the average of the maximum distance between recaptures for captured animals) to the edge of the trapping grid area. We estimated variances for densities following Otis *et al.* (1978).

Because of low capture and recapture probabilities, program CAPTURE failed to provide estimates on a number trapping occasions. Therefore, we compared population densities

TABLE 1.—Mean density of plants (number/m<sup>2</sup>) in three different forest blowdown categories from four study sites in the Boundary Waters Canoe Area Wilderness, Minnesota, 2000–2001

Plant species	Blowdown category						KW	
	<33%		33–66%		>66%		H	P
	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE		
<i>Abies balsamea</i>	1.08	0.60	1.00	0.54	0.92	0.51	0.13	0.973
<i>Acer spicatum</i>	0.08	0.84	0.42	0.19	0.17	0.17	3.29	0.193
<i>Aralia nudicaulis</i>	1.25	0.66	0.92	0.42	0.58	0.50	0.69	0.707
<i>Aster</i> spp.	1.33	1.03	1.00	0.58	0.42	0.29	0.38	0.828
<i>Clintonia borealis</i> *	0.08 <sup>a</sup>	0.84	1.75 <sup>b</sup>	0.76	0.00 <sup>a</sup>	0.00	6.29	0.043
<i>Coptis groenlandica</i>	0.00	0.00	1.08	1.08	0.00	0.00	2.00	0.368
<i>Cornus canadensis</i>	2.41	1.73	3.17	1.54	1.25	0.73	0.02	0.988
<i>Equisetum</i> sp.	0.50	0.36	0.00	0.00	0.00	0.00	4.11	0.128
<i>Ledum groenlandicum</i> *	0.00 <sup>a</sup>	0.00	0.00 <sup>a</sup>	0.00	2.42 <sup>b</sup>	1.69	6.34	0.042
<i>Maianthemum canadensis</i> *	3.66 <sup>a</sup>	1.48	0.17 <sup>ab</sup>	0.17	0.75 <sup>b</sup>	0.59	6.82	0.033
<i>Mitchella repens</i>	0.00	0.00	1.83	1.24	1.67	1.67	2.01	0.367
<i>Picea glauca</i>	0.17	0.11	0.92	0.54	1.67	0.85	1.44	0.488
<i>Rubus idaeus</i>	0.50	0.36	0.33	0.33	1.92	1.03	1.57	0.457
<i>Thuja occidentalis</i>	0.17	0.11	1.00	1.00	1.08	0.62	1.14	0.567
<i>Trientalis borealis</i>	0.67	0.51	1.67	1.24	0.00	0.00	3.18	0.204
<i>Vaccinium angustifolium</i>	2.25	1.04	1.50	1.02	1.30	1.24	1.67	0.433
<i>Vaccinium macrocarpon</i>	0.00	0.00	0.00	0.00	1.67	1.67	2.00	0.368
Average Blowdown (%)*	2.08 <sup>a</sup>	1.14	35.83 <sup>ab</sup>	5.96	70.00 <sup>b</sup>	6.57	27.88	<0.001

\* Kruskal-Wallis (KW) tests indicate whether plant density or mean amount of blowdown differed among blowdown categories. Lettered superscripts indicate significant paired comparisons, using the Dunn procedure and an  $\alpha = 0.05$ ; for all KW tests,  $df = 2$

for both species across time and between blowdown categories using the minimum number known alive (MNKA), recognizing that it can be a negatively biased indicator of small mammal abundance (Nichols and Pollock, 1983). We compared diversity indices and MNKA for both species across years and among blowdown categories with a RM-ANOVA (von Ende, 2001). We compared the age structure (juveniles: adults) of red-backed vole and woodland jumping mice across blowdown categories and between years (2001) with log-likelihood ratio tests (Zar, 1999).

## RESULTS

*Vegetation.*—Ground cover sampling indicated that each field site was within the range of the predetermined blowdown categories (<33%, 33–66% or >66% blowdown; Table 1). However, the percent of blowdown at all sites was on the lower end of the established blowdown categories (Table 1). Species composition of plant communities was similar among the blowdown categories; the density of only three of 17 plant species, *Clintonia borealis*, *Maianthemum canadensis* and *Ledum groenlandicum*, differed among the blowdown categories (Table 1). *Clintonia borealis* was most abundant in 33–66% blowdown compared to other blowdown categories (all  $Q_4 > 2.94$ ,  $P < 0.020$ ), whereas *M. canadensis* was more abundant in <33% blowdown than in 33–66% ( $Q_4 = 2.79$ ,  $P = 0.033$ ), but only marginally higher ( $Q_4 = 2.52$ ,  $P = 0.077$ ) compared to the >66% blowdown sites. *Ledum groenlandicum* was only present at sites with >66% blowdown (Table 1).

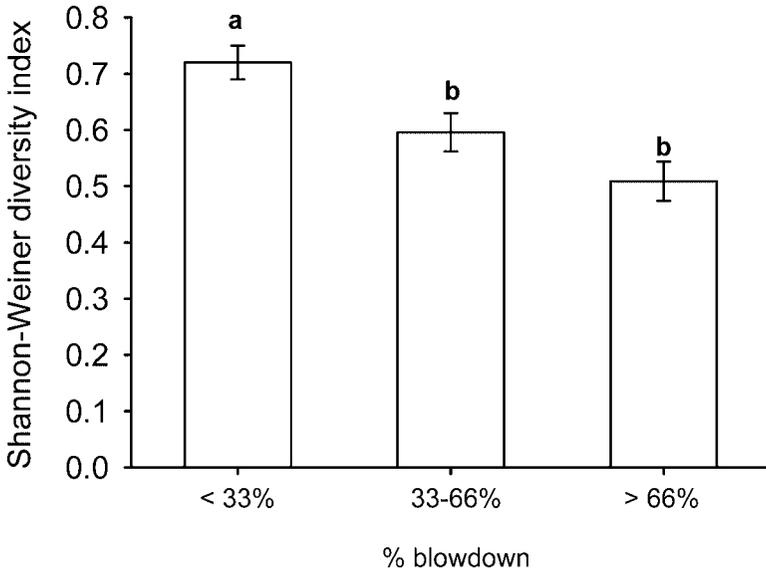


FIG. 1.—Shannon-Weiner indices (mean  $\pm$  1 SE) of small mammal diversity in three forest blowdown categories in the Boundary Waters Canoe Area Wilderness, Minnesota, 2000–2001. Statistical differences are denoted with lettered superscripts; for each blowdown category  $n = 4$

*Species diversity.*—We captured eight species of small mammals from 2000–2001 (capture data available from the authors upon request), including voles (*C. gapperi* and *Microtus chrotorrhinus*), mice (*N. insignis* and *Peromyscus maniculatus*), sciurids (*Tamiasciurus hudsonicus* and *Tamias minimus*) and shrews (*Sorex cinereus* and *S. hoyi*). At all trapping sites, however, red-backed voles constituted the majority of individuals captured. Shannon-Weiner diversity indices differed among blowdown categories ( $F_{2,9} = 10.22$ ,  $P = 0.005$ ) and exhibited a temporal trend, increasing from 2000 to 2001 ( $F_{1,9} = 9.37$ ,  $P = 0.014$ ). Diversity indices did not, however, exhibit a significant interaction between blowdown categories and time ( $F_{2,9} = 0.26$ ,  $P = 0.78$ ). Small mammal diversity increased by 82% from 2000 ( $\bar{x} = 0.438$ ,  $SE = 0.065$ ) to 2001 ( $\bar{x} = 0.779$ ,  $SE = 0.056$ ), irrespective of blowdown category. Among blowdown categories, small mammal diversity was highest in stands with the least blowdown (Fig. 1). At sites with <33% blowdown, diversity was slightly higher than at the 33–66% blowdown category ( $t_6 = 2.76$ ,  $P = 0.033$ ) and nearly 2 $\times$  higher compared to the >66% blowdown category ( $t_6 = 4.53$ ,  $P = 0.004$ ; Fig. 1). Diversity did not differ between the 33–66% and >66% blowdown categories ( $t_6 = 1.77$ ,  $P = 0.13$ ; Fig. 1).

*Population size and structure (red-backed voles and woodland jumping mice).*—Animal densities and associated 95% confidence intervals were determined for woodland jumping mice (Table 2) and red-backed voles (Table 3). However, program CAPTURE provided estimates for only 41 of the 48 trapping occasions. Failure to provide estimates was due primarily to low capture and recapture success for woodland jumping mice (Table 2). Nonetheless, the 41 density estimates obtained from CAPTURE were significantly correlated with densities derived from MNKA for both woodland jumping mice ( $r^2 = 0.807$ ,  $df = 17$ ,  $P < 0.001$ ) and red-backed voles ( $r^2 = 0.621$ ,  $df = 22$ ,  $P < 0.001$ ). Therefore, we used densities from MNKA for subsequent statistical analyses.

TABLE 2.—Estimates of woodland jumping mice density (individuals/ha) in three different forest blowdown categories on four study sites in the Boundary Waters Canoe Area Wilderness, Minnesota, 2000–2001 (95% CI in parentheses). Densities were generated using program CAPTURE; NR and NC denotes densities that were incalculable because of no recaptures and no captures, respectively

Site	Blowdown category and year					
	<33%		33–66%		>66%	
	2000	2001	2000	2001	2000	2001
1	5 (5–12)	31 (22–54)	3 (3–3)	8 (6–22)	1 (1–1)	16 (12–33)
2	1 (1–1)	NR	8 (8–8)	10 (9–23)	NC	5 (5–20)
3	8 (8–8)	20 (9–32)	6 (6–10)	NR	NC	6 (5–13)
4	8 (8–15)	28 (18–51)	3 (3–3)	15 (10–33)	NC	NR

Red-backed vole density differed between years ( $F_{1,9} = 68.3$ ,  $P < 0.001$ ) and among blowdown categories ( $F_{2,9} = 14.2$ ,  $P = 0.002$ ), but did not exhibit an interaction between years and blowdown intensity ( $F_{2,9} = 0.44$ ,  $P = 0.66$ ). From 2000 to 2001 mean density of red-backed voles fell by 63%, from 33.3 individuals/ha ( $SE = 2.3$ ) to 12.4 individuals/ha ( $SE = 1.4$ ). Disregarding year, vole density was lowest in the <33% blowdown category (all  $t_6 > 3.37$ ,  $P < 0.015$ ) and reached peak densities in stands with >33% blowdown (Fig. 2). Red-backed vole densities did not differ between the 33–66% and >66% blowdown categories ( $t_6 = 1.34$ ,  $P = 0.23$ ; Fig. 2).

Similarly, density of woodland jumping mice differed between years ( $F_{1,9} = 26.3$ ,  $P = 0.001$ ) and among blowdown categories ( $F_{2,9} = 6.42$ ,  $P = 0.019$ ), but did not exhibit an interaction between years and blowdown category ( $F_{2,9} = 3.92$ ,  $P = 0.06$ ). Mean density of woodland jumping mice nearly doubled from 2000 to 2001, from 3.8 individual/ha ( $SE = 1.0$ ) to 7.5 individuals/ha ( $SE = 1.1$ ). Further, density of woodland jumping mice exhibited an inverse relationship with the percent of blowdown (Fig. 2). Densities in the >66% blowdown category were lower compared with densities from both the <33% ( $t_6 = 3.40$ ,  $P = 0.015$ ) and 33–66% ( $t_6 = 2.52$ ,  $P = 0.045$ ) blowdown categories, but did not differ between the <33% and 33–66% blowdown categories ( $t_6 = 1.38$ ,  $P = 0.22$ ; Fig. 2). Regardless of blowdown intensity or year, red-backed vole and woodland jumping mouse densities exhibited a strong, negative correlation (Fig. 3).

Age ratios (juveniles: adults) for red-backed vole populations did not differ between years ( $G_1 = 2.38$ ,  $P = 0.13$ ), but differed among blowdown categories ( $G_2 = 15.2$ ,  $P < 0.001$ ).

TABLE 3.—Estimates of red-backed vole density (individuals/ha) in three different forest blowdown categories on four study sites in the Boundary Waters Canoe Area Wilderness, Minnesota, 2000–2001 (95% CI in parentheses). Densities were generated using program CAPTURE; NR denotes densities that were incalculable because of no recaptures

Site	Blowdown category and year					
	<33%		33–66%		>66%	
	2000	2001	2000	2001	2000	2001
1	24 (21–34)	29 (18–78)	42 (37–56)	36 (25–71)	43 (38–57)	21 (16–44)
2	29 (29–34)	6 (6–14)	46 (22–149)	33 (32–39)	22 (18–27)	11 (11–20)
3	28 (28–35)	15 (11–40)	43 (16–200)	27 (18–64)	33 (33–38)	39 (24–91)
4	26 (25–33)	NR	30 (28–39)	39 (35–42)	40 (39–48)	35 (22–81)

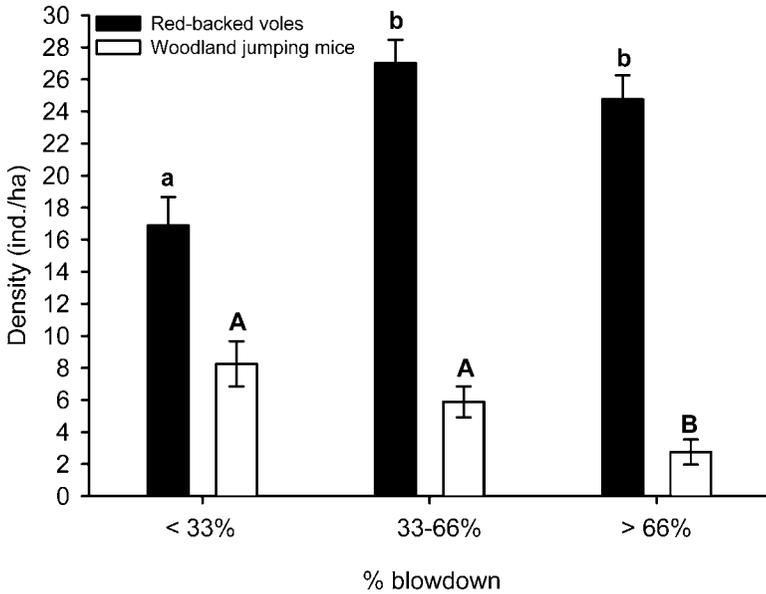


FIG. 2.—Mean ( $\pm 1$  SE) density (individuals/ha) of red-backed voles and woodland jumping mice in three forest blowdown categories in the Boundary Waters Canoe Area Wilderness, Minnesota, 2000–2001. Estimates are based on the minimum number of individuals known alive, averaged over both years and study sites. Red-backed vole density was highest in stands with the most blowdown, whereas woodland jumping mice attained highest densities in stands with the least blowdown. Statistical differences are denoted with lettered superscripts; for each blowdown category  $n = 4$

Juveniles predominated in the 33–66% blowdown, with age ratios of 2.2: 1, significantly higher than those of 1.2: 1 the <33% blowdown category ( $G_1 = 8.78$ ,  $P = 0.003$ ) and 1.0: 1 found in the >66% blowdown category ( $G_1 = 12.9$ ,  $P < 0.001$ ). Vole age ratios did not differ between the <33% and >66% blowdown categories ( $G_1 = 0.74$ ,  $P = 0.39$ ). In contrast to voles, age ratios of woodland jumping mice populations (1.1: 1) did not differ between years ( $G_1 = 1.49$ ,  $P = 0.22$ ) or among blowdown categories ( $G_2 = 0.35$ ,  $P = 0.84$ ).

#### DISCUSSION

Although our ground cover results indicate that the USFS and MN DNR preliminary blowdown categories of <33%, 33–66% and >66% tended to overestimate the actual percent of blowdown in forest stands, all of our trapping grids were located within the expected range of blowdown percentages. Vegetation on the forest floor was only moderately altered as a result of blowdown; the abundance of only three plant species differed across the blowdown categories. The relative uniformity of forest vegetation across blowdown sites may reflect highly variable vegetation data precluding a detection of actual differences. Alternatively, the data may be a result of forest stands in an early or arrested stage of succession (*i.e.*, windthrow had not yet settled and begun to decompose). Our results are in accordance with Powell and Brooks (1981) findings of minimal ground cover alterations secondary to blowdown in coniferous forests. Indeed, Powell and Brooks (1981) only detected differences in the abundance of five species of plants between blowdown and

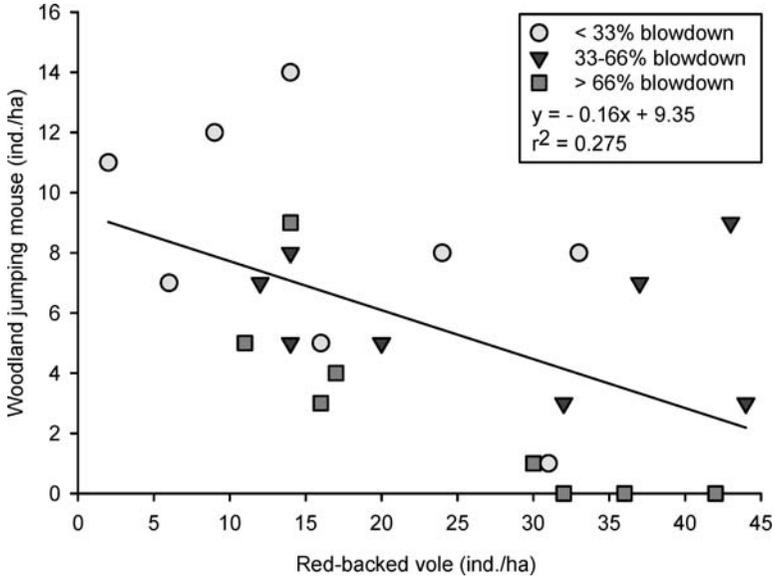


FIG. 3.—Relationship between density (individuals/ha) of red-backed voles and woodland jumping mice in the Boundary Waters Canoe Area Wilderness, Minnesota, 2000–2001. Density of both species were from forest stands that had experienced varying intensity of blowdown (<33%, 33–66% and >66%). Regardless of year or blowdown intensity, densities of red-backed voles and woodland jumping mice exhibited an inverse relationship

intact forest stands. Therefore, it appears that the immediate effects of blowdown on ground vegetation are limited; multiple years may be required before substantive changes in ground vegetation can be detected.

We found that small mammal diversity was highest in stands with the least blowdown and declined as the percent of blowdown increased. However, our estimates of species diversity, even in stands with minimal blowdown (<33%), were considerably lower than have been reported in other studies of small mammal communities in northern forests. For example, Silva (2001) found that small mammal diversity in fragmented forests on Prince Edward Island, Canada, averaged 1.06, and Sullivan and Sullivan (2001) reported that indices of small mammal diversity ranged from 1.06–1.27 in undisturbed forests in British Columbia, Canada. The factors behind lower mammalian diversity in the BWCAW, including in relatively intact stands of forest, compared with those from other northern coniferous forests could have been an artifact of our field methods or simply a feature of small mammal communities in the BWCAW. In contrast to Silva (2001) and Sullivan and Sullivan (2001), who employed pitfall and Longworth traps, we employed Sherman live traps, which generally have lower success for capturing lightweight mammals, such as shrews (Pucek, 1969; Allen *et al.*, 1997). The paucity of shrews in our sample could have resulted from our trapping methods and contributed to our relatively low estimates of mammalian diversity.

Nevertheless, our results demonstrate that small mammal diversity is reduced by blowdown. The mechanism behind lower diversity in blowdown sites is unclear, but we suspect it is not a direct consequence of blowdown. Rather, red-backed vole predominance at sites with blowdown seemed to impact the incidence and abundance of other species. Red-backed voles were most abundant at sites with a high proportion of blowdown and the

presence and abundance of other species, woodland jumping mice in particular, were negatively correlated with vole abundance (Fig. 3). Thus, through direct or apparent competition (Brower and Cade, 1966; Holt *et al.*, 1994), it appears that voles were displacing other species of small mammals and responsible for reducing diversity at blowdown sites. This hypothesis is also supported by our multiyear data on red-backed vole abundance and small mammal diversity. At all sites, regardless of blowdown category, red-backed voles were more abundant in 2000 than 2001. In contrast, small mammal diversity exhibited the opposite trend; diversity indices decreased from 2000 to 2001. Therefore, it appears that red-backed vole numerical dominance contributed to lower diversity in forest stands.

Habitat use by the two most abundant species, red-backed voles and woodland jumping mice differed. Red-backed voles predominated in all sites but achieved peak densities in extensive blowdown. In contrast, woodland jumping mice had their highest densities in minimal blowdown. Many studies have shown that red-backed voles select sites with large amounts of coarse woody debris (CWD; Yahner, 1986; Keinath and Hayward, 2003). For red-backed voles, it appears that CWD serves as cover for feeding (Maser *et al.*, 1978), reproducing and resting (Wywiałowski, 1987; Keinath and Hayward, 2003) and as enhanced foraging habitat (Amaranthus *et al.*, 1994). Clearly, forest stands that have experienced a blowdown provide ample quantities of CWD, presumably benefiting red-backed vole populations.

In addition to selecting sites with large amounts of CWD, red-backed voles select mesic sites (Burt, 1957; Merritt, 1981), apparently because they need a plentiful water supply to compensate for the relatively large amount of metabolic water that they lose (Odum, 1944; McManus, 1974). Indeed, red-backed voles consume more than twice as much water (0.64 g H<sub>2</sub>O/g/day) as their predicted mass relative value (Brower and Cade, 1966; McManus, 1974) and are drought intolerant (Yahner, 1986). High temperatures increase metabolic water loss and requirements in rodents (Chew, 1965). For red-backed voles, any increase in water loss could result in unattainable water requirements. Blowdown appears to both provide for more available water and ameliorate high water demands. Blowdowns create numerous cradle-knolls, a microtopographic pit and mound formed as a result of a tree uprooting, which allows for rainwater accumulation and generates large quantities of CWD that reduces evaporative loss from these otherwise ephemeral puddles (Harmon *et al.*, 1986). Coarse woody debris also moderates ground temperatures (Greenberg, 2001), which should reduce metabolic water loss for small mammals. Thus, blowdown may create ideal habitat for red-backed voles: large quantities of CWD for cover, abundant food and water sources, and improved environmental stability.

In contrast, whereas woodland jumping mice share a slight preference for vegetative cover with red-backed voles (Lovejoy, 1973), they do not select for habitats with abundant surface water (Brower and Cade, 1966). Therefore, woodland jumping mice selection for stands with blowdown may not be as great. Previous research suggested that red-backed voles were extremely territorial, displacing other species from habitats via aggressive encounters (Brower and Cade, 1966). Indeed, woodland jumping mice, in particular, apparently avoid areas where red-backed voles are abundant (Brower and Cade, 1966; Lovejoy, 1973). In this study, woodland jumping mice were more abundant in the less disrupted regions, while red-backed voles predominated in areas with blowdown. Woodland jumping mice and red backed voles also exhibited inverse densities across years; from 2000 to 2001 vole density decreased on all sites, while woodland jumping mice densities increased. Thus, densities of woodland jumping mice and red-backed voles exhibited a strong negative relationship between years and among blowdown categories (Fig. 3). The data presented here and those published previously suggest that both species may select blowdown habitat, but that red-backed voles displace woodland jumping mice from their preferred habitat.

It is somewhat surprising that vole densities fell between 2000 and 2001 in the BWCAW because red-backed vole populations typically exhibit non-cyclical dynamics (Merritt *et al.*, 2001; Sullivan and Sullivan, 2001). The decline in vole abundance might be explained by interactions with predators or with the depletion of food sources. For example, high vole densities in 2000 could have stimulated a functional response by predators, such as martens (*Martes americana*), weasels (*Mustela* spp.) and boreal owls (*Aegolius funereus*), elevating predation pressure and reducing vole density in 2001. Alternatively, red-backed voles could have reached sufficient densities to reduce plant and seed availability, which is their primary food source during winter (Merritt, 1981). Whatever the underlying mechanism, similar temporal oscillations in red-backed vole abundance have been previously observed following habitat alterations from fires (Krefting and Ahlgren, 1974) and logging (Martell and Radvanyi, 1977).

Powell (1972) observed that the majority of red-backed voles in blowdown were sexually inactive and concluded that they were juveniles. From these data he postulated that red-backed voles select forests with little blowdown and displaced juvenile conspecifics to the marginal (blowdown) habitat. Similarly we found that juveniles predominated at sites with 33–66% blowdown, but, in contrast, reason that blowdown is preferred habitat for red-backed voles. Powell (1972) equated sexual inactivity with juveniles and, therefore, likely overestimated juvenile abundance and was, in contrast, indexing reproductive activity. Similar to our study Powell (1972) found that vole densities were greatest in blowdown habitats, which may account for lower reproduction in blowdown habitats due to density dependent effects previously described. Further, the explanation of sex ratios given by Powell (1972) does not explain either the complementary population densities of woodland jumping mice or the fact that juvenile red-backed voles predominated only in the moderate blowdown (33–66%) categories. Thus, we conclude that blowdown benefits red-backed voles, which appear to select for and displace other small mammal species from these stands.

Small mammals play crucial roles in forest regeneration. Red-backed voles, in particular, may dramatically influence forest succession (Terwilliger and Pastor, 1999) because of their dual role as predators of sapling trees and seeds (Sullivan and Sullivan, 2001) and as dispersers of mycorrhizal fungal spores (Maser *et al.*, 1978). Therefore, changes in small mammal communities subsequent to a large-scale disturbance may alter the trajectory of forest succession. Future research should seek to identify the effects of large-scale disturbances on animal populations and the subsequent effects of small mammal community assemblages on forest structure and succession.

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